

1 **Title: Resurrection of the island rule – human-driven extinctions have obscured a basic**
2 **evolutionary pattern**

3

4 **Keywords:** anthropocene, body size, evolution, islands, mammals

5

6 The manuscript contains five supplementary figures and a supplementary excel sheet containing
7 information on body size and island status of all mammals.

8 This manuscript is intended to be a “Note.”

9

10 **Authors:** Søren Faurby^{a,b*}, Jens-Christian Svenning^a

11 ^a Section for Ecoinformatics & Biodiversity, Department of Bioscience, Aarhus University, Ny Munkegade 114,
12 DK-8000 Aarhus C, Denmark.

13 ^b Department of Biogeography and Global Change, Museo Nacional de Ciencias Naturales, CSIC, Calle José
14 Gutiérrez Abascal 2, Madrid 28006, Spain

15

16

17

18 **Abstract**

19 Islands are or have been occupied by unusual species, such as dwarf proboscideans and giant rodents.
20 The discussion of the classical but controversial “island rule,” which states that mammalian body sizes
21 converge on intermediate sizes on islands, has been stimulated by these unusual species. In this paper,
22 we use an unprecedented global data set of the distributions and the body sizes of mammals and a novel
23 analytical method to analyze body size evolution on islands; the analyses produced strong support for
24 the island rule. Islands have suffered massive human-driven losses of species, and we found that the
25 support for the island rule was substantially stronger when the many late-Quaternary extinct species
26 were also considered (particularly, the tendency for dwarfing in large taxa). In this study, the decisive
27 support generated for the island rule confirmed that evolution is markedly different on islands and that
28 human impact may obscure even fundamental evolutionary patterns.

29

30 **Introduction**

31 Before the arrival of humans, many oceanic islands housed bizarre mammal faunas. Dwarf
32 proboscideans used to occur on Mediterranean islands, the Channel Islands in California, and the island
33 of Timor in Southeast Asia, but all are extinct (Faurby and Svenning 2015). Similarly, giant rats were
34 frequent on islands, with only a few species that are extant (Faurby and Svenning 2015), although in
35 some cases with much reduced ranges, e.g., the Malagassy giant rat (*Hypogeomys antimena*) (Burney et
36 al. 2008). In addition to these clades with numerous deviant island forms, many other clades also had a
37 single or a few odd-sized island species, e.g., the extinct dwarf hippos of Crete and Madagascar and the
38 extinct Sardinian giant pika (Stuenes 1989, Angelone et al. 2008).

39 These bizarre island mammals stimulated the proposal of the island rule, which states that
40 mammalian body sizes converge on intermediate sizes on islands (Van Valen 1973). However, the
41 island rule has been intensely debated in recent years and is viewed as both a near universal rule
42 (Lomolino et al. 2011) and a sample or publication artifact (Meiri et al. 2008, Raia et al. 2010), with
43 intermediate positions also argued (Welch 2009). Both the opponents and the proponents of the island
44 rule acknowledge the apparent abundance of giants and dwarfs on islands (Meiri et al. 2008, Lomolino
45 et al. 2011). The two schools have strongly argued whether the island rule represents a general
46 evolutionary pattern, the idiosyncratic changes in individual lineages or even the human tendency to
47 see patterns in all datasets (Van Valen 1973, Meiri et al. 2008, Raia et al. 2010, Lomolino et al. 2011).

48 Critics of the island rule argue two primary points, both of which we overcome in the
49 present study. The first point concerns sampling bias. The studies that support the island rule have
50 generally been meta-analyses of published comparisons between the mainland and island populations

51 of the same species (Van Valen 1973, Lomolino et al. 2011). As discussed for the related Bergmann's
52 rule (Meiri et al. 2004), these studies may be a nonrandom subset of all populations and therefore a
53 significant pattern matching expectation may be generated by a reporting bias. In this study, we
54 removed the possibility for such sampling bias by generating and analyzing a database that contained
55 the body sizes for approximately 99% of all extant and recently extinct species of mammals (see
56 Materials and Methods).

57 The second critique of the basis for the island rule is that of phylogenetic
58 nonindependence, because previous studies showed diminished support for the rule when the
59 phylogeny was accounted for in the intraspecific analyses (Meiri et al. 2008, McClain et al. 2013). This
60 problem is a form of pseudo-replication that inflates the estimates of precision and thereby potentially
61 generates false significances. The magnitude (or existence) of this problem, however, depends on what
62 model is used as the null model. The classical studies, which compared only sister lineages (e.g.,
63 Lomolino 1985), are compatible with body sizes that evolved via simple models such as the Brownian
64 motion (Felsenstein 1985) or the Ornstein-Uhlenbeck (OU) models (Hansen 1997). The studies that
65 analyzed the ratios between the sizes of island and mainland mammals in a phylogenetic context (e.g.,
66 Meiri et al. 2008) might also be compatible with such models, when one assumes an identical age for
67 all island populations or that the island populations have reached a new equilibrium size.

