



Body size evolution in insular vertebrates: generality of the island rule

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ABSTRACT

Aim My goals here are to (1) assess the generality of the island rule – the graded trend from gigantism in small species to dwarfism in larger species – for mammals and other terrestrial vertebrates on islands and island-like ecosystems; (2) explore some related patterns of body size variation in insular vertebrates, in particular variation in body size as a function of island area and isolation; (3) offer causal explanations for these patterns; and (4) identify promising areas for future studies on body size evolution in insular vertebrates.

Location Oceanic and near-shore archipelagos, and island-like ecosystems world-wide.

Methods Body size measurements of insular vertebrates (non-volant mammals, bats, birds, snakes and turtles) were obtained from the literature, and then regression analyses were conducted to test whether body size of insular populations varies as a function of body size of the species on the mainland (the island rule) and with characteristics of the islands (i.e. island isolation and area).

Results The island rule appears to be a general phenomenon both with mammalian orders (and to some degree within families and particular subfamilies) as well as across the species groups studied, including non-volant mammals, bats, passerine birds, snakes and turtles. In addition, body size of numerous species in these classes of vertebrates varies significantly with island isolation and island area.

Main conclusions The patterns observed here – the island rule and the tendency for body size among populations of particular species to vary with characteristics of the islands – are actually distinct and scale-dependent phenomena. Patterns within archipelagos reflect the influence of island isolation and area on selective pressures (immigration filters, resource limitation, and intra- and interspecific interactions) within particular species. These patterns contribute to variation about the general trend referred to as the island rule, not the signal for that more general, large-scale pattern. The island rule itself is an emergent pattern resulting from a combination of selective forces whose importance and influence on insular populations vary in a predictable manner along a gradient from relatively small to large species. As a result, body size of insular species tends to converge on a size that is optimal, or fundamental, for a particular body plan and ecological strategy.

Keywords

Body size, dwarfism, evolution, gigantism, island area, island biogeography, island rule, isolation, vertebrates.

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INTRODUCTION

In response to the special characteristics of island environments, animals often undergo evolutionary changes that are both remarkable and of fundamental importance for evolutionary biologists, ecologists and biogeographers (Foster, 1964; Carlquist, 1974; Hooijer, 1976; Sondaar, 1977; Heaney, 1978; Reyment, 1983; Lomolino, 1985; Adler & Levins, 1994; Brown & Lomolino, 1998; Grant, 1998; Whittaker, 1998). Typically small, herbaceous plants take on the forms of trees, birds and insects lose the power of flight, and many insular forms become dwarfs or giants in comparison with their mainland relatives. In mammals, body size variation of insular populations seemed so general that Van Valen (1973) termed it the 'island rule'. In the first comprehensive review of the pattern, Foster (1964) described it as a set of different tendencies among taxonomic groups; i.e. toward dwarfism in insular carnivores, lagomorphs (rabbits and hares) and artiodactyls (deer and other, even-toed ungulates), and gigantism in insular rodents and possibly insular marsupials as well. Later, others reinterpreted the pattern as a graded trend across, as well as within taxa, from gigantism in the typically smaller species of mammals to dwarfism in the larger species (Heaney, 1978; Lomolino, 1985).

Lomolino's (1985) analysis of body size patterns of 71 species of non-volant mammals, in particular, provided results consistent with the predicted pattern. Potential causal explanations, although many, include the effects of limited insular resources, the paucity of interspecific competition and predation (especially that from large mammals, which are often absent from oceanic islands), and the challenge of dispersing to, but not emigrating from, islands (see also McNab, 2002). In one of his discussions of evolution of insular biotas, Darwin's (1859, p. 177) metaphor of 'shipwrecked mariners' provided an insightful view of natural selection and evolution on islands:

As with a mariner shipwrecked near a coast, it would have been better for the good swimmers if they had been able to swim still further, whereas it would have been better for the bad swimmers if they had not been able to swim at all and had stuck to the wreck.

Many of the remarkable and apparently anomalous ecological and evolutionary characteristics of insular biotas may simply result from predictable responses to radically divergent selection regimes of mainland and insular environments. As Darwin's statement also implies, evolutionary divergence of insular life forms may result from changes in selective pressures between those operating during immigration and those operating following colonization: selection during immigration for those that could 'swim still further' followed by selection for those that 'had stuck to the wreck', i.e. for those that lost the ability or propensity for long-distance dispersal.

Body size evolution is one of the most fundamental responses to island environments because it influences a multitude of characteristics including those associated with immigration potential, ecological interactions and resource requirements. For example, many birds undergo evolutionary

changes associated with ecological release on oceanic islands lacking ground-dwelling mammals, losing the power (and the energetic costs) of flight and reducing their metabolic rates, while often increasing in overall body size, shifting their diets and adopting niches typically occupied by large grazing and browsing mammals on the mainland (McNab, 1994a,b, 2001, 2002; see also Arnold, 1979).

To the degree to which species differ with respect to their relevant characteristics – most notably those morphological, physiological and behavioural traits influencing resource requirements, interspecific interactions and immigration abilities – and the degree to which these characteristics vary as functions of body mass, we expect the general pattern among species (the island rule) to emerge. We know, however, that body mass is not a perfect, nor is it the sole determinant of resource requirements, interspecific interactions and immigration abilities. Just as important, islands vary markedly in primary productivity and available resources, in the diversity and intensity of ecological interactions, and in their isolation (the latter affected both by island age and geographical distance). The overall effect of all this is that, while insular populations often exhibit a strong signal – the island rule – there remains substantial, unexplained variation about the trend line (i.e. that describing the relative size of insular forms as a function of body size of the species on the mainland; Figs 1, 2 & 4). While this residual variation might be viewed as nuisance noise or perhaps evidence that there is no underlying pattern, it may provide invaluable insights for those attempting to deconstruct (*sensu* Huston, 1994; see also Marquet *et al.*, 2004) the pattern in order to identify factors and processes influencing body size evolution, in general. In fact, studies that focus on within-archipelago patterns in body size variation of a particular species or lineage may provide especially important clues to the factors influencing evolution and assembly of biotic communities (e.g. Heaney, 1978; Lomolino, 1984; see Fig. 3).

It is now two decades since the second, comprehensive survey of body size patterns in insular mammals (Lomolino, 1985). During that time, and especially during the last decade, numerous authors have studied body size patterns in these and other terrestrial vertebrates inhabiting islands and island-like ecosystems. My goal here is to stimulate and foster continuing advances in this research area by reanalysing the pattern for insular mammals (data from Lomolino, 1983, 1985, but this time analysed at the population level; see Methods), comparing these patterns to those emerging for non-volant mammals inhabiting other types of isolated systems (namely, anthropogenically disturbed areas of continental ecosystems) and for other insular vertebrates (including bats, birds, snakes and turtles), and then suggesting some potentially fruitful directions for future research.

METHODS

Reanalysis of body size patterns in insular mammals

For simplicity and clarity of presentation, Lomolino (1985) analysed patterns of body size variation in insular mammals at

