The island rule: made to be broken?

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The island rule is a hypothesis whereby small mammals evolve larger size on islands while large insular mammals dwarf. The rule is believed to emanate from small mammals growing larger to control more resources and enhance metabolic efficiency, while large mammals evolve smaller size to reduce resource requirements and increase reproductive output. We show that there is no evidence for the existence of the island rule when phylogenetic comparative methods are applied to a large, high-quality dataset. Rather, there are just a few clade-specific patterns: carnivores; heteromyid rodents; and artiodactyls typically evolve smaller size on islands whereas murid rodents usually grow larger. The island rule is probably an artefact of comparing distantly related groups showing clade-specific responses to insularity. Instead of a rule, size evolution on islands is likely to be governed by the biotic and abiotic characteristics of different islands, the biology of the species in question and contingency.

Keywords: body size evolution; dwarfism; gigantism; island rule; mammals;
phylogenetic comparative methods

1. INTRODUCTION

The quaternary fauna of the island of Flores has drawn much recent attention. Flores is today home to one of the world's largest murid rodents (*Papagomys armandvillei*) and the world's largest lizard (*Varanus komodoensis*). During the Middle Pleistocene (900 000 years ago), Flores also harboured a dwarf relative of modern elephants (*Stegodon sondaari*) and a giant tortoise (van den Bergh *et al*. 2001; Rolland & Crockford 2005). Public imagination, however, was mostly captivated by the finding of what is argued to be a dwarf species of human (*Homo floresiensis*, Brown *et al*. 2004), living on Flores a mere 18 000 years ago.

While some aspects of the anatomy of *H. floresiensis* are hotly debated (e.g. Jacob *et al*. 2006), its diminutive size is taken as a natural outcome of its insularity (Diamond 2004; Bromham & Cardillo 2007). This is because size decrease is a well-known feature of diverse groups of island mammals such as elephants (Roth 1992) and artiodactyls (Lister 1996). The presence of giant rats and lizards on Flores is also perceived as a natural attribute of island faunas, because many rodent and lizard species seem to increase in size on islands (Adler & Levins 1994; Meiri 2007).

Differences in the body size of closely related island and mainland populations of mammals were first quantified by Foster (1964), who showed that rodents often evolve large size on islands whereas carnivores and artiodactyls usually grow smaller there. Even though Foster (1964) did not find compelling evidence for size increase in shrews, his results were interpreted as a trend of size increase in small mammals on islands and size decrease in large mammals, and named 'the island rule' by Van Valen (1973). Lomolino (1985) quantified this rule by plotting the body size ratio

(SR) of the island populations relative to that of their mainland conspecifics against body mass of the latter. He showed a significant decrease in SR as body masses increased: species smaller than approximately 700 g tended to increase in size on islands, while larger species became smaller (Lomolino 1985; Meiri *et al*. 2004).

Recently, there has been much interest in the island rule, with similar patterns to those described for mammals as a whole being described in some taxa (birds, Clegg & Owens 2002; snakes, Boback & Guyer 2003; bats, Lomolino 2005; primates, Bromham & Cardillo 2007) but not in others (rodents, Lawlor 1982; carnivores, Meiri *et al*. 2004; mammals, Meiri *et al*. 2006; ungulates, Raia & Meiri 2006; lizards, Meiri 2007). The datasets used in most of the studies that have examined the island rule to date have been criticized for using either poor size indices, very large islands, or mainland populations that are only distantly related to the insular ones (Lawlor 1982; Lomolino 2005; Lomolino *et al*. 2005; Meiri *et al*. 2006). Furthermore, the effects of factors such as island area and isolation, competition, predation levels and the trophic level of the focal species on body size evolution of island species have all been debated recently (Dayan & Simberloff 1998; Michaux *et al*. 2002; Meiri *et al*. 2005*a*; Lomolino 2005; Meiri 2007; White & Searle 2007).

The effects of phylogeny, however, have never been explicitly examined. Lomolino *et al*. (2005) postulated that phylogeny would have an important effect on size evolution, with different 'types' of animals each having particular optimal sizes. They predicted that a similar pattern—a negative correlation between SRs and body size—would prevail within all clades or ecological groupings, although the slopes and intercepts would differ.