68 However, with the assumption that the rate of evolutionary change is a function of traits,
69 which are also evolving, i.e., via the correlation between generation length and evolutionary rate
70 (Welch et al. 2008, Thomas et al. 2010), phylogenetic nonindependence is a problem for studies that do
71 not integrate phylogeny. Such a correlation is not a problem for studies that incorporate phylogeny and
72 that focus on the ratios between the island and mainland species, but these studies also require an

73 identical age of all island populations or that the island populations have reached a new equilibrium
74 size. Imagine, for example, an analysis that contained two sets of rodent mainland /island sister pairs
75 with short generation times and therefore potentially fast evolutionary rates and that contained two sets
76 of elephant mainland/island species pairs with longer generation times and therefore potentially lower
77 evolutionary rates. If the rate is evolving over time, the comparisons of the magnitude of change
78 between the species pairs will need phylogenetic correction because larger relative differences between
79 the mice species pairs than the elephant species pairs could be a null expectation. Irrespective of
80 whether the rate is evolving, however, the null expectations would remain a 50% decrease in size in
81 both the mice and the elephants. To solve the potential problem of phylogenetic nonindependence
82 without requiring an identical age of all island populations or that the island populations have
83 previously reached a new equilibrium size, we restricted the analyses to focus only on the directionality
84 and not on the magnitude of change (see the Materials and methods). We stress that this restriction did
85 not imply that body size did not evolve as a Brownian motion process (there are strong indications that
86 it often does (Blomberg et al. 2003)) but that our analysis (explained below) did not make that
87 assumption. Moreover, the analysis was almost independent of the assumed model of body size
88 evolution.

89 In addition to the potential problems with the studies that support the island rule, the
90 primary interspecific study that dismisses the island rule (Raia et al. 2010) also has potential problems.
91 The study used a somewhat incomplete body size database (Smith et al. 2003) and a partially outdated
92 phylogeny (Bininda-Emonds et al. 2007). Raia et al. (2010) also included bats, whereas the classic
93 studies that support the island rule focused on non-flying mammals (Lomolino 1985) or analyzed bats
94 separately (Lomolino 2005). If supported, the island rule is likely a consequence of island isolation, and

95 the substantially lower levels of endemism in bats than in non-flying mammals (Weyeneth et al. 2011)
96 indicates that the island bat fauna is less isolated compared to non-flying mammalian fauna. Thus, the
97 island rule would be expected to establish a weaker pattern for bats than for non-bats.

98 In this paper, we reanalyzed the magnitude of the island rule in an interspecific context
99 using a novel, near-complete body size database and a recent mammalian phylogeny (Faurby and
100 Svenning 2015) solely focusing on the directionality and not on the magnitude of body size changes in
101 island lineages. To determine the potential importance of the factors responsible for the apparent lack
102 of support for the island rule in the earlier studies that integrated phylogenetic relationships between
103 species, we estimated the effects of including or excluding bats and extinct species and different
104 definitions of islands.

105

106 **Materials and methods**

107 **Data generation**

108 For all analyses, we used the taxonomy and the phylogeny of a recent mammalian phylogeny, which
109 included all species with dated occurrences within the last 130,000 years, but no likely chronospecies
110 (Faurby and Svenning 2015). Notably, most extant mammal species existed throughout this period and
111 therefore coexisted with the extinct species, and there is increasing evidence that *Homo sapiens* were
112 the primary cause of these extinctions (Sandom et al. 2014), particularly on islands (Turvey and Fritz
113 2011).

114 We generated a new body size database, which included almost all species of mammals (5673
115 of 5747 species; of the 74 species without data, 8 represented extinct, but undescribed, species). The
116 new database was partly based on an older database (Smith et al. 2003) but was heavily modified. The
117 information for 3629 of the 5673 species was used from the older database, but our complete database
118 contained information from a total of 709 separate data sources (644 articles published in 146 separate
119 journals, 55 books, 8 web resources and personal information from 2 experts; the complete database is
120 available in the Supplementary Data, in addition to information on which islands all island endemic
121 species are found). For the species for which the weight data were not available, the weights were
122 generally estimated with the assumption of strict isometries for related similar sized species. The
123 isometry was generally assumed for forearm length in bats and body length (excluding tail) for the
124 remaining species, but other measures were also used occasionally.

125 We scored island endemic or remainder as a binary character and defined island endemics based
126 on three definitions. The loose and classical definition was any species endemic to any area, which are
127 the oceanic islands at the current sea levels. The species that are currently restricted to islands (or were
128 restricted until their extinction in historical times) but with former Holocene occurrences on the
129 mainland, e.g., the Tasmanian devil (*Sarcophilus harrisii*) and the Tasmanian tiger (*Thylacinus*
130 *cynocephalus*) (Johnson and Wroe 2003), were not scored as island endemics. The strict definition was
131 for any species that was not found on any continent or any island connected to a continent during the
132 ice ages (i.e., any island for which the deepest water-level between the island and a continent was less
133 than 110 meters deep). Using this restricted definition, the island endemics were species for which the
134 majority of their evolutionary history were restricted to islands instead of species that happened to be
135 on islands with the current sea levels. For the few species that evolved by rapid speciation since the last

136 ice age on land-bridge islands (e.g., Anderson and Hadley 2001), this definition may be overly
137 restrictive because the species would have been island endemics for their entire evolutionary history.
138 Therefore, we also used a semi-strict definition, which was a relaxation of the strict island definition,
139 and any species that did not occur on large land-bridge islands (larger than 1000 km²) were also scored
140 as island endemics. We acknowledge that this threshold was somewhat arbitrary, but rapid speciation
141 since the end of the last ice age likely required a small population size and therefore a limited area. The
142 largest island with a strong candidate for such recent speciation would be Coiba (503 km²) with the
143 endemic agouti *Dasyprocta coibae*, whereas the colobus monkey *Procolobus kirkii* from Zanzibar
144 (1658 km², the smallest land-bridge island above 1000 km² that contained an endemic species)
145 appeared to have been isolated for substantially longer than the end of the last ice age (Ting 2008).