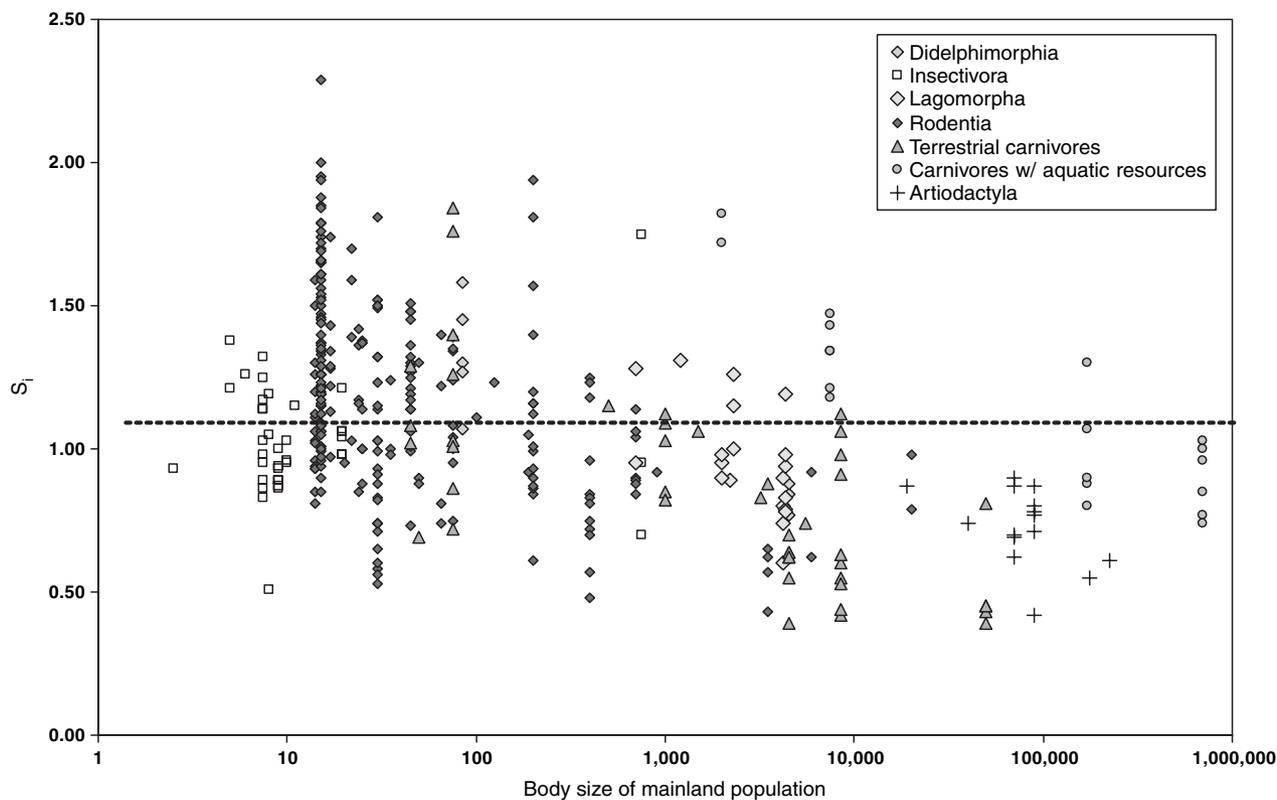


Figure 1 Body size trends for populations of insular mammals. S_i = relative size of insular forms expressed as a proportion of body mass of their mainland relative.

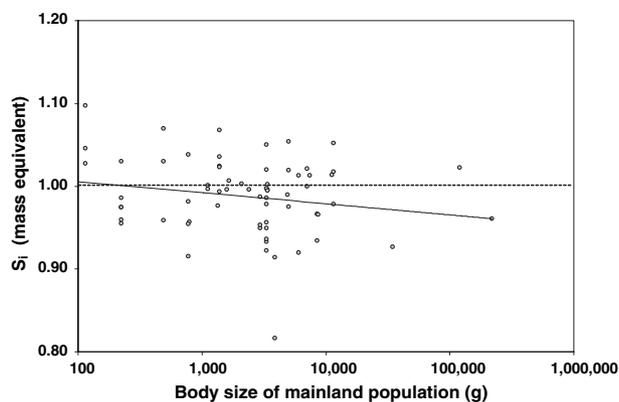


Figure 2 Body size trends in insular carnivores (Mammalia, Carnivora) based on skull (condylo-basal length) measurements of populations from relatively large islands (88% of the islands were > 1000 square miles, 61% > 10,000 square miles; after Meiri *et al.*, 2004). S_i is relative size of insular form (in mass equivalents) as a proportion of that of their mainland relative [the probability that this trend is not consistent with the island rule (i.e. that the slope is not < 0.0) is < 0.05].

the species level (71 species from six orders of mammals). These data, however, represent species means taken from a variable number of insular populations for each species, many of those populations inhabiting islands that varied substantially in area, isolation, climate, biotic diversity and age – all of

these factors potentially influencing body size of insular populations (Fig. 3). Since the phenomenon under study, evolutionary divergence, occurs across islands and insular populations, and because causal explanation are appropriately framed at that scale, population-level analyses of the pattern are clearly most appropriate. One additional advantage of analysing these data at this scale is that we can assess the trend at finer taxonomic scales, i.e. within orders, families and, in some cases, subfamilies as well.

The data used in this reanalysis is the same as that collected for my earlier analysis (Lomolino, 1983, 1985). This includes data from studies reporting body sizes of 385 insular populations of mammals and their nearest, mainland relatives. These data were compiled before computer assisted literature searches were available, and so the survey was conducted by manually searching bibliographies of relevant papers and all available relevant journals in Cornell University's Library system. These data include measurement of adults, only, and comparisons of masses of adult males when available. When measurements in the form of mass were not available, I used linear measurements of body size (preferentially body length, excluding the tail, but when this information was not available, I used skull length). Measures of tooth size or other dimensions of skulls or other parts of the skeletal system were not used because shape, relative size and scaling relationships of these measures may vary between mainland and insular forms and among insular populations as well (Sondaar, 1977,

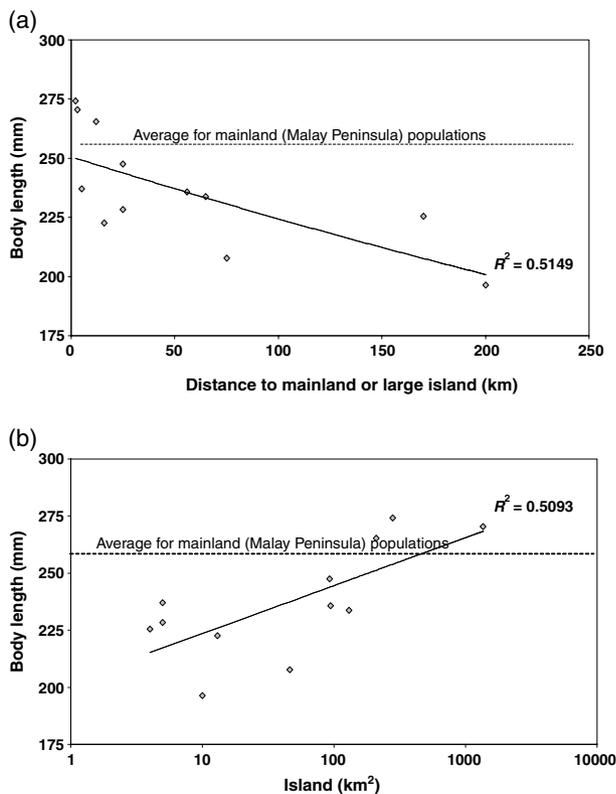


Figure 3 Body size of the tri-coloured squirrel (*Callosciurus prevosti*) as a function of (a) island isolation and (b) island area (Heaney, 1978; the probability that the slopes of these trends do not differ from 0 is < 0.05).

pp. 683–686). Body size divergence (S_i) was expressed as body mass of an insular population divided by that of its nearest, mainland relative (for linear measures of body size, S_i was calculated as the quotient of the cubed, linear dimensions). Although S_i is a useful measure for visualization of patterns with respect to the island rule (i.e. tendencies for gigantism or dwarfism), I also analysed the statistical significance of body size trends by regressing actual size of insular forms (as mass or mass equivalents) as a function of size of mainland forms to avoid possible statistical problems and artefacts associated with regressions using ratios (see Atchley *et al.*, 1976; M. L. Rosenzweig, pers. comm., 1984; Packard & Boardman, 1988; Prairie & Bird, 1989). Finally, because these data were collected from over 80 different sources, it is highly unlikely that any emerging patterns would derive from biases in collecting or interpreting the data, especially given the complex nature of the pattern being tested (a trend that switches from gigantism to dwarfism) and the fact that most of these measurements were taken and reported before the pattern was clearly articulated.

Body size patterns in other insular vertebrates

The generality of the island rule was also evaluated by comparing trends emerging for the above data set with those

of other insular mammals [including an earlier review of body size in insular bats (Krzanowski, 1967) and a recent study of variation in skulls and teeth of carnivores on large islands (Meiri *et al.*, 2004)], of mammals that were isolated and have persisted in fragmented forests of Denmark for c. 175 years (Schmidt & Jensen, 2003), and for relatively large, Australian marsupials (those > 5 kg) that survived through the late-Pleistocene and Holocene following the colonization and subsequent activities of Australia's Aborigines (Flannery, 1994). In addition, recent studies by Clegg & Owens (2002), Boback & Guyer (2003) and N. Karraker (unpublished manuscript) provide relevant data to test the generality of this island rule for other vertebrates (birds, snakes and turtles, respectively).

RESULTS AND DISCUSSION

Insular mammals

Reanalysis of trends for terrestrial non-volant mammals

Analyses of body size trends of populations of insular mammals yielded results consistent with earlier analyses conducted at the species level (Lomolino, 1985), and also provided sample sizes adequate to test for the predicted pattern at finer taxonomic scales (i.e. within orders, families and, in some cases, within subfamilies; Fig. 1, Table 1). Regression results indicate that regardless of the regression models used, the clear majority of the trends are consistent with that predicted by the island rule; i.e. a graded trend from gigantism in the smaller species to dwarfism in the larger species [with 18 of 21 trends being consistent with the rule, 12–13 of these (depending on the regression model) significant at the 0.05 level; Table 1]. The only anomalous trends were for the Insectivora, for rodents of the subfamily Murinae, and for carnivores of the family Procyonidae. In the first case, the trend was slightly positive, but became negative and consistent with the island rule when just the more species rich group of insectivores – the soricids (shrews) – were considered separately. In the latter two cases (Murinae and Procyonidae), the trends were positive (i.e. contrary to the general pattern), but in both cases the analyses were based on data from just two levels of the independent variable (i.e. groups with species of just two body sizes in the mainland form).