Comparative tests of such hypotheses need to consider phylogeny if they are to be statistically valid or powerful (Gittleman & Luh 1992). If closely related species tend to have similar SRs and similar body sizes, they are likely to
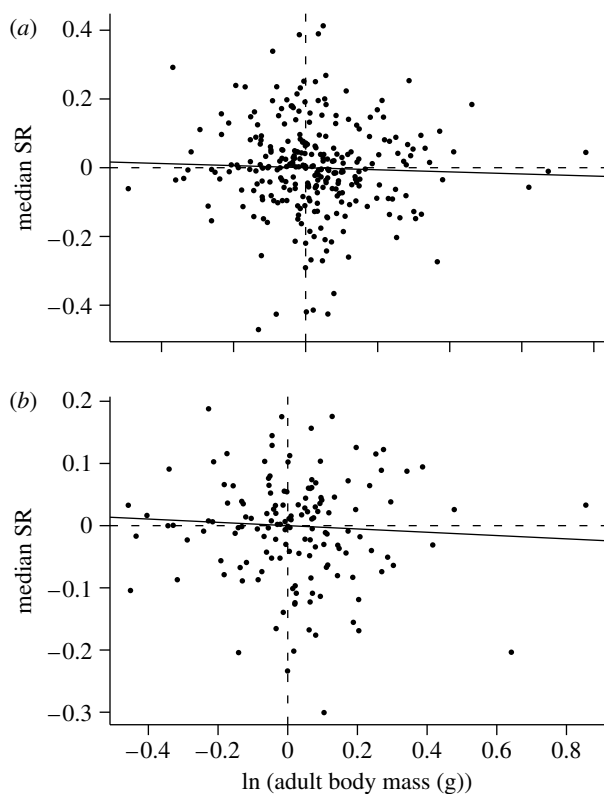

Figure 1. Regressions through the origin of independent contrasts showing the relationship between median SR and adult body mass (g). (*a*) All species (slope = −0.03, $t_{209} = -0.68$, $R^2 < 0.01$, $p = 0.50$) and (*b*) well-sampled species only (slope = −0.03, $t_{112} = -0.76$, $R^2 = 0.01$, $p = 0.45$).

be pseudoreplicates in tests of whether SR depends on body size. Thus, an apparently significant relationship could arise simply because, say, rodents (rather than all small mammals) get larger on islands whereas artiodactyls (not all large mammals) get smaller. Alternatively, the predicted negative relationship may hold within each family or order, but different intercepts (Lomolino 2005) might obscure the within-clade patterns when all data are pooled (Gittleman & Luh 1992; figure 1). Despite these issues, none of the studies of the island rule to date have explicitly considered phylogeny.

We therefore assembled a new dataset of body sizes of insular mammals and their mainland counterparts designed to minimize the possible sources of error that may have affected earlier attempts (see above). We use this dataset to evaluate the rule as laid out by Foster (1964), Van Valen (1973) and Lomolino (1985) asking the following questions: (i) are there mammalian clades that consistently tend towards either insular gigantism or insular dwarfism, (ii) is the island rule valid for mammals, (iii) is there a similar pattern when phylogeny is taken into account, and (iv) do island area, island isolation, species trophic level or predation influence the mode of size evolution on islands.

2. MATERIAL AND METHODS

(a) *Data*
We used published records of mammalian sizes on islands and their nearest mainlands including all the sources used in earlier tests of the island rule, recent comparative studies and new sources (appendix 1 in the electronic supplementaty material). From these we extracted data on body sizes of island populations and their near-mainland relatives according to

strict morphological, phylogenetic and geographical criteria. Some of the datasets used to demonstrate the existence or absence of the island rule were criticized for using inadequate size indices (Lomolino 2005; Meiri *et al.* 2006), distantly related island–mainland pairs (Lawlor 1982), exceedingly large islands (Lomolino 2005) and phylogenetically non-independent data (Lawlor 1982). We therefore used only data that are, in these respects, relatively problem free by adopting the following measures: to best control for possible differences in measurement techniques, seasonal and year-by-year variation, reproductive condition and comparisons of field and museum measurements, we only compared populations if island and mainland body sizes were reported in the same study. Because populations on even nearby islands can have drastically different body sizes (e.g. Jessop *et al.* 2006), we only used populations that we were certain were derived from a single island. We used only those studies that reported body size of mainland populations geographically closest to the island in question (Lawlor 1982). Some insular populations have their nearest sister taxon on a mainland area which is a considerable distance away (e.g. Hafner *et al.* 2001). The paucity of good intraspecific phylogenetic data, however, precludes us from identifying the closest relatives for most insular populations and we therefore use geographical distance to approximate phylogenetic affinity.