146

147 **Analyses**

148 The phylogeny used in this study consisted of the 1000 separate, random fully bifurcating trees from a
149 posterior distribution of trees that represented the phylogenetic uncertainty from Faurby and Svenning
150 (2015). Separate analyses were initially performed for each of the 1000 trees after which the results
151 from each tree were combined.

152 For each island endemic species (IE), we found the largest clade that contained only island
153 endemics (C_{Island}) and the smallest clade that contained both island endemics and nonendemics and
154 removed all members of C_{Island} from this clade (hereafter C_{Mainland}). We then estimated ancestral
155 $\log_{10}(\text{Weight})$ for all C_{Island} and C_{Mainland} , assuming Brownian motion. With the removal of the island
156 endemics for the calculation of C_{Mainland} , we allowed body size evolution to differ between island and

157 mainland clades but did not enforce such differences. Following this procedure, we sampled all the
158 island endemic species in random order, listed all members of C_{Island} and, if the sampled species was
159 not a member of the C_{Island} of any previously sampled species, noted the size of the ($\text{Size}_{\text{Mainland}}$) and
160 whether this size was smaller or larger than $\text{Size}_{\text{Island}}$. Therefore, our end products were a vector of
161 ancestral mainland weights for independent island invasions and a corresponding vector with binary
162 information on whether the island invaders were smaller than the mainland ancestors. To reduce the
163 effects of measurement errors on weight, we discarded from further analyses all island invasions for
164 which the difference in weight between $\text{Size}_{\text{Mainland}}$ and $\text{Size}_{\text{Island}}$ was smaller than 10%. Supplementary
165 analyses were performed using 0%, 5%, 15% and 20% weight difference thresholds, but the results
166 changed very little, although there was a tendency for a weaker island rule with the 0% threshold,
167 which was likely a consequence of the increased noise in the data (see Supplementary Figures S1-S5)

168 We then fitted zero to the 4th degree polynomial models of the probability of size decrease as a
169 function of the $\text{Size}_{\text{Mainland}}$ using a logistic regression ($M_{0_{\text{Tree } i}}, M_{1_{\text{Tree } i}}, M_{2_{\text{Tree } i}}, M_{3_{\text{Tree } i}}, M_{4_{\text{Tree } i}}$) and
170 calculated their respective AIC weights ($w_{0_{\text{Tree } i}}, w_{1_{\text{Tree } i}}, w_{2_{\text{Tree } i}}, w_{3_{\text{Tree } i}}, w_{4_{\text{Tree } i}}$). For all the
171 potential values of $\text{Size}_{\text{Mainland}}$ between 0.0 and 6.0 (i.e., untransformed weights between 1 g and 1 ton)
172 in steps of 0.1 for all models, we then calculated the means and the variances,
173 ($\mu_{M_{0.0_{\text{Tree } i}}} \dots \mu_{M_{6.0_{\text{Tree } i}}}$) and ($\sigma^2_{M_{0.0_{\text{Tree } i}}} \dots \sigma^2_{M_{6.0_{\text{Tree } i}}}$), respectively, for the untransformed fitted
174 values for all five models.

175 The results were thereafter combined for all five models for each potential value of C_{Mainland} as a
176 mixture of the normal distributions from the five models, with the weight of each model equal to the
177 AIC weight. Therefore, the combined result was that the predicted effect for any k would be in the

178 distribution $\text{Predict}_{k_{Tree\ i}} = \sum_{j=0}^4 w_{j_{Tree\ i}} \times N\left(\mu_{M_{j_{k_{Tree\ i}}}}, \sigma^2_{M_{j_{k_{Tree\ i}}}}\right)$. Following this procedure, the
179 results were combined for all trees as $\text{Combined}_k = \sum_{i=1}^{1000} \text{Predict}_{k_{Tree\ i}}$. Finally, the median and
180 several quantiles for the Combined_k were transformed into probabilities.

181 We tested the effect of the definition of an island endemic, the potential effect of the
182 anthropogenic extinctions to bias the results and the effect of including bats in the analysis. The
183 analysis was performed separately for each of the twelve combinations of the three definitions of island
184 endemics (classical, semi-strict, strict), for the exclusion or inclusion of bats and for the exclusion or
185 inclusion of extinct species.

186 All analyses were performed in R 3.0.2 (R Core Team. 2013) using functions from the libraries
187 ape (Paradis et al. 2004), phylobase (R Hackathon et al. 2014) and qpcR (Spiess 2014).

188

189 **Model justification**

190 Because our analysis included approximately 99% of all mammal species, the issue of publication bias
191 was dismissed. However, we acknowledge that small biases might remain because of taxonomic
192 practices, e.g., whether island populations that diverged more in size from their mainland relatives were
193 more likely to be classified as separate species. One example of such a small bias is the island endemic
194 pygmy sloth (*Bradypus pygmaeus*) (Anderson & Handley, 2001). These questionable populations or
195 species are generally found on land-bridge islands (as with the pygmy sloth), and therefore, this type of
196 bias is a problem that should affect only the classical or semi-strict but not the strict island endemic
197 definition.