Carnivore skull measures

Meiri *et al.*'s (2004) recent study of skull measurements in Carnivora also provides results that are consistent with the island rule (Fig. 2), although trends within some carnivore families seem anomalous and residual variation about the trend line is more substantial than that of the above described patterns. The substantial unexplained variation about the general relationship is not that surprising, however, given the methods employed by these authors. First, Meiri *et al.* (2004) did not use mass, but relied on the

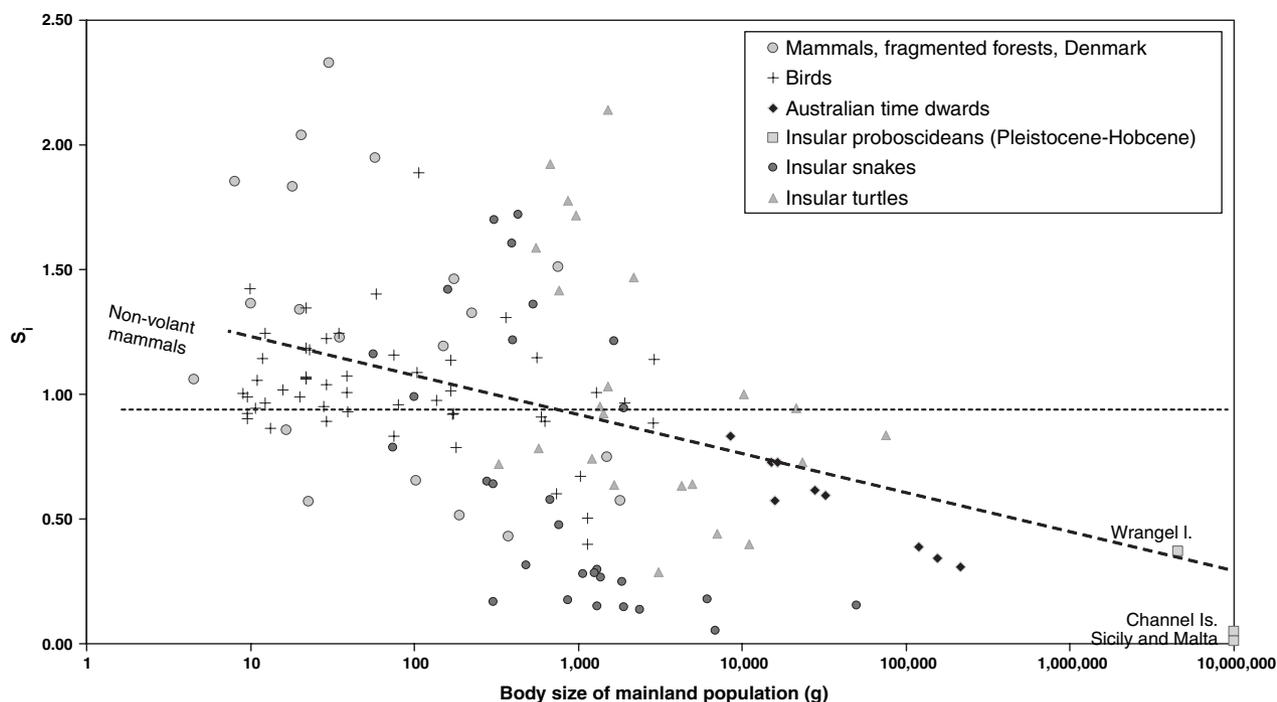


Figure 4 Body size trends in insular vertebrates (see Table 2). S_i is relative size of insular forms as a proportion of the mass of their mainland relative. Sources: mammals of fragmented forests in Denmark: Schmidt & Jensen (2003); insular birds: Clegg & Owens (2002); insular snakes: Boback & Guyer (2003); insular turtles: N. Karraker (unpublished manuscript); Australian marsupial, Pleistocene–Holocene ‘time-dwarfs’: Flannery (1994). The dashed line indicates the trend for populations of non-volant, terrestrial mammals on islands (Lomolino, 1985 and this paper; Figure 1).

author’s measurements of skulls and teeth from museum specimens (condylo-basal length, maximum diameter of upper canine, and length of the first lower molar). While each of these measures are correlated with body size (mass), they are features that, to different degrees, also reflect differences in shape, in diet, and in other more labile characteristics of insular populations adapting to a diversity of insular environments. In fact, Meiri *et al.*’s analyses of these data reveal different patterns of variation for the three different measures, and Meiri & Dayan’s (2003, p. 331) study of a related pattern (Bergmann’s rule) found that ‘studies using body mass in mammals show the greatest tendency to adhere [to the predicted pattern, while] linear measurements and dental measurements show a weaker tendency’. Finally, Meiri *et al.*’s quite laudable restriction of their data to those derived from museum collections with large numbers of specimens of each insular population may have unintentionally reduced the power for assessing the island rule. As an apparent result, most of the insular populations they included were from relatively large islands (88% of the islands were larger than 2590 km² in area, 61% were larger than 25,900 km²). These are very large islands, indeed, including Great Britain, Newfoundland, Sumatra and Borneo (these particular islands ranging from 22,979 to 670,434 km²). Given the asymptotic nature of the predicted relationship between body size of insular populations and island area (see Heaney, 1978), it is much more difficult to

detect a significant body size trend if most islands are relatively large (i.e. mainland-like). Despite all this, the pattern for skull size of insular carnivores (based on condylo-basal length of males) was consistent with the island rule [i.e. S_i decreasing with body size of mainland populations; linear regression of S_i on $\log(\text{CBL})$ in males; t (slope is not < 0.0) = 1.698, $P = 0.047$; Fig. 2].

Insular bats

Krzanowski’s (1967) survey of body size patterns in insular bats was published soon after Foster’s (1964) paper on non-volant mammals, and his approach was similar, albeit presented primarily in a long series of descriptions rather than tables, which would have made the data much more readily accessible to others. While an updated review of body size trends in insular bats is certainly overdue, Krzanowski’s survey provides some interesting insights. He reported that, although the range in body size of bats is similar to those of rodents and insectivores, unlike the latter groups bats tend to exhibit dwarfism on islands (the ratio of dwarfs to giants was 15 : 6 for megachiropterans, and 52 : 29 for microchiropterans). Krzanowski (1967, p. 339) hypothesized that the dwarf forms resulted from altered selection pressures (islands typically lacking large, ground-dwelling mammals), from increased pressures of intraspecific competition (in his terms, resulting from ‘qualitatively strong populations’), and from resource

Table 1 Summary of regression statistics for relative body size (S_i) of insular populations as a function of body size of nearest mainland population