Island populations were compared to mainland conspecifics (using the taxonomy of Wilson & Reeder 1993) unless the insular species was endemic, and phylogenetic data showed that it was derived from, or sister species of, the mainland species. Very large islands are 'mainland like' in terms of the number of predators and competitors a species is likely to encounter (Lomolino 2005). Meiri *et al.* (2006) found that similar patterns of size evolution are obtained when the area of the largest islands included are less than 50 000 km², and we therefore restrict our analysis to such islands (The largest island in our database is Axel Heiberg, 43 178 km², and the smallest island omitted is Svalbard, 62 700 km².)

When more than one size index was reported for a population pair, we preferred indices based on mass, then body lengths, then cranial, then dental lengths (Lomolino 2005). We did not use bat wing length because wing lengths of island bats have been shown to vary in relation to wind speed and foraging strategies (Iliopoulou-Georgudaki 1986; Jacobs 1996). We used data only from adults ('young adults' and juveniles were omitted). We used data only from sexed specimens when the sex of some or all specimens was reported, and used data for unsexed specimens in non-dimorphic species only where no data on sexed specimens were available. When similar size indices and sex data existed, we chose data based on insular then mainland sample size (treating unreported sample sizes as zero).

We assembled a dataset consisting of 1184 island–mainland population pairs, representing 276 species in 45 families and 15 orders (appendix 2 in the electronic supplementaty material). Of these 276 species, 147 had sufficiently large sample sizes that both mainland and island sizes were based on at least six individuals. We refer to these as well-sampled species.

(b) *Variables*
For each island–mainland comparison, we calculated the ratio of island to mainland body size (SR). Where data existed for both sexes, we averaged SRs of males and females. In species-level analyses, we used the median SR of each species, because the median may be less influenced by anomalous measurements than the mean if the number of populations is small.

In order to compare ratios based on mass to those based on linear measurements, we cubed linear ratios (Lomolino 1985). If the value of SR calculated was dependent on the trait used, then different indices will be incomparable. We tested that by regressing body mass median SR against body length median SR^3, and against cranial length median SR^3, and body length median SR^3 against cranial length median SR^3 for all the species in our dataset that had data allowing median SR to be calculated on all traits. All of these regressions had intercepts not significantly different from zero and slopes not significantly different from one (appendix 3 in the electronic supplementaty material), suggesting that there was no effect of the trait used on the value of SR so using different traits as body size indices should not affect the results.

Species (rather than population)-specific body masses (g), for use as an explanatory variable (only, not for calculating SRs), were mainly taken from the PanTheria Traits database (K. E. Jones *et al.* 2007, unpublished data). Trophic level (carnivores, omnivores or herbivores) was taken from PanTheria and from Nowak (1999; appendix 4 in the electronic supplementaty material). For the other variables (island area, island isolation and number of carnivore species), we used the value associated with the population with the median SR. Island area, island isolation and number of carnivore data were obtained from the literature (mostly from Meiri *et al.* 2005b), the United Nations Environment Programme website (http://islands.unep.ch) and maps (e.g. NIMA 1997; appendix 5 in the electronic supplementaty material).

All numeric variables were log transformed prior to analyses except median SR which was normally distributed. We used R v. 2.1.1 in all analyses (R Development Core Team 2006).

Many species median SR values were based on just a few island and mainland individuals. If these individuals were uncharacteristic of the species they could bias the results. Therefore, for all the analyses, we first used all the species in the dataset, then repeated the analysis omitting species for which SR values were based on fewer than six specimens from the island and/or mainland population (although if similar mainland areas were compared with more than one island, these may actually represent fewer specimens). These sampling differences could reflect island area if only a few specimens were sampled on small islands. There was, however, no significant relationship between number of specimens and island area ($t_{108} = -0.22$, slope $= -0.01$, $R^2 < 0.01$, $p = 0.83$), so using well-sampled species should not bias our results towards larger islands.

(c) *Non-phylogenetic analyses*

To examine whether different mammalian clades generally evolve larger or smaller body sizes on islands, we tested whether species within orders and families (where these contained at least five species) had median SR values significantly different from unity.