198 However, a problem noted by Meiri et al. (2008) might have affected our analysis. For the
199 two vectors A and B , the correlation between B and B/A is significantly negative the majority of the
200 time when A and B are independent. Meiri et al. (2008) extended this basic mathematical result to the
201 island rule and argued that the island rule pattern would occur when the body sizes of the populations
202 or species on the islands were independent of the body sizes of their mainland relatives. To assess the
203 effect of this relationship, we randomized the body sizes of all species, of all species within families, or
204 of all species within genera for the analysis with the apparent strongest island rule (i.e., strict island
205 endemic definition, excluding bats and including extinct species). For this analysis, the body sizes were
206 randomized anew for each of the 1000 trees.

207

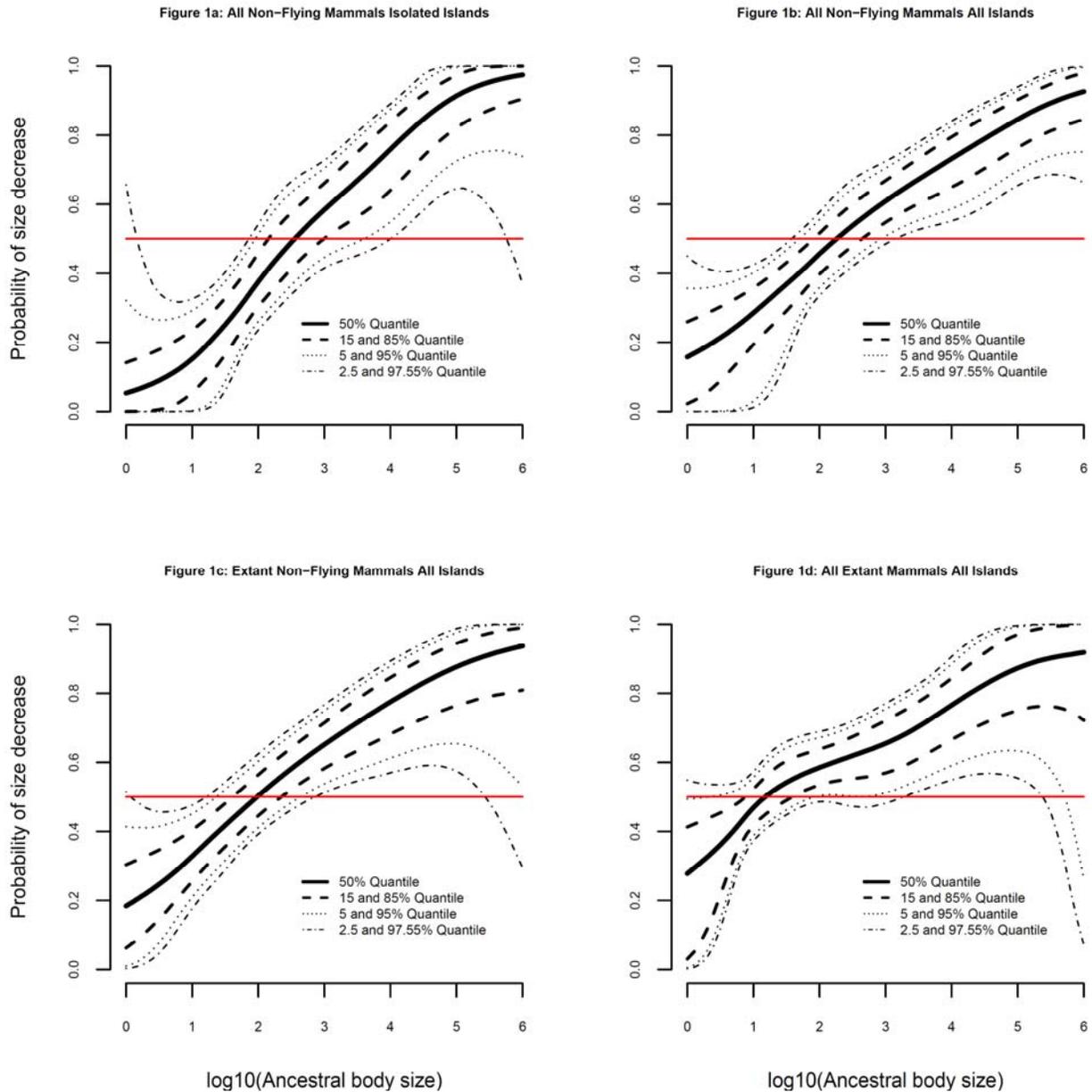
208 **Results**

209 Strong support for the island rule was provided when bats were excluded from the analysis but only
210 weak support when the bats were included. Among the 12 combinations of island-type definitions and
211 included species, the strongest support for the island rule (measured as the difference between the
212 predicted probability for size increase species for species with a size of 1 ton and 1 gram) was with the
213 strict island definition and the exclusion of bats but the inclusion of extinct species (Table 1, Figure 1,
214 Figures S1-S5). The inclusion of bats in the analysis consistently led to markedly lower support for the
215 island rule, and the addition of the bats removed or at least reduced the tendency for small mammals to
216 increase in size on islands. The inclusion of the extinct species and the application of the strict or semi-
217 strict island definitions provided stronger support for the island rule, but only when bats were excluded.