Taxonomic group	<i>n</i>	Intercept (b_0)	SE	Slope (b_1)	SE	<i>P</i>	r^2 adj	Mass (g) where $S_i = 1.0$
(a) Regression model: $S_i = b_0 + b_1[\log_{10}(\text{mass mainland, g})]$ (<i>P</i> values indicate probabilities that the slope (b_1) is not < 0.0)								
All mammals	384	1.35540	0.02979	-0.11991	0.01194	0.00000	0.207	920
Terrestrial populations	365	1.40989	0.03058	-0.15646	0.01328	0.00000	0.275	417
Marupials, Didelphimorpha, Diddlephidae (two levels of independent variable, mass)	8	1.89812	0.18444	-0.29238	0.06812	0.00180	0.713	
Insectivora*	38	0.98509	0.07633	0.04421	0.06186	0.76033	-0.013	
Insectivora, Soricidae	35	1.07714	0.14906	-0.05424	0.15339	0.36291	-0.026	26
Lagomorpha, Leporidae	20	2.39105	0.49491	-0.41818	0.14433	0.00462	0.280	2120
Rodentia	240	1.54322	0.05238	-0.22316	0.03014	0.00000	0.184	272
Rodentia, Sciuridae	25	1.36785	0.30472	-0.16949	0.11461	0.07609	0.047	
Rodentia, Muridae	186	1.51515	0.09005	-0.17153	0.06251	0.00334	0.034	
Rodentia, Muridae, arvicolinae	44	1.89104	0.31468	-0.41486	0.18889	0.01676	0.082	
Rodentia, Muridae, murinae (two mass levels)*	24	-1.60937	1.34636	2.36448	1.14593	0.97473	0.124	
Rodentia, Muridae, sigmodontinae	118	1.55911	0.11011	-0.17444	0.07875	0.01435	0.032	
Rodentia, Heteromyidae	19	1.25812	1.05767	-0.29412	0.71094	0.34199	-0.048	
Carnivora (terrestrial and aquatic)	63	1.27739	0.13881	-0.09111	0.03570	0.00660	0.082	
Terrestrial carnivores	44	1.59497	0.13171	-0.23092	0.03912	0.00000	0.440	377
Carnivores with aquatic prey	19	2.49658	0.18993	-0.28136	0.03887	0.00000	0.741	208,485
Carnivora, Procyonidae (two mass levels)*	11	-4.02761	3.93891	1.20924	1.00865	0.87089	0.042	
Carnivora, Canidae	14	1.35602	0.27141	-0.18209	0.06706	0.00883	0.329	
Carnivora, Mustelidae	17	1.50300	0.29970	-0.16519	0.13127	0.11315	0.035	
Artiodactyla	15	1.99569	0.66553	-0.25924	0.13580	0.03849	0.159	6931
Artiodactyla, Cervidae	14	1.77745	0.73214	-0.21316	0.15017	0.08965	0.072	
(b) Regression model: $\log_{10}(\text{mass, insular population, g}) = b_0 + b_1[\log_{10}(\text{mass, mainland population, g})]$ (<i>P</i> values indicate probabilities that the slope (b_1) is not < 1.0)								
All mammals	384	0.13558	0.01218	0.94603	0.00488	0.00000	0.990	
Terrestrial populations	365	0.16234	0.01236	0.92840	0.00537	0.00000	0.988	
Marupials, Didelphimorpha, Diddlephidae (two mass levels)	8	0.34866	0.06306	0.88223	0.02329	0.00073	0.995	
Insectivora*	38	-0.00170	0.03263	1.00694	0.02644	0.60277	0.975	
Insectivora, Soricidae	35	0.01442	0.06892	0.98969	0.07092	0.44265	0.851	
Lagomorpha, Leporidae	20	0.61731	0.22597	0.81202	0.06590	0.00509	0.888	
Rodentia	240	0.20635	0.01979	0.90682	0.01139	0.00000	0.964	
Rodentia, Sciuridae	25	0.15245	0.15297	0.92307	0.05753	0.09688	0.914	
Rodentia, Muridae	186	0.18173	0.03007	0.93798	0.02087	0.00168	0.916	
Rodentia, Muridae, arvicolinae	44	0.32456	0.12077	0.84786	0.07249	0.02088	0.760	
Rodentia, Muridae, murinae (two mass levels)*	24	-0.97827	0.48575	1.88313	0.41344	0.97823	0.462	
Rodentia, Muridae, sigmodontinae	118	0.19869	0.03519	0.93477	0.02517	0.00538	0.922	
Rodentia, Heteromyidae	19	0.05617	0.54567	0.89561	0.36678	0.38959	0.216	
Carnivora (terrestrial and aquatic)	63	0.09204	0.06685	0.95927	0.01720	0.01049	0.980	
Terrestrial carnivores	44	0.28259	0.06555	0.88024	0.01947	0.00000	0.979	
Carnivores with aquatic prey	19	0.54134	0.07116	0.89643	0.01456	0.00000	0.995	
Carnivora, Procyonidae (two mass levels)*	11	-3.61366	2.36596	1.87723	0.60586	0.91087	0.462	
Carnivora, Canidae	14	0.35496	0.18541	0.85740	0.04581	0.00412	0.964	
Carnivora, Mustelidae	17	0.16797	0.10762	0.94335	0.04714	0.12344	0.961	
Artiodactyla	15	0.64898	0.44832	0.83747	0.09148	0.04867	0.855	
Artiodactyla, Cervidae	14	0.50654	0.49395	0.86754	0.10131	0.10686	0.848	

S_i = mass of insular population as proportion of that of mainland relative. r^2 adj, adjusted *r*-square value.

*Results not consistent with the island rule are marked by asterisks.

limitation ('the limitation of space and, in consequence, among other things, of food supply...'). He also noted that '...smaller specimens [had] greater chances of finding shelter and hiding from predators' (in this case, avian predators).

Although not the most prevalent response to insularity, Krzanowski (1967) did report at least 35 cases of gigantism on islands. Again, his explanation was based on insular selection pressures and some of the advantages of being large, which

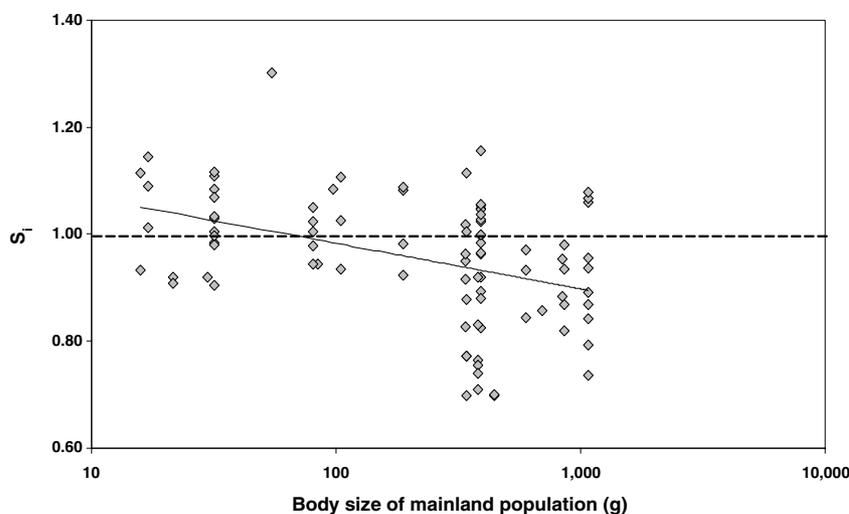


Figure 5 Body size trends in insular bats (megachiropterans). S_i is relative size of insular forms expressed as proportion of size of their nearest mainland relative [forearm length data after Krzanowski, 1967; the probability that this trend is not consistent with the island rule (i.e. that the slope is not < 0) is < 0.05].

include a greater ability to survive during short-lived periods of hunger, greater ability to withstand the relatively cool climates of insular environments, and superior immigration abilities. In Krzanowski's (1967, p. 30) words, '...the stronger and so, for the most part, bigger specimens of the original population managed to cover the distance separating these islands from the mainland. So far as the characters [body size] are hereditary, they were transmitted to the offspring. As a result, a variety of larger than the initial form have sprung up'.

Analyses of Krzanowski's (1967) data reveal that megachiropterans also exhibit the island rule pattern (Fig. 5; Krzanowski did not present comparable data for microchiropterans; see also Barclay & Brigham, 1991).

Mammals of other, island-like ecosystems

Schmidt & Jensen's (2003) recent analysis of mammals inhabiting anthropogenically fragmented forests of Denmark indicate that body size changes can occur quite rapidly (see also Lister, 1989, 1996), and that these changes are consistent with the pattern expected for mammals of true islands. In just 175 years of isolation, it appears that larger species are undergoing dwarfism, while smaller species tend to increase in size, with the size at which mammals of these fragmented forests are neither increasing or decreasing in size being between 0.1 and 0.4 kg (Fig. 4 & Table 2; Schmidt & Jensen, 2003). These results are limited to just one system and should therefore be taken as preliminary, but the possibility of anthropogenic changes in body mass of native species certainly warrants increased attention from biogeographers and conservation biologists (see Lomolino *et al.*, 2001 for accounts of anthropogenic changes in body size in fish, birds, skinks and turtles, respectively; also see Brown *et al.*, 1992, Smith *et al.*, 1997; Summer *et al.*, 1999; Aponte *et al.*, 2003; Campbell & Echternacht, 2003).

Flannery (1994) has reported a similar trend for Australian marsupials following colonization and transformation of native landscapes by aborigines *c.* 60,000 yr BP. Within a few millennia, Australia's marsupial megafauna (those > 500 kg)

began to suffer extinction, while those smaller than 5 kg were largely unaffected, at least until recent times. Marsupials between 5 and 500 kg, however, exhibited an intriguing phenomenon Flannery (1994) termed 'time-dwarfing'. Throughout the late-Pleistocene, these species [including spotted-tailed quolls (*Dasyurus maculatus*), Tasmanian devils (*Sarcophilus harrisii*), yellow-footed rock wallabies (*Petrogale xanthopus*), koalas (*Phascolarctos cinereus*), swamp wallabies (*Wallabia bicolor*), agile wallabies (*Wallabia agilis*), wallaroos (*Macropus robustus*), grey kangaroos (*Macropus giganteus*) and red kangaroos (*Macropus rufus*)] all survived, but underwent dwarfing. Consistent with the island rule, the degree of dwarfing was highest for the largest species (Fig. 4).