A pattern consistent with the island rule may emerge if animals below a certain size threshold grow larger, and/or animals above this threshold grow smaller, even if there are no such patterns for small or large mammals when considered separately. We therefore examined whether median SRs were significantly different for species above and below body mass thresholds of 100 g, 500 g, 1 kg, 5 kg and 10 kg, using *t*-tests with the Welch approximation of degrees of freedom. These body mass thresholds correspond roughly to where changes from gigantism to dwarfism were expected to occur under

different models of size evolution (e.g. Heaney 1978; Brown *et al.* 1993; Damuth 1993; reviewed in Meiri *et al.* (2005b)).

(d) *Phylogenetic analyses*

Previous analyses of the relationship between median SR and species body size never explicitly considered the phylogenetic non-independence of species. We therefore calculated Pagel's (1999) λ statistic for each variable to determine whether each showed significant phylogenetic structure using the R package GEIGER (Harmon *et al.* in press). We used likelihood ratio tests to test whether values of λ were significantly greater than zero. If traits are independent of phylogeny, λ is zero; however, if λ is significantly greater than zero it indicates that the species values are not independent data points and also indicates the need to consider phylogeny in the analyses. We repeated each analysis described below non-phylogenetically, so that our results could be compared to those of previous studies and to the phylogenetically corrected results.

We performed these phylogenetic analyses using independent contrasts generated using PENDEK v. 1.03 (A. Purvis, C. D. L. Orme & R. Grenyer 2006, unpublished), the R package APE (Paradis *et al.* 2005) and a mammal supertree (Bininda-Emonds *et al.* 2007) to which we added *Callosciurus erythraeus* (as a sister species to *Callosciurus finlaysoni*, Herron *et al.* 2004), and *Mystacina robusta* (as a sister species to *Mystacina tuberculata*). Independent contrasts were calculated after optimizing branch-length power transformations to minimize the correlation between absolute scaled contrasts and their standard deviations (Garland *et al.* 1992; Cardillo *et al.* 2005). We performed regressions through the origin of independent contrasts to investigate the relationship between median SR and body mass using all species, then repeated the analyses for each order that was represented by five or more species. We repeated the analyses within trophic levels. Previous works often used population—rather than species-level analyses; thus we also performed a non-phylogenetic population-level analysis to test whether SR was negatively correlated with body mass.

We investigated the effects of any highly influential points (those with a studentized residual exceeding ± 3, Jones & Purvis 1997), by deleting them and repeating our analyses. Where the deletion made a qualitative difference, we report the results both before and after deletion.

(e) *Other predictors of size evolution*

To examine the influence of island area, island isolation, species trophic level and the number of carnivore species on the island (as a surrogate for predation pressure) on body size evolution, we repeated regressions of median SR against body mass including each in turn as predictors. The presence/absence of carnivores may be more important than carnivore species richness in determining species responses (Meiri *et al.* 2005a). We therefore repeated the analysis using presence/absence of carnivores using brunch contrasts (Purvis & Rambaut 1995) generated in 'CAIC in R' (Orme in preparation). Body size evolution is sometimes thought to interact with island area to produce different patterns for small, medium-sized and large mammals (Heaney 1978). We consequently included an interaction between body mass and island area. We also added an interaction term between carnivore number and body mass since small mammals may respond differently to the presence of carnivores than large ones. Finally, we fitted a model where all the above terms (except presence/absence of carnivores) were used as

Table 1. Clade-specific tendencies towards gigantism or dwarfism. (Results of *t*-tests performed on orders and families of mammals (where the order or family was represented by five or more species) to test whether median SR is significantly different from one. $^*p < 0.05$, $^{**}p < 0.01$, $^{***}p < 0.001$. Mean SR $\pm$ 95% CIs are given for each order or family.)