218

Figure 1. Relationships between ancestral body size and directionality of evolutionary size change after island invasion.

The estimated probability of a size decrease as a function of the ancestral body size of the island invading clade. The thick black line shows the median of the distribution of potential predicted values, whereas the three stippled lines show the 2.5/97.5%, 5/95% and 15/85% quantiles. Because the response variable is binary, the values below the horizontal line indicate that a clade is most likely to increase in size, and the values above the horizontal line indicate that a clade is most likely to decrease in size. The first panel shows the relationship for non-flying mammals, including both extinct and extant species for isolated islands. The last panel shows the relationship for both flying and non-flying mammals but only for extant species and using all islands. The three differences between the panels are changed one by one; the last three panels use all the islands, the last two panels only analyze extant species and the last panel analyzes all mammals without restricting the analysis to non-flying species.



219

220

221

222

223

The definitions of island endemics and the exclusion or inclusion of bats and extinct

species also changed the shape of the relationship between body size and body size change on islands,

in addition to influencing the magnitude of the island rule. For the strict island definition, when bats

were excluded but extinct species were included, the apparent optimal size (the body size for which

224 size increases and decreases are equally likely) was 500 gram ($10^{2.7}$ g). On the other hand, for the
225 classical island definition, when bats were included and, extinct species were not included, the optimal
226 size was only 20 gram. (Table 1).

227 Our analysis of the effect of randomization of body sizes showed no support for the island
228 rule under realistic randomization scenarios. Of the average of 143.3 independent island invasions from
229 each of the 1000 separate trees, an average of 38.5 consisted of island endemic genera. When these
230 genera were removed from the analysis with randomization within genera, almost no relationship
231 between the body size and the directionality of size change was detected (Figure 2a). A slightly
232 stronger but still weak pattern was found when the island endemic genera were included in the analysis
233 (Figure 2b); however, randomization at the family level (Figure 2c) was required to falsely generate a
234 pattern with substantial support for the island rule (the pattern with complete randomization was almost
235 identical to the pattern for randomization at the family level, results not shown). The results of these
236 randomizations strongly suggested that the support for the island rule was not an analytical artifact.

237

Figure 2. Relationships between ancestral body size and directionality of evolutionary size change for randomized body sizes.

All panels show the effect of randomization of body sizes for the strict island rule, when extinct species are included but bats are excluded (analogous to Figure 1d). In Figure 2a, body sizes are randomized across all genera but with all island endemic genera excluded from the analysis, whereas in Figure 2b, body sizes are randomized across all species within genera and the island endemic genera are included in the analysis. In Figure 2c, body sizes are randomized

across all species within families.