Evolution of insular body size in other terrestrial vertebrates

The island rule may be more general than previously suggested, applying to other vertebrates in addition to mammals. Until recently it appeared that, although birds exhibited a general trend toward increasing bill size on islands (Lack, 1947; Grant, 1965; Blondel, 2000; but see Clegg & Owens, 2002), they failed to exhibit trends in body size consistent with the island rule (at least when wing length was used as a surrogate of body size; Grant, 1965). On the other hand, some relatively small birds such as wrens and possibly fruit pigeons tend to exhibit gigantism on islands (Williamson, 1981; McNab, 1994a,b; Grant, 1998) while larger birds such as rails, ducks and ratites tend toward insular dwarfism (Wallace, 1857; Lack, 1947; Greenway, 1967; Weller, 1980). Cassowaries are large by most avian standards, but as Wallace noted in 1857, the New Guinea form (*Casuaris bennetti*) is small compared with its relative on the Australian mainland [*C. casuarinus*; body lengths of 52 inches (132 cm) vs. 65 inches (165 cm), respectively]. Emus (*Dromaeius novaehollandiae*) of the small islands of Bass Strait are much smaller than those of Tasmania and the Australian mainland (Greenway, 1967). Thus, the trends suggest a possible, general pattern.

Table 2. Results of regression analyses for body size trends in insular vertebrates

Taxonomic group (source)	Regression model (mass in g, carapace length, CL in mm)	<i>n</i>	Intercept (<i>b</i> ₀)	SE	Slope (<i>b</i> ₁)	SE	<i>P</i>	<i>r</i> ² adj	Mass where <i>S</i> _i = 1.00
Bats (Megachiropterans, this study, after Krzanowski (1967))	$S_i = b_0 + b_1[\log_{10}(\text{mass on mainland})]$ $\log_{10}(S_i) = b_0 + b_1[\log_{10}(\text{mass on mainland})]$	90	1.1532	0.0486	-0.0851	0.0204	0.0001	0.156	63 g
Birds (Clegg & Owens, 2002)	$S_i = b_0 + b_1[\log_{10}(\text{mass on mainland})]$ $\log_{10}(S_i) = b_0 + b_1[\log_{10}(\text{mass on mainland})]$	51	1.2121	0.0838	-0.1009	0.0418	0.0097	0.088	126 g
Snakes (Boback & Guyer, 2003)	$S_i = b_0 + b_1[\log_{10}(\text{mass on mainland})]$ $\log_{10}(S_i) = b_0 + b_1[\log_{10}(\text{mass on mainland})]$	51	0.1012	0.0375	-0.0553	0.0187	0.0024	0.134	68 g
Non-volant mammals	$S_i = b_0 + b_1[\log_{10}(\text{mass on mainland})]$ $\log_{10}(S_i) = b_0 + b_1[\log_{10}(\text{mass on mainland})]$	30	2.4875	0.5158	-0.6076	0.1759	0.0009	0.274	281 g
Fragmented Forests of Denmark (Schmidt & Jensen, 2003)	$S_i = b_0 + b_1[\log_{10}(\text{mass on mainland})]$ $\log_{10}(S_i) = b_0 + b_1[\log_{10}(\text{mass on mainland})]$	30	1.0400	0.2933	-0.4740	0.1000	0.0000	0.425	156 g
Australian time-dwarfed Marsupials (Flannery, 1994)	$S_i = b_0 + b_1[\log_{10}(\text{mass on mainland})]$ $\log_{10}(S_i) = b_0 + b_1[\log_{10}(\text{mass on mainland})]$	20	1.8106	0.3158	-0.3102	0.1596	0.0035	0.127	411 g
Turtles (N. Karraker, unpublished manuscript)	$S_i = b_0 + b_1[\log_{10}(\text{mass on mainland})]$ $\log_{10}(S_i) = b_0 + b_1[\log_{10}(\text{Max CL})]$	20	0.2794	0.1223	-0.1278	0.0618	0.0263	0.147	154 g
		9	2.1646	0.1677	-0.3500	0.0365	0.0000	0.919	2125 g
		9	1.0875	0.1169	-0.2973	0.0255	0.0000	0.944	4544 g
		23	2.8972	0.9940	-0.7832	0.4151	0.0362	0.104	265 mm (3779 g)*
		23	0.7000	0.4431	-0.3108	0.1850	0.0536	0.076	179 mm (1181 g)*

n, Number of observations; *r*² adj, adjusted *r*-square value; *P* values indicate probabilities that the slope (*b*₁) is not consistent with the island rule.

*Conversion from carapace length to mass based on allometric equation for male *Testudo hermanni*; $\log(\text{mass, g}) = -3.160 + 2.967 \log(\text{carapace length, g})$ (Willemssen *et al.*, 2002).

Clegg & Owens (2002) provided a much clearer and more comprehensive assessment of morphological variation in insular birds, revealing that both bill length and body mass of a sample of 110 insular populations vary in a manner consistent with the island rule; i.e. a graded trend from gigantism in smaller birds to dwarfism in the larger birds (Fig. 4 & Table 2; see also Cassey & Blackburn, 2004).

Insular reptiles show a diversity of patterns in body size evolution, but again a general trend may be emerging. Much as Foster (1964) first reported for mammals, different reptilian orders and families appear to exhibit different evolutionary tendencies. Gigantism, for example, is common in insular iguanids, herbivorous lizards, whiptails, tiger snakes and possibly tortoises (Mertens, 1934; Case, 1978, 1979; Case & Bolger, 1991; Case & Schwaner, 1993; Petren & Case, 1997; Caccone *et al.*, 1999), while rattlesnakes tend to be dwarfed on islands (Schwaner & Sarre, 1990). Boback & Guyer's (2003) recent and more comprehensive analysis of body size variation of insular snakes, however, reveals a pattern consistent with the island rule (Fig. 4 & Table 2). Similarly, N. Karraker's (unpublished manuscript) ongoing studies of body size variation in insular turtles also reveals a graded trend from gigantism in the smaller species to dwarfism in the larger species (Fig. 4 & Table 2; see also Aponte *et al.*, 2003; Boback, 2003).

A fundamental, or 'optimal', size

For each of the above groups of species, within or among classes of vertebrates, there is a body size in Figs 1, 2 and 4 at which the trend line intersects the dashed line marking the point where *S*_i = 1.0; i.e. where body size of insular populations tends not to diverge from that of their mainland counterparts. With a healthy degree of caution, some scientists have interpreted the body size corresponding to this intersection point to be a crude estimate of the fundamental or 'optimal' body size for species of a particular bau plan and ecological strategy (e.g. flying insectivorous endotherm or large grazing mammal; see Case, 1978; Maurer *et al.*, 1992; Brown *et al.*, 1993; Jones & Purvis, 1997; Marquet & Taper, 1998; Boback & Guyer, 2003). In smaller, more isolated, or ecologically more simple communities, larger species will undergo dwarfism, smaller species will undergo gigantism, all converging on this characteristic size. On the species-rich and environmentally heterogeneous mainland, however, modal body size of particular species groups might converge on this body size except for the challenges of interspecific interactions, and temporal and spatial variation in environmental characteristics that combine to increase variation about the modal size.

Macroecologists have reported related patterns in body size variation that also suggest an optimal size. For example, Marquet & Taper (1998) discovered that along a gradient of decreasing island area and declining species diversity, the range in body size of insular bird communities decreased, with sizes converging on that approximating the modal size for these

birds. Similarly, Maurer *et al.* (1992) found that along a gradient of decreasing land area, maximum body size increases and median body size converges on the hypothetical optimum estimated from the island rule for these mammals (see also Brown *et al.*, 1993; Marquet & Taper, 1998). More recently, Boback & Guyer (2003) have conducted similar analyses of body size trends in insular snakes. Along a gradient of decreasing diversity, body size of insular assemblages of snakes converges on a size similar to the modal size for these vertebrates and one similar to the apparent 'optimal' body size estimated independently from analysis of the island rule (i.e. the size at which insular snakes tend not to diverge in size from their mainland relatives).

Interpretation of this feature of the island rule remains in its preliminary stages, but since the potential insights are so intriguing, preliminary comparisons of trends in fundamental sizes (S_f = sizes where species tend to exhibit neither gigantism nor dwarfism) among groups seem justified, if only to raise some questions for future studies. For example, how should these values vary among species with fundamentally different bau plans or for those with similar bau plans but different feeding strategies? For mammals, S_f values tend to be much higher for species with aquatic prey (i.e. the piscivorous mink and otter), which are much less constrained by limited terrestrial resource of islands than are the more

terrestrial mammals (Fig. 1) (Lomolino, 1985; Gordon, 1986; Hilderbrand *et al.*, 1999; McNab, 2002). Regression results presented in Tables 1a and 2 can be used to estimate fundamental sizes for different groups of mammals by solving for the mainland mass that yields $S_f = 1.0$. Again cautioning on the preliminary nature of this line of research, the differences among groups are nonetheless interesting and worthy of future study (see values reported in last column of Tables 1a & 2). The S_f value for all non-volant mammals combined is 920 g, but it is just 417 g for the terrestrial species, and varies from just 26 g in shrews, 272 g in rodents and 2120 g in rabbits and hares, to over 6 kg in grazing and browsing ungulates (*Artiodactyla*) and over 200 kg in carnivores with aquatic prey (Table 1a).