all species	family	all species			species with greater than five mainland and island specimens		
		N	mean SR	t	n	mean SR	t
all	all	276	1.00 ± 0.03	-0.04	147	1.02 ± 0.03	1.21
Artiodactyla	all	12	0.88 ± 0.10	-2.59^*	6	0.90 ± 0.14	-1.88
	Cervidae	7	0.84 ± 0.17	-2.26	—	—	—
Carnivora	all	57	0.94 ± 0.04	-2.82^{**}	35	0.98 ± 0.04	-1.21
	Canidae	8	0.96 ± 0.16	-0.62	6	0.99 ± 0.20	-0.16
	Herpestidae	5	0.85 ± 0.11	-3.63^*	—	—	—
	Mustelidae	24	1.00 ± 0.06	0.06	15	1.01 ± 0.05	0.35
	Viverridae	10	0.84 ± 0.08	-4.55^{**}	5	0.87 ± 0.15	-2.28
Chiroptera	all	32	0.99 ± 0.05	-0.57	17	0.96 ± 0.07	-1.29
	Pteropodidae	9	1.04 ± 0.12	0.72	8	0.99 ± 0.06	-0.33
	Rhinolophidae	8	0.97 ± 0.08	-1.01	—	—	—
	Vespertilionidae	11	0.97 ± 0.11	-0.61	5	0.93 ± 0.26	-0.78
Diprotodontia	all	5	1.07 ± 0.31	0.66	—	—	—
Insectivora	all	26	1.00 ± 0.09	-0.09	15	1.03 ± 0.08	0.73
	Soricidae	19	1.00 ± 0.10	< -0.01	14	1.04 ± 0.08	0.98
Lagomorpha	all (Leporidae)	10	1.03 ± 0.14	0.54	—	—	—
Primates	all	30	0.92 ± 0.09	-1.72	—	—	—
	Cercopithecidae	16	0.88 ± 0.15	-1.68	—	—	—
Rodentia	all	86	1.08 ± 0.07	2.26^*	56	1.07 ± 0.06	2.18^*
	Heteromyidae	7	0.74 ± 0.28	-2.31	5	0.83 ± 0.10	-4.46^*
	Muridae	54	1.07 ± 0.09	3.98^{***}	35	1.14 ± 0.07	3.98^{***}
	Sciuridae	19	0.99 ± 0.11	-0.20	14	1.00 ± 0.15	-0.01
Scandentia	all (Tupaiidae)	9	0.94 ± 0.08	-1.85	6	0.97 ± 0.07	-1.04

Table 2. Mass-specific tendencies towards gigantism or dwarfism. (Results of Welch two sample *t*-tests testing for differences in median SR above and below various body mass thresholds. SR, size ratio. $^*p < 0.05$, $^{**}p < 0.01$, $^{***}p < 0.001$.)

body mass threshold	all species			species with greater than five mainland and island specimens		
	d.f.	mean median SR above/below threshold	t	d.f.	mean median SR above/below threshold	t
100 g	188	0.96/1.05	-2.84^{**}	137	1.00/1.04	-1.35
500 g	267	0.95/1.04	-3.55^{***}	141	0.99/1.04	-1.60
1 kg	266	0.94/1.04	-3.76^{***}	105	0.98/1.03	-1.78
5 kg	89.5	0.94/1.01	-2.14^*	23.7	0.97/1.02	-1.50
10 kg	38.0	0.91/1.01	-3.11^{**}	16.0	0.94/1.02	-2.33^*

explanatory variables. The analyses above were carried out both phylogenetically and non-phylogenetically, so the results could be compared to those from previous work. We adjusted *p*-values for multiple tests using the Benjamini & Yekutieli method of controlling for false discovery rates (Benjamini & Yekutieli 2001).

3. RESULTS
(a) *Clade tendency towards gigantism or dwarfism*
Overall, there is no tendency for island populations to be larger or smaller than mainland ones in either the whole dataset (paired *t*-test: $t_{274} = -0.04$, $p = 0.97$) or just the well-sampled species ($t_{145} = 1.21$, $p = 0.23$). However, some taxa did show significant trends (table 1). Artiodactyls and carnivores (in particular, herpestids and viverrids) tend to become smaller on islands, whereas insular rodents

(especially murids) tend to be larger than their mainland counterparts. Only the size increase in murids remains significant when only well-sampled species (see above) were used, and heteromyid rodents tend towards size decrease, suggesting that data quality may be an issue.

There is some support for the hypothesis that median SR differs either side of a threshold body size (table 2), although only the difference above and below 10 kg body mass remained significant when only well-sampled species were analysed.

(b) *SRs as a function of body size*
SR values were not independent of phylogeny (all species, $n = 276$, $\lambda = 0.316$; well-sampled species, $n = 147$, $\lambda = 0.256$; appendix 6 in the electronic supplementaty material) indicating the probable need for phylogenetic comparative methods to avoid pseudoreplication when

Table 3. The island rule: regressions of SRs against body mass. (Results from regressions of median SR against body mass (g) for subgroups of the dataset. Phylogenetic analyses consisted of regressions through the origin of independent contrasts, using all species in each subgroup. (a) All comparisons. (b) Analyses use only those species in each subgroup represented by greater than five specimens from both the island and the mainland populations. $^*p<0.05$, $^{**}p<0.01$, $^{***}p<0.001$.)