Figure 2a: Randomisation within genera
Excluding island endemic genera

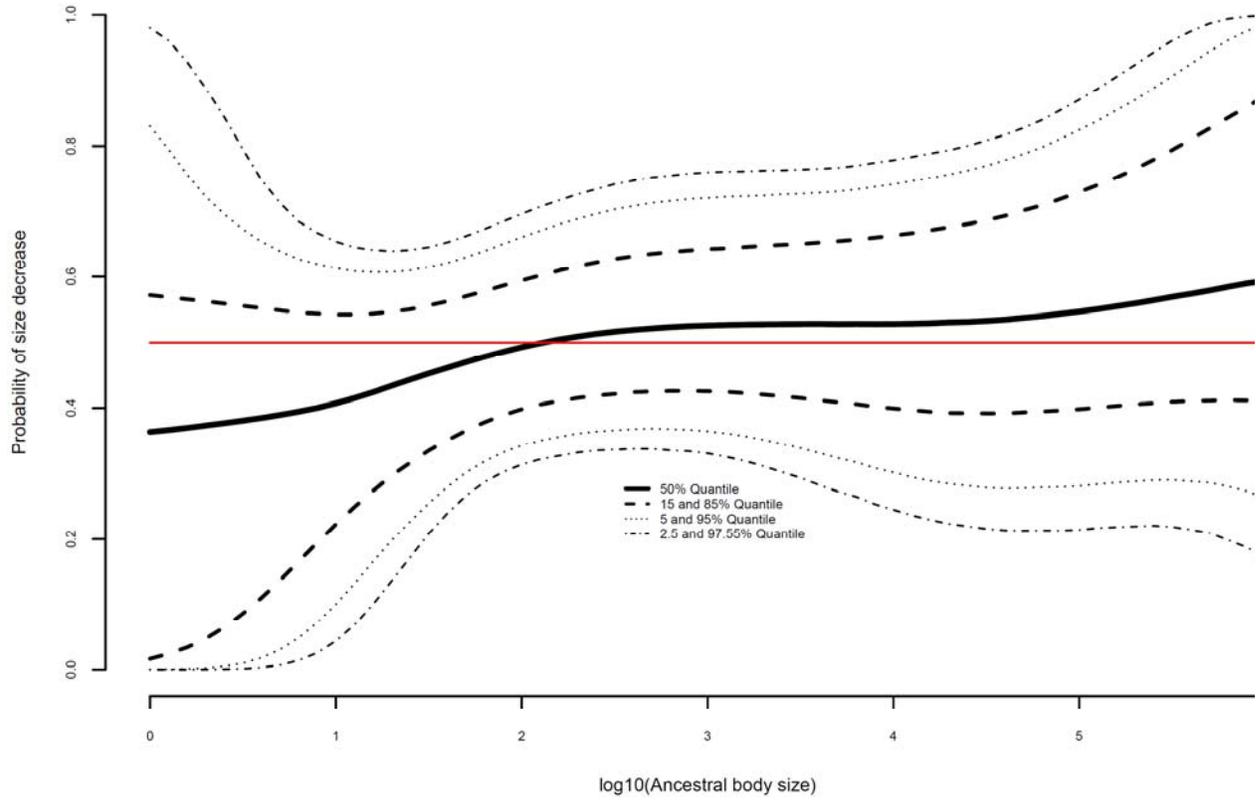


Figure 2b: Randomisation within genera

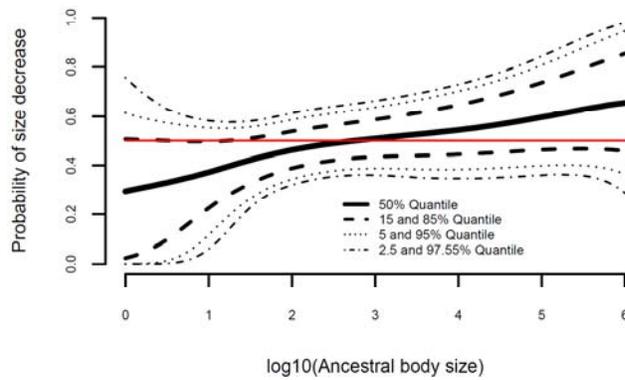
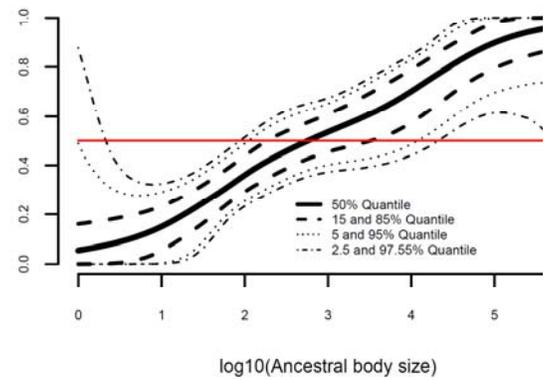


Figure 2c: Randomisation within families



238

239

240 **Discussion**

241 The validity of the island rule was clearly supported with our results. Therefore, we suggest that part of
242 the explanation for the lack of evidence for the island rule in the earlier interspecific study (Raia *et al.*
243 2010) was not because of the incorporation of the phylogeny, as the authors suggested, but because of
244 the choice to disregard the ecological difference between flying and non-flying mammals and, to a
245 lesser extent, the choice of definition of island endemics and the incomplete inclusion of historically
246 extant species (i.e., species that occurred within the Late Pleistocene or Holocene). In this regard, we
247 do not state explicitly that the models that excluded bats in our analysis provided a better fit to the data
248 than the models that included bats; however, we do state that the estimated effect of body size (i.e., the
249 island rule) is substantially stronger in the models that excluded bats.

250 The effects of including or excluding land-bridge islands and bats into the analysis can
251 potentially be seen as two sides of the same story. If the primary factor for the island rule was
252 ecological release, the rule would only be realized on islands with reduced numbers of predators or
253 competitor species. Therefore, the island rule would not apply or would be much less applicable to the
254 land bridge islands, which were part of the continental mainland during the last glaciation, in addition
255 to many earlier periods during the Pleistocene. The species on the land-bridge islands would have
256 experienced similar faunas as on the current mainland for a large part of their evolutionary history, and
257 therefore these species would not have experienced ecological release, or only relatively brief release.
258 Similarly, island bats were not likely to experience a significant ecological release because the primary
259 predators of bats are birds such as raptors and owls (Rydell and Speakman 1995). These birds are
260 typically strong fliers and therefore even long isolated islands tend to harbor well-developed predatory

261 bird faunas. Thus, for the native bat fauna on land-bridge islands, predator release would be limited or
262 would not occur.

263 Our focus on interspecific patterns enables us to disentangle the different factors driving
264 the island rule. The selection of immigrants for larger body sizes (as discussed in Lomolino, 2011)
265 could potentially be important for relatively new intraspecific comparisons. Considering the
266 evolutionary rates over small to medium time scales (Gingerich 2001), any effect of immigrant
267 selection would disappear in interspecific analyses unless other selective forces were maintaining the
268 changed body size (see Jaffe et al. (2011) for a similar argument regarding body size evolution in island
269 tortoises). Therefore, our results indicated that selection caused by the novel ecology on islands was
270 driving both the dwarfing and gigantism observed in different lineages.

271 With the arrival of humans, island faunas suffered severe extinctions. Our data set
272 included 589 non-flying and 223 flying island endemics based on the strict island definition, with
273 overall late-Quaternary extinction rates of 20% and 4%, respectively (the corresponding number for all
274 the islands was 916 non-flying and 323 flying species with extinction rates of 13% and 3%,
275 respectively; see Supplementary Data). These extinctions are often tightly linked to human arrival and
276 to evidence of human hunting or other anthropogenic factors (Turvey and Fritz 2011). Based on our
277 analysis, the inclusion of the extinct species strongly increased the support for the island rule. The
278 incorporation of the extinct island species was previously advocated for ecological studies (Griffiths et
279 al. 2009, Hansen and Galetti 2009), but our results highlighted the necessity to also include these
280 species in evolutionary studies. The recent human-driven extinctions most likely obscured signals
281 related to the long-term evolutionary responses to island environments, for example, the elimination of
282 the most specialized of the island lineages (Lomolino et al. 2013). In this regard, we note that we

283 expect both dwarfing and gigantism to be an evolutionary consequence of predator release. Therefore,
284 the species that showed the largest changes in body size on islands would be expected to be the most
285 sensitive to predation by humans or by our commensal animals.