Viewed over relatively long temporal scales, the diversification of various lineages of vertebrates may have involved relatively long periods of gradual diversification and increased variation in body size within groups of similar bau plans and ecological strategies (following Cope's Rule; see Cope, 1887; Gould, 1997; Jablonski, 1997; Alroy, 1998; Gould & MacFadden, 2004), alternating with periods of more dramatic evolution and diversification in body size when lineages diverged to invade or define new bau plans and ecological strategies (i.e. those with markedly different fundamental or optimal sizes; Fig. 6). In particular, development of flightlessness and associated morphological and physiological changes

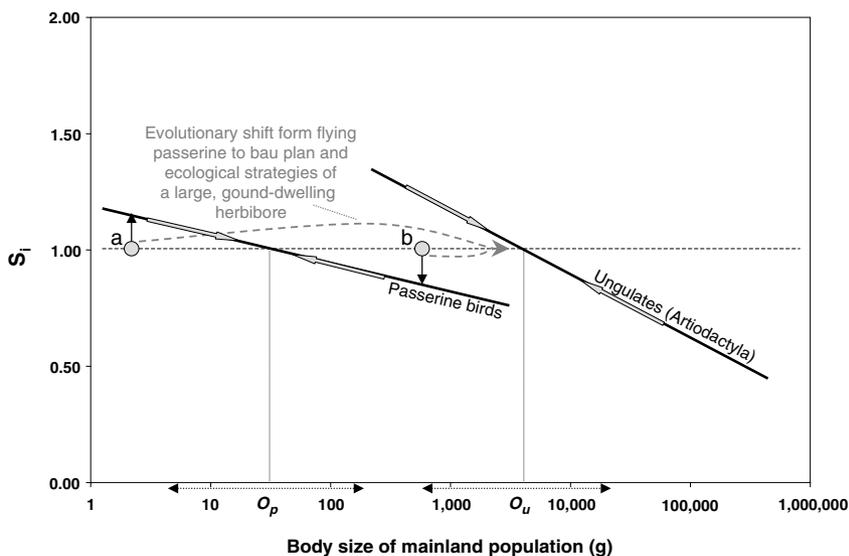


Figure 6 In species-rich mainland communities, interspecific interactions (especially competition and predation) facilitate evolutionary divergence and increased variation in morphological and ecological characteristics of component species (horizontal dotted arrows along the abscissa refer to evolutionary divergence in body size within lineages inhabiting species-rich, mainland communities). On the other hand, the paucity of such selective pressures on species-poor islands may facilitate reduction in this variation and convergence on the 'optimal', or fundamental size and behaviour for a particular bau plan and ecological strategy (solid grey arrows). In addition to these relatively gradual evolutionary changes, which are features of the island rule (i.e. gigantism in smaller species and dwarfism in larger species – vertical arrows for species a and b), major evolutionary transformations, such as the loss of flight and development of gigantism in insular birds may involve shifts in fundamental sizes, bau plans and ecological strategies in response to the distinctive selective pressures on islands. As McNab (1994a,b, 2002) suggested, the lack of ground-dwelling, mammalian predators and competitors may have shifted selective pressures to favour individuals that commit less energy to flight muscles, evolving towards the bau plan and ecological strategy of a non-volant, large herbivore (dashed grey arrows) – in this case an ungulate which, in comparison with insectivorous and granivorous birds, has a much larger fundamental (optimal) size (O_p and O_u refer to optimal sizes for passerines and ungulates, respectively).

in birds may have involved these fundamental changes and adaptations to the special challenges of insular environments (in Darwin's terms, 'sticking to the wreck'). Rather than just shifting to occupy the fundamental niche and size of some vacant group of species (e.g. large grazing mammals), these transformations more than likely involved development toward niches and body plans novel to those insular forms. That is, insular forms such as elephants, birds and bats may seem convergent on the characteristics of ungulates, but they are not equivalent (see Brown & Lomolino, 1998).

The short-tailed bats of New Zealand comprise a fascinating case in point. Unlike birds, it appears that bats have never evolved flightlessness, at least no concrete evidence has been presented for this. Despite this, the evolution of insular bats, in particular of the short-tailed bats of New Zealand, is nonetheless remarkable, involving fundamental changes in their ecological niche and the morphological, physiological and behavioural characters that support it (Lloyd, 2001). New Zealand has three native bats: the long-tailed wattled bat (*Chalinolobus tuberculatus*), the lesser, short-tailed bat (*Mystacina tuberculata*) and the greater, short-tailed bat (*M. robusta*). The latter species has not been observed since 1967 and is presumed extinct. Its closest relative, the short-tailed bat, persists, although it is considered a species of the highest conservation priority. According to Lloyd (2001, p. 69), the diet and range of foraging modes of this species is the most diverse of any bat in existence, including feeding on fruits, nectar, pollen and a variety of invertebrates captured while 'hawking, flycatching, gleaning and terrestrial foraging'. Accordingly, the morphology and physiology of these bats supports a diversified ecology. Perhaps most remarkable among their adaptations is that, although these bats remain fairly good flyers, they are the most terrestrial of all bats, often foraging on the ground and sometimes roosting in burrows. Morphological adaptations to terrestrial foraging include wing and tail membranes that can be furled along the axis of the forelimb, robust hind limbs and talons, and a relatively wide range of movements of the femur (Lloyd, 2001). Greater short-tailed bats had similar adaptations, supporting a diet and niche that was also diversified, but in this case more carnivorous than that of its surviving relative. That is, in addition to feeding on invertebrates and plants, *M. robusta* also preyed or scavenged on vertebrates (birds and reptiles).

In summary, evolution of these and perhaps many other island forms involved major shifts and expansions in their fundamental niches, converging on particular traits of vacant species, but creating novel niches shared by no other species on the mainland or otherwise.

SYNTHESIS: EXPLANATIONS FOR THE ISLAND RULE

Like other very general patterns in ecology, biogeography and evolution (e.g. the species–area relationship, latitudinal gradients in diversity and Cope's Rule), the generality of body size patterns in insular vertebrates may result, not from one factor,

but from a combination of convergent forces – each having similar effects but varying in importance depending on the particular species and spatial and temporal scales. All of these selective forces contribute to the overall, emergent pattern across species – in this case, the graded trend on islands from gigantism in the smaller species to dwarfism in the larger species.

The generality as well as the variability about the general trend are reflections of the multi-scale nature of the overall patterns. That is, the island rule is an emergent pattern across species and archipelagoes, resulting from natural selection operating among individuals and populations within particular islands. Evolutionary divergence among different islands is to be expected given the often marked differences in their histories, environmental characteristics and associated selective pressures. While many forces and factors influence optimal body size of a given species on each island it inhabits, as islands become smaller and more isolated (i.e. more island-like), species diversity declines while population densities of the few insular inhabitants increases, sometimes rivalling or exceeding those of species-rich communities on the mainland (see discussion of density compensation in Lomolino *et al.*, 2005). As a result, key selective forces switch from those most closely associated with interspecific pressures (e.g. predation, parasitism and interspecific competition) on the mainland or large, species-rich islands, to those more closely associated with intraspecific competition for limited resources on species-poor islands. Thus, explanations for body size trends in insular vertebrates often include ecological release (from predation, parasitism and interspecific competition) and resource limitation on islands, the latter mediated by relatively high densities of conspecifics and intense, intraspecific competition (Grant, 1965; Case, 1978; Lomolino, 1985).

In addition to these selective forces (ecological release and resource limitation), both of which operate long after populations have colonized and spread across an island, natural selection may also operate during immigration. As evident from Darwin's metaphor of 'shipwrecked mariners', selective pressures during immigration may be fundamentally different from those influencing established populations; the latter often producing insular marvels such as flightless beetles and birds, or the insular giants and dwarfs discussed here. On the other hand, founding populations and biotas of isolated islands may comprise a highly non-random subset of the mainland species pool – one biased in favour of the better immigrants (see Reymont, 1983; Lomolino, 1984). Some of the effects of selection for better immigrants (those that could 'swim still further') may persist long after colonization, provided of course that selective pressures following colonization do not operate counter to any initial biases in founding populations. For active immigrants, such as the vertebrates discussed here, immigration abilities should increase with body size and, therefore, larger individuals should be favoured (at least during the early stages of colonization).