subgroup	phylogenetic				non-phylogenetic			
	d.f.	t	slope	R^2	d.f.	t	slope	R^2
(a)								
all species	209	-0.68	-0.03	<0.01	274	-2.98^{**}	-0.02	0.03
Artiodactyla[a]	10/9	$-2.70^*/-0.49$	$-0.10/-0.01$	0.42/0.03	10	-1.66	-0.05	0.22
Carnivora	49	-1.48	-0.01	0.04	55	1.14	0.02	0.02
Chiroptera	23	-0.144	-0.01	<0.01	30	0.77	0.02	0.02
Diprotodontia	3	0.46	0.03	0.06	3	0.77	0.04	0.17
Insectivora	18	0.04	0.01	<0.01	24	-1.05	-0.03	0.04
Lagomorpha[a]	8/7	$-0.88/-3.62^{**}$	$-0.19/-0.56$	0.09/0.65	8	-1.73	-0.18	0.27
Primates	26	0.47	0.26	0.01	28	-0.72	-0.02	0.02
Rodentia	47	-1.25	-0.76	0.03	84	-1.09	-0.02	0.01
Scandentia	1	-0.02	<-0.01	<0.01	7	-0.62	-0.05	0.05
Carnivores	47	0.87	0.02	0.02	61	1.75	0.01	0.05
Omnivores	109	-1.24	-0.21	0.01	147	-4.67^{***}	-0.04	0.03
Herbivores	55	-1.30	-0.29	0.03	62	-1.34	-0.02	0.03
(b)								
all species	112	-0.76	-0.03	0.01	145	-1.74	-0.01	0.02
Artiodactyla	4	-2.38	-2.11	0.59	4	-1.91	-0.05	0.48
Carnivora	30	1.42	0.06	0.06	33	0.81	0.01	0.02
Chiroptera	14	-0.02	<-0.01	<0.01	15	-0.33	-0.01	<0.01
Insectivora	9	-0.23	-0.06	0.01	13	-1.46	-0.07	0.14
Lagomorpha	—	—	—	—	1	-0.48	-0.06	0.19
Rodentia	33	-1.55	-0.71	0.07	54	-0.87	-0.02	0.01
Scandentia	—	—	—	—	4	-1.45	-0.10	0.34
Carnivores	28	0.86	0.02	0.03	32	1.59	0.01	0.07
Omnivores	64	-0.04	-0.01	<0.01	85	-2.59^*	-0.02	0.07
Herbivores	21	-1.01	-0.23	0.05	24	-2.59	-0.01	0.03

[a] Results are displayed both before and after a deletion of one highly influential datum (result before deletion/result after deletion).

Table 4. Predictors of SRs. (Results from multiple regressions of median SR against body mass (g) plus a range of additional predictors. Phylogenetic analyses consisted of regressions through the origin of independent contrasts. (a) Analyses use all species. (b) Analyses use only those species in each subgroup represented by greater than five specimens from both the island and the mainland populations.)

additional predictor	phylogenetic				non-phylogenetic			
	d.f.	t	slope	R^2	d.f.	t	slope	R^2
(a)								
area	102	-0.85	-0.01	0.01	119	-1.70	-0.02	0.04
area–body mass interaction	102	-0.50	<-0.01	<0.01	118	0.52	<0.01	0.04
isolation	102	-1.56	-0.03	0.02	119	-1.35	-0.03	0.03
trophic level	168	-0.15	-0.01	<0.01	193	-0.12	-0.02	0.03
number of carnivores	96	-1.00	-0.03	0.01	110	-1.43	-0.05	0.04
number of carnivores–body mass interaction	96	-1.17	-0.01	0.02	109	-0.51	-0.01	0.04
(b)								
area	23	-0.61	<-0.01	0.09	28	-1.40	-0.03	0.07
area–body mass interaction	23	-0.03	<-0.01	<0.07	27	0.73	0.01	0.09
isolation	23	-0.43	-0.04	0.08	28	-1.01	-0.04	0.04
trophic level	92	-0.71	-0.04	0.01	103	-0.91	-0.02	0.02
number of carnivores	19	-0.59	-0.06	0.06	22	-0.99	-0.08	0.06
number of carnivores–body mass interaction	19	-0.73	-0.13	0.07	21	-0.24	-0.01	0.06

testing putative correlates. All of the correlates, except isolation, had values of λ which were significantly greater than zero at least when only the well-sampled species were considered (appendix 6 in the electronic supplementaty material), again indicating the need to consider phylogeny.