286 The apparent optimal body size of 500 gram determined in our analysis using the strict
287 island model and excluding bats but including extinct species (the model that showed the strongest
288 support for the island rule) was similar to an estimate of optimal body size derived from the patterns in
289 the intraspecific changes for terrestrial mammals on islands, which was 474 grams (Lomolino, 2005).
290 However, several arguments against a global optimal body size have been developed (discussed in Raia
291 et al. (2010)), and the similarity of the above results was possibly accidental. The potential accidental
292 nature of the similarity of these results was also supported by the variation in the suggested global
293 optimal size, if such an optimal size can be determined, with estimates of both 100 gram and 1 kg
294 suggested previously (Brown et al., 1993; Damuth, 1993).

295 In this study, the decisive support for the island rule highlighted that the function of island
296 ecosystems is fundamentally different from that of mainland systems (cf. Millen 2006) and that these
297 differences drive divergent evolutionary dynamics on islands and the mainland. Notably, our results
298 were consistent with the weakening of ecological interactions on islands that caused body sizes to shift
299 to intermediate biomasses, irrespective of the ancestral body size or the phylogenetic lineage.
300 Conversely, the strong support for the island rule also implied that much of the large variation in body
301 sizes or the repeated evolution of similar maximum body sizes in mainland systems (Smith et al. 2010)
302 was a consequence of the intense ecological interactions in these settings.

303

304 **Supplementary Materials**

305 Figures S1-S5.

306 Supplementary data. A database of body size and island species endemism.

307

308 **References**

309 Anderson, R.P., and C.O. Handley. 2001 A new species of three-toed sloth (Mammalia: Xenarthra) from
310 Panama, with a review of the genus *Bradypus*. Proceedings of Biological Society of Washington 114:
311 1:33.

312

313 Angelone, C., Tuveri, C., Arca, M., Martinez, N.L., and T. Kotsabis. 2008. Evolution of *Prolagus*
314 *sardus* (Ochotonidae, Lagomorpha) in the Quaternary of Sardinia Island (Italy). Quaternary
315 International 182: 109-115.

316

317 Bininda-Emonds, O.R.P., et al. 2007. The delayed rise of present-day mammals. Nature 446: 507-512.

318

319 Blomberg, S.P., Garland, T.G., and A.R. Ives. 2003. Testing for phylogenetic signal in comparative
320 data: Behavioral traits are more labile. Evolution 57: 717-745.

321

- 322 Brown, J.H., Marquet, P.A., and M.L. Taper. 1993. Evolution of body-size – consequences of an
323 energetic definition of fitness. *American Naturalist* 142: 573–584
- 324
- 325 Burney, D.A., Vasey, N., Godfrey, L.R., Ramilisonina, Jungers, W.L., Ramarolahy, M., and L.
326 Raharivony. 2008. New findings at Andrahomana Cave, Southeastern Madagascar. *Journal of Cave and*
327 *Karst Studies* 70: 13–24.
- 328
- 329 Damuth, J. 1993. Cope’s rule, the island rule and the scaling of mammalian population-density. *Nature*
330 365: 748–750
- 331
- 332 Faurby, S., and J.C. Svenning. 2015. A species-level estimate of the phylogeny for all extant and Late
333 Quaternary extinct mammals using a novel hierarchical Bayesian approach. *Molecular Phylogenetics*
334 *and Evolution* 84: 14-26.
- 335
- 336 Felsenstein, J. 1985. Phylogenies and the comparative method. *American Naturalist* 125: 1-15.
- 337
- 338 Gingerich, P.D. 2001. Rates of evolution on the time scale of the evolutionary process. *Genetica* 112–
339 113: 127–144.
- 340

- 341 Griffiths, C.J., Hansen, D.M., Jones, C.G., Zuël, N., and S. Harris 2009. Resurrecting extinct
342 interactions with extant substitutes. *Current Biology* 21: 762-765.
- 343
- 344 Hansen, D.M., and M. Galetti. 2009. The forgotten megafauna. *Science* 324: 42-43.
- 345
- 346 Hansen, T.F. 1997. Selection and the comparative analysis of adaptation. *Evolution* 51: 1341-1351.
- 347
- 348 Jaffe, A.L., Slater, G.J., and M.E. Alfaro. 2011. The evolution of island gigantism and body size
349 variation in tortoises and turtles. *Biology letters* 7: 558-561.
- 350
- 351 Johnson, C.N., and S. Wroe. 2003. Causes of extinction of vertebrates during the Holocene of mainland
352 Australia: arrival of the dingo, or human impact? *The Holocene* 6:941-948.
- 353
- 354 Lomolino, M.V. 1985. Body size of mammals on islands: the island rule re-examined. *American*
355 *Naturalist* 125: 310-316.
- 356
- 357 Lomolino, M.V. 2005. Body size evolution in insular vertebrates: generality of the island rule. *Journal*
358 *of Biogeography* 32: 1683-1699.