It may be especially instructive to explore the residual variation about the general signal – the island rule – along with

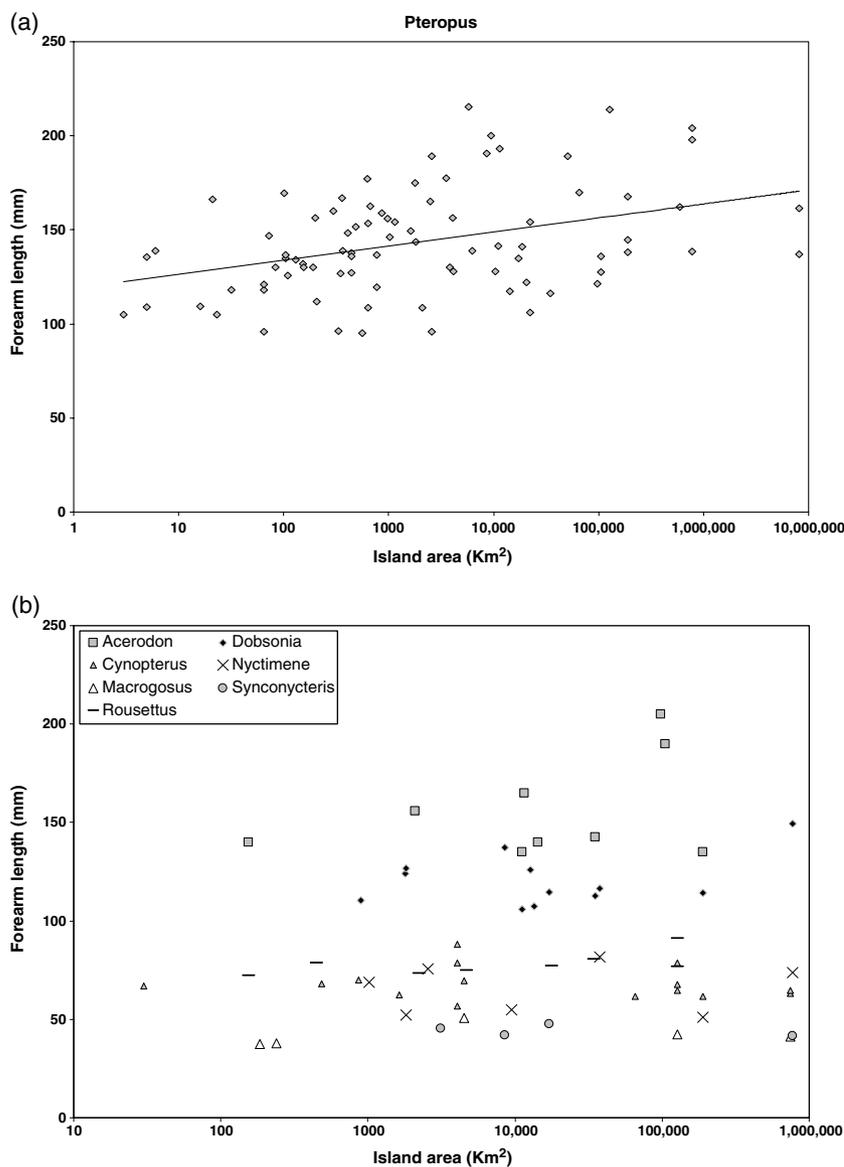


Figure 7 Body size variation as a function of island area in megachiropteran bats of the genera (a) *Pteropus* and (b) *Acerodon*, *Cynopterus*, *Macroglossus*, *Rousettus*, *Dobsonia*, *Nyctimene* and *Synconycteris* (data after Krzanowski, 1967).

some corollary patterns that are evident at finer scales. Given that the effects of immigrant selection should vary with isolation, and that those of ecological release and resource limitation should vary with area, isolation and diversity of insular communities, then body size of insular populations of a particular species should be correlated with area and isolation of the islands it inhabits. In fact, such correlations have been reported for a variety of insular vertebrates, and for some invertebrates as well (Figs 3 & 7, Table 3). As McNab (2002, p. 699) has noted, energy conservation can also be achieved by undergoing torpor and by decreasing basal metabolic rates – phenomena that have been documented for insular doves (*Drepanoptilia holosericea*), pigeons (*Ducula* spp.) and bats (*Pteropus* spp. and *Dobsonia* spp.). Consistent with this energy conservation hypothesis, the magnitude of decreases in metabolic rates is greatest for those populations inhabiting the smaller islands, i.e. where resource supplies should be most

limiting (see McNab, 2002, Fig. 3). Again, variation in island characteristics (i.e. that within archipelagos) may account for much of the total variation in body size of insular vertebrates. While the patterns within species might be viewed as corollaries of the island rule, they actually contribute to residual variation rather than the general, emergent signal (Fig. 8).

At a more general level, the island rule is a pattern emerging from processes influencing insular populations on hundreds of islands varying greatly in area, isolation and other factors that influence resource levels, productivity, species diversity, ecological interactions and the likelihood of colonization. If differences among islands contribute only to variation about the trend, what then accounts for the island rule? First, the island rule is actually a complex pattern: not gigantism or dwarfism, but a graded trend from gigantism in the smaller species to dwarfism in the larger species. That there is a graded trend suggests that the relative importance of selective forces

Table 3 Intraspecific and intrageneric correlations of body size of insular populations with island isolation and island area

Taxon (class, order)	Independent variable	Region/archipelago	Source
Mammalia			
Proboscidea			
<i>Elaphus falconeri</i> (late-Pleistocene)	+Area	Mediterranean Is.	Heaney (1978)
Rodentia			
<i>Apodemus sylvaticus</i>	+Isolation*	British Isles	Berry (1969)
<i>Mus musculus</i>	+Isolation	British Isles	Berry (1964)
<i>Microtus pennsylvanicus</i>	+Isolation*	Thousand Is., USA	Lomolino (1984)
<i>Microtus agrestis</i>	+Isolation*	Stockholm Archi., Sweden	Ebenhard (1988)
<i>Peromyscus maniculatus</i>	+Isolation*	Queen Charlotte Is.	Lomolino (1983), after Foster (1963)
<i>Peromyscus maniculatus</i>	+Isolation*; -area*	Gulf of British Columbia	Lomolino (1983), after Redfield (1976), Melton (1982)
<i>Peromyscus sitkensis</i>	+Isolation*	Queen Charlotte Is.	Lomolino (1983), after Cowan (1935)
<i>Peromyscus eremicus</i>	+Isolation*; -area*; +depth*	Gulf of California	Lawlor (1982)
<i>Callosciurus prevosti</i>	+Isolation*; +area*	Sunda Shelf, Indonesia	Heaney (1978)
Xenarthra			
<i>Bradypus</i> spp.	+Area*	Bocas del Toro Is., Panama	Anderson & Handley (2002)
Chiroptera			
<i>Pteropus</i> spp.	+Area*	Indonesia	McNab (2002); this study, analysis of data in Krzanowski (1967)
<i>Rousettus</i>	+Area*	Indonesia	This study, analysis of data after Krzanowski (1967)
Insectivora			
<i>Blarina brevicauda</i>	+Isolation*	Thousand Is., USA	Lomolino (1984)
<i>Sorex obscurus</i>	+Isolation*	Queen Charlotte Is.	Lomolino (1983), after Foster (1963)
Aves			
Gruiformes			
<i>Gallinula</i> spp.	+Area*	Pacific Islands	McNab (1994a)
<i>Porphyrio</i> spp.	+Area*	Pacific Islands	McNab (1994a)
Passeriformes			
<i>Troglodytes troglodytes</i>	+Isolation*	British and Scottish Is.	Rensch (1959)
Anseriformes			
<i>Anas platyrhynchos</i>	+Area	Polynesia	McNab (1994a), after Weller (1980)
Reptilia			
Squamata			
<i>Lacerta galloti</i>	+Area*	Canary Is.	Carlquist (1965)
<i>Anolis</i> spp.	+Area*	Greater Antilles	Filin & Ziv (2004)
<i>Ameiva</i> spp.	+Area*	Lesser Antilles	Case (1978)
<i>Uta stansburiana</i>	+Isolation*	Gulf of California	Soulé (1966)
Insecta			
Coleoptera			
<i>Asida planipennis</i>	+Area*	Balearic Is.	Palmer (2002)

+ and - indicate positive and negative correlations of body size with island area or isolation; * $P < 0.05$.

varies in a predictable manner across a gradient from the smallest to the largest species (Fig. 9). Resource limitation (intensified by high population densities and intense intraspecific competition on species-poor islands) should confer higher fitness to smaller individuals because they require less energy to survive and reproduce. The resultant tendency toward insular dwarfism should be most prevalent for those requiring the most energy, i.e. the largest species.