We found that the response of SR to body size is essentially linear (see appendix 7 in the electronic supplementaty material). Phylogenetic comparative analysis shows no relationship between median SR and body mass (figure 1) in either the whole dataset or the well-sampled species, and the relationship is significant within only one of the nine mammalian orders (Lagomorpha, $n=$ seven contrasts; table 3a. This remained significant after correcting for multiple tests, $p=0.024$), and in none of six orders that contained enough well-sampled species to be analysed (table 3b).

Non-phylogenetic analysis of all populations shows a significant but weak negative relationship ($t_{1170}=-7.89$, slope $=-0.02$, $R^2=0.05$, $p<0.01$); a similar analysis of all species is also significant and weak ($t_{274}=-2.98$, slope $=-0.02$, $R^2=0.03$, $p<0.01$; figure 2a). Well-sampled species show no significant relationship ($t_{145}=-1.74$, slope $=-0.01$, $R^2=0.02$, $p=0.08$; figure 2b). None of the orders shows a significant relationship, though omnivores (but neither carnivores nor herbivores) do (table 3; this remained significant after correcting for multiple tests: all species: $p<0.001$; well-sampled species: $p=0.021$).

(c) *Other predictors of size evolution*
Island area, island isolation, trophic level, carnivore numbers and the island area–body mass interaction failed to predict SR in the full dataset using phylogenetic or non-phylogenetic analyses (table 4). SRs do not differ between islands where carnivores are present and those where carnivores are absent (all species: $F_{2,53}=1.52$, $R^2=0.05$, $p=0.23$; well-sampled species only: $F_{2,6}=0.20$, $R^2=0.06$, $p=0.83$).

4. DISCUSSION
Phylogenetic comparative analyses provide no support for the predictions of the island rule either for all mammals or within clades. When species are instead viewed as independent points, small mammals have a weak, but significant, tendency to grow large on islands, whereas large mammals evolve smaller size on islands ($R^2=0.03$). However, that the pattern is significant may be influenced by the large sample size, the probable non-independence of many of the data points, and the statistical tendency for a negative correlation between ratios and their denominators (Smith 1999; Brett 2004). Some clades show a tendency for gigantism (murid rodents) or dwarfism (artiodactyls, heteromyids and some carnivores), in line with the findings of Foster (1964), suggesting that the small versus large dichotomy in previous work (e.g. Van Valen 1973) may be an artefact of contrasting groups showing clade-specific (rather than size-specific) responses to insularity.

We did not find convincing evidence that larger size leads to insular size reduction within mammals in general (using independent contrasts) or within clades. Neither do we find that, as a rule, large mammals dwarf on islands nor that small mammals grow large (e.g. shrews, squirrels and
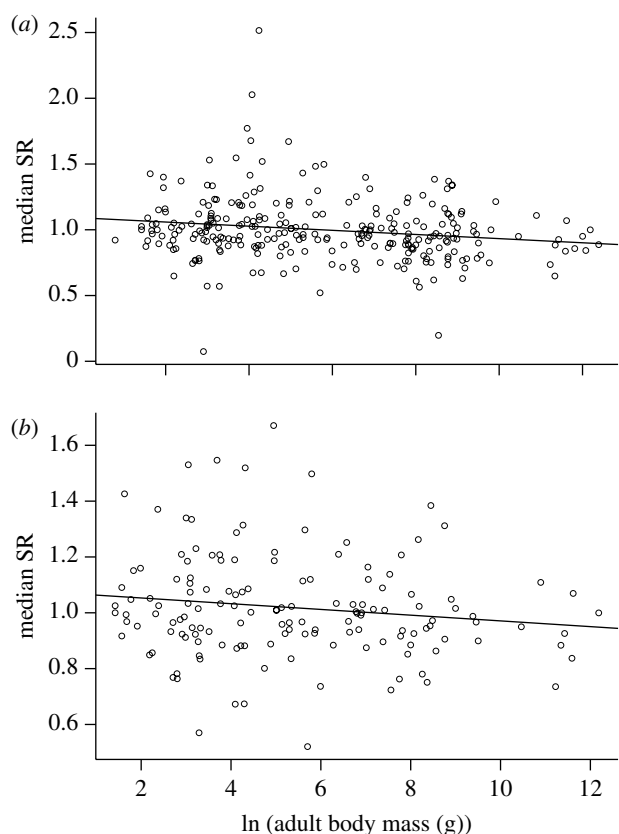