The effects of ecological release should also vary with body size of the ancestral or mainland species. On the mainland,

optimal body size results from a compromise between demands to survive in the face of a diversity of predators, parasites, competitors, mutualists and other symbionts. Small vertebrates often avoid predators by remaining small enough to utilize small refugia. Likewise, these same species may coexist with other, relatively large competitors by remaining small so that their total energy demands are less and their diets can be more specialized and more efficient than larger species. In less diverse communities such as those on islands, large predators and competitors are typically absent so these

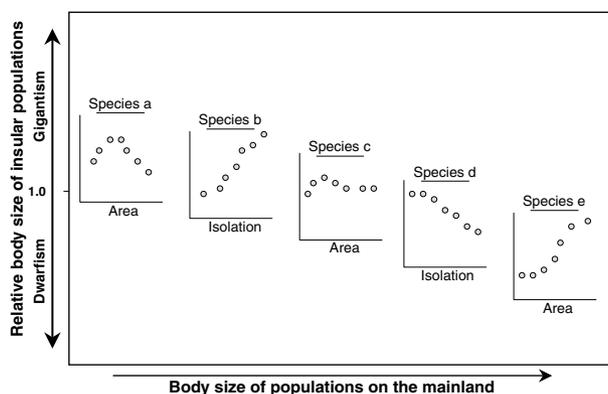


Figure 8 A multi-scale view of variation in body size of insular populations and species. Body size variation within species and within archipelagos (insets) reflects differences in ability to survive on and colonize islands (functions of island area and isolation, respectively; see Fig. 3 & Table 3). Shown here are expected trends for five hypothetical species ranging in body size from relatively small to large species (species a–e, respectively), each predicted to exhibit different patterns of body size variation with island area and island isolation. These trends within archipelagos and species contribute to residual variation about the general trend for the island rule, while the trend itself is an emergent one resulting from predictable variation in importance of different selective forces among species of small to large size (see Fig. 9).

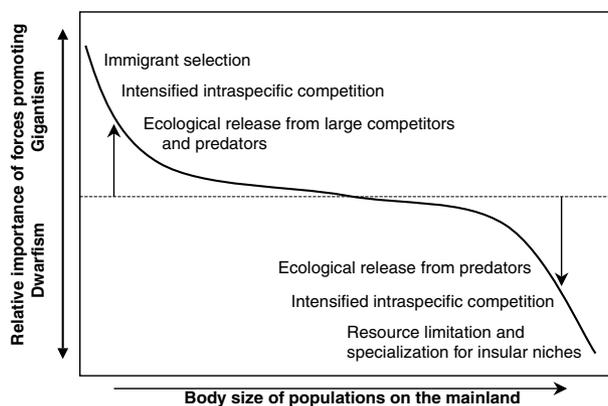


Figure 9 The island rule is an emergent pattern resulting from a combination of selective pressures whose importance and influence on insular populations change in a predictable manner along a gradient from relatively small to relatively large species.

advantages of remaining small will be lessened and the advantages of being larger and hence dominating conspecifics increases, thus promoting increased size or gigantism in the otherwise small vertebrates.

The responses of larger species to insular conditions should be just the opposite. These are species that, at least on the mainland, dominated other competitors or avoided predators by outgrowing them. Large size also has its disadvantages, however. One of the most relevant of these is an increase in

total energy and resource requirements, which would be especially problematic on small islands and those with few predators, but with high population densities and intense intra-specific competition. Thus, dwarfism is prevalent in large vertebrates species, not just as a result of resource limitation, but also from predatory release. In the absence of predators, the energy used to outgrow, outrun or outfly predators on the mainland can be used to adapt more efficiently to insular environments and their ecologically simple communities (see McNab, 1994a,b, 2001, 2002). Unfortunately, these evolutionary adaptations and many other remarkable features of insular biotas, including dwarfed mammoths and hundreds of species of flightless birds, carry grave liabilities, at least when these species are subjected to what Darwin referred to as the ‘strangers craft of power’. When exotic predators and competitors colonize (or more likely are introduced from the mainland by humans), they often cause a wave of extinctions in the ecologically naive natives – dwarfs and giants alike. As McNab (2002, p. 702) observed:

humans have all but eliminated the ‘fantasy’ world on oceanic islands of terrestrial faunas dominated by reptiles, large flightless browsing and grazing birds, and bird lineages that found their last refuge from continental competition living in or at the edge of forests of woody ‘herbs’, where mammals at best were marginally represented by a few bats. We are converting islands into minicontinents, thereby facilitating the irrevocable loss of species that would contribute to our understanding of the responses of life to environments liberated from the tyranny of mammalian predation.

In terms of explaining the island rule’s emergent pattern, it may simply boil down to the effects of selective pressures whose influences vary among species of different size (Fig. 9). Immigrant selection and ecological release from larger competitors and predators – which promote gigantism – are most important in the smaller species, while resource limitation and release from the need to outgrow predators – which promote dwarfism – should be most important in the larger vertebrates. In the absence or paucity of interspecific interactions (defining characteristics of ecologically simple islands), intraspecific pressures become paramount and the characteristics of insular populations often converge on those best suited to meet challenges of surviving and reproducing within the limited and ecologically simple, insular environs. This fundamental or ‘optimal’ size differs among vertebrates with different bau plans and ecological strategies, but some and perhaps many species appear able to undergo evolutionary transformations from one bau plan to another. For example, many birds including hundreds of species of insular rails have experienced shifts similar to those described in Wilson’s (1959, 1961) taxon cycles. Rather than simply increasing or decreasing in size and converging on the fundamental size for these birds, they have instead become more specialized for insular environments, decreasing investment in energy intensive flight muscles and,

instead, converging on the bau plan and ecological strategies of large, herbivorous non-volant vertebrates such as ungulates, which are typically absent from oceanic islands (Fig. 6; McNab, 2001, 2002).

CONCLUSION

The island rule remains a very general pattern – in one sense a relatively complex combination of patterns across a range of spatial and temporal scales, but in another sense relatively simple in that the emergent pattern results from predictable differences in selective pressures among species of different size, and from a tendency for convergence toward phenotypes that seem optimal for particular bau plans and ecological strategies. The recent resurgence of interest in this very general pattern, and corollary patterns as well, is very encouraging and likely to contribute some insights of fundamental importance to ecology, biogeography and evolution, with possible relevance for conservation biologists as well (see Lomolino *et al.*, 2001; Lomolino, 2004).

Research into this and related patterns in body size evolution should recognize and capitalize on the multi-scale nature of the pattern and apply the lessons and strategies of the comparative approach and macroecology (Brown, 1995; Gaston & Blackburn, 2000). Perhaps some of the most valuable insights into forces influencing body size evolution will be based on deconstruction (*sensu* Huston, 1994) of the emergent pattern into those characteristic of different taxa and functional groups of species, and on patterns that should vary across spatial and temporal scales based on putative causal forces. For example, body size trends should vary among groups of species with different resource requirement (e.g. ectotherms vs. endotherms, and herbivores vs. carnivores) and different immigration abilities (e.g. birds and bats vs. non-volant mammals). These differences in trends among functional groups should also be evident at the scale of populations within species, but in this case body size should also be correlated with characteristics of the islands and archipelagos, especially those characteristics most closely associated with diversity, productivity and immigration (e.g. area, latitude and isolation of the islands).

In this time of continuing advances in our abilities to collect and analyse biogeographical information, we are certain to benefit from future efforts to update and conduct more comprehensive assessments of body size patterns and potential causal explanations. While most of the earlier studies of the island rule focused on non-volant mammals and a limited variety of other terrestrial vertebrates, some truly fundamental insights may come from analogous studies across a much broader diversity of taxa including other orders of mammals (especially bats and primates), other classes of vertebrates and invertebrates, and perhaps other phyla as well.

There exists a perhaps surprising but largely untapped wealth of information on body size variation among insular populations of our own species, such that an extensive review and analyses should provide some especially intriguing

insights for anthropologists, biogeographers and evolutionary biologists; see recent reports on dwarfed insular hominins of Flores Island (Brown *et al.*, 2004; Morwood *et al.*, 2004) and earlier work on Bergmann's rule in human populations (Roberts, 1953, 1978; Bindon & Baker, 1997) and on biogeography of insular humans, in general (e.g. see Houghton, 1986, 1990; Terrell, 1986). Each of these investigations should draw on the ever-improving phylogenetic information and, when possible, on fossils and subfossils to make better informed comparisons and to reconstruct body size evolution within selected island lineages (see Gould & MacFadden, 2004).

Finally, only a very limited number of studies have explored body size evolution in other, island-like systems. The potential changes in body size of populations inhabiting montane ecosystems, naturally and anthropogenically fragmented ecosystems, nature reserves, zoos, aquaria and botanical gardens should attract many scientists attempting to understand and conserve biological diversity.

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