Figure 2. Slope of a non-phylogenetic regression of median SR against adult body mass (g). (a) All species (slope $=-0.02$, $t_{274}=-2.98$, $R^2=0.03$, $p=0.003$) and (b) well-sampled species only (slope $=-0.01$, $t_{145}=-1.74$, $R^2=0.02$, $p=0.08$).

bats do not show a tendency towards gigantism). We find very little evidence to suggest that the pattern we obtain (non-phylogenetically) across the dataset as a whole is mirrored within clades (Lomolino 2005). This suggests that results showing a graded trend from insular gigantism to insular dwarfism (Van Valen 1973; Lomolino 1985; Lomolino 2005) may have stemmed from pseudoreplication, with many small rodents (mostly mice) showing gigantism and many large artiodactyls (mostly deer) showing dwarfism. Dwarfism does not seem a general attribute of all clades containing large species or only of such clades: while the fossil record indicates elephants usually dwarf on islands our results suggest heteromyid rodents also tend towards insular dwarfism (see also Lawlor 1982). There is little in our data to suggest that the island rule is a general pattern shared by all mammalian clades (Lomolino *et al.* 2005).

Size evolution on islands is often thought to be tightly related to characteristics of the islands and their mammalian faunas, such as island area, isolation and the presence or absence of carnivores (Heaney 1978; Michaux *et al.* 2002). We found little evidence that these factors have a consistent influence on body size evolution. Admittedly, it is difficult to gauge what index best reflects isolation (e.g. distance to the nearest mainland, the nearest larger island, the nearest more species-rich island). Similarly, the effects of carnivores on different mammalian species are likely to be complex: predation pressure is probably more related to predator abundance and identity than to their richness. With the commonly used indices for these variables, we find no indication that they have a consistent effect on size

evolution. In fact, although we use different subsets of our database, we find few significant factors affecting insular size evolution regardless of the analytical method employed. Thus, insularity does not result in simple patterns of size evolution that manifest themselves along single axes such as body size. Detailed studies of more coherent clades that explicitly model the biotic composition of different islands and the biology of the focal species (e.g. Lawlor 1982; Angerbjörn 1985; Smith 1992; Raia & Meiri 2006) may shed more light on the mechanisms that affect size evolution than a general macroecological study of all mammals.

Some striking cases of evolution on islands captivate the mind of the general public and scientists alike. Body size evolution is often one of the most striking consequences of insularity with 100 kg elephants, 36 kg red deer (Lister 1996) and perhaps even smaller humans (Brown *et al.* 2004) inhabiting some islands at different stages of the Pleistocene. Consider as well the existence on islands of 600 kg elephant birds (Murray & Vickers-Rich 2004) and 200 kg rodents (Biknevicius *et al.* 1993) and insular size evolution seem truly extraordinary. Restricting ourselves to within-species comparisons, we did not analyse these most extreme cases and it may be that comparing more distantly related taxa would reveal stronger patterns. Perhaps size evolution only expresses itself fully over longer time periods than those separating the population pairs we used here. On the other hand, some of the popular images of island dwarves and giants cohabiting may obscure the true picture: *H. floresiensis*, if it existed, probably shared Flores with a large, not dwarfed *Stegodon* (Rolland & Crockford 2005), and not all insular elephants were, or indeed are, small. While the most extreme examples are highly compelling, they do not show the enormous variation characterizing the pathways of insular size evolution and do not amount to a general rule.

We suspect that size evolution on islands is highly contingent on history, community composition and the biology of the colonizing species, and that only a close scrutiny of these factors will enable us to detect generalities (Case 1978; Lawlor 1982; Raia & Meiri 2006). We found that some clades show a tendency for insular gigantism, others for insular dwarfism. Contrasting those with clades that show no such tendencies may help unravel the biological attributes that govern size evolution (Lawlor 1982). The broad-brush approach we used here revealed very little of these intricacies. Therefore, we were able to explain very little of the considerable variation in the ways mammals respond to the selective forces that drive size evolution. A more useful approach (Simberloff 2006) may involve quantifying the strength of ecological interactions that are thought to select for different sizes, taking into account the unique autecological conditions encountered by different populations. As a rule, the biotic and abiotic environment a population finds itself in will shape how its body size evolves.

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