359

360 Lomolino, M.V., Sax, D.F., Palombo, A.R., and A.A. Van der Geer. 2011. Of mice and mammoths:
361 evaluations of causal explanations for body size evolution in insular mammals. *Journal of*
362 *Biogeography* 39: 842-854.

363

364 Lomolino, M.V., Van der Geer, A.A., Lyras, G.A., Palombo, M.R., Sax, D.F., and R.S. Rozzi. 2013.
365 Of mice and mammoths: generality and antiquity of the island rule. *Journal of Biogeography* 40:1427-
366 1439.

367

368 McClain, C. R., Durst, P. A. P., Boyer, A. G., and C. D. Francis. 2013. Unravelling the determinants of
369 insular body size shifts. *Biology Letters* 9: 20120989

370

371 Meiri, S., Cooper, N., and A. Purvis. 2008. The island rule: made to be broken? *Proceedings of the*
372 *Royal Society of London Series B, Biological Sciences* 275: 141–148.

373

374 Meiri, S., Dayan, T., and D. Simberloff. 2004. Carnivores, biases and Bergmann's rule. *Biological*
375 *Journal of the Linnean Society* 81: 579–588.

376

377 Millen, V. 2006. Morphological evolution is accelerated among island mammals. *PLoS Biology* 4:
378 e321.

379

380 R Core Team. 2013. R: A Language and Environment for Statistical Computing. [http://www.R-](http://www.R-project.org/)
381 [project.org/](http://www.R-project.org/).

382

383 R Hackathon et al. 2014. phylobase: Base package for phylogenetic structures and comparative data. R
384 package version 0.6.8. <http://CRAN.R-project.org/package=phylobase>.

385

386 Raia, P., Carotenuto, F., and S. Meiri. 2010. One size does not fit all: no evidence for an optimal body
387 size on islands. *Global Ecology and Biogeography* 19: 475–484.

388

389 Rydell, J., and J.R. Speakman. 1995. Evolution of nocturnality in bats: Potential competitors and
390 predators during their early history. *Biological Journal of the Linnean Society* 54: 183-191.

391

392 Smith, F.A., Lyons, S.K., Ernest, S.K.M., Jones, K.E., Kaufman, D.M., Dayan, T., Marquet, P.A.,
393 Brown, J.H., and J.P. Haskell. 2003. Body mass of late Quaternary mammals. *Ecology* 84: 3403.

394

395 Smith, F.A., et al. 2010. The evolution of maximum bod sizes in terrestrial mammals. *Science* 266:
396 1216-1219.

397

398 Spiess, A.N. 2014. qpcR: Modelling and analysis of real-time PCR data. R package version 1.4-0.
399 <http://CRAN.R-project.org/package=qpcR>.

400

401 Stuenes, S. 1989. Taxonomy, Habits, and Relationships of the Subfossil Madagascan Hippopotami
402 *Hippopotamus lemerlei* and *H. madagascariensis*. *Journal of Vertebrate Paleontology* 9: 241-268

403

404 Thomas, J.A., Welch, J.J., Lanfear, R., and L.A. Bromham. 2010. Generation time effect on the rate of
405 molecular evolution in invertebrates. *Molecular Biology and Evolution* 27: 1173-1180.

406

407 Ting, N. 2008. Mitochondrial relationships and divergence dates of the African colobines: evidence of
408 Miocene origins for the living colobus monkeys. *Journal of Human Evolution* 55: 312-325.

409

410 Turvey, S.T., and S.A. Fritz. 2011. The ghosts of mammals past: biological and geographical patterns
411 of global mammalian extinction across the Holocene. *Philosophical Transactions of the Royal Society*
412 *of London series B* 366: 2564-2576.

413

414 Van Valen, L. 1973. Pattern and the balance of nature. *Evolutionary Theory* 1: 31–49.

415

416 Welch, J.J. 2009. Testing the island rule: primates as a case study. *Proceedings of the Royal Society of*
417 *London Series B, Biological Sciences* 276: 141–148.

418

419 Welch, J.J., Bininda-Emonds O.R.P., and Bronham L. 2008. Correlates of substitution rate variation in
420 mammalian protein-coding sequences. *BMC Evolutionary Biology* 8: 53-64.

421

422 Weyeneth, N., Goodman, S.M., and M. Ruedi. 2011. Do diversification models of Madagascar's biota
423 explain the population structure of the endemic bat *Myotis goudoti* (Chiroptera: Vespertilionidae)?
424 *Journal of Biogeography* 38: 44–54.

Table 1. The estimated strength of the island rule under the 12 different analyzed scenarios

Island definition	Including extinct species	Including bats	log10 of the body size with equal probability of size increase and decrease	Difference between the predicted probability of size increase for species of 1 ton and 1 gram
Classical	No	Yes	1.3	0.641
Classical	No	No	2.1	0.753
Classical	Yes	Yes	1.6	0.602
Classical	Yes	No	2.4	0.769
Semi-strict	No	Yes	1.5	0.578
Semi-strict	No	No	2.4	0.867
Semi-strict	Yes	Yes	2.0	0.583
Semi-strict	Yes	No	2.6	0.893
Strict	No	Yes	1.4	0.589
Strict	No	No	2.4	0.893
Strict	Yes	Yes	2.0	0.616
Strict	Yes	No	2.7	0.922

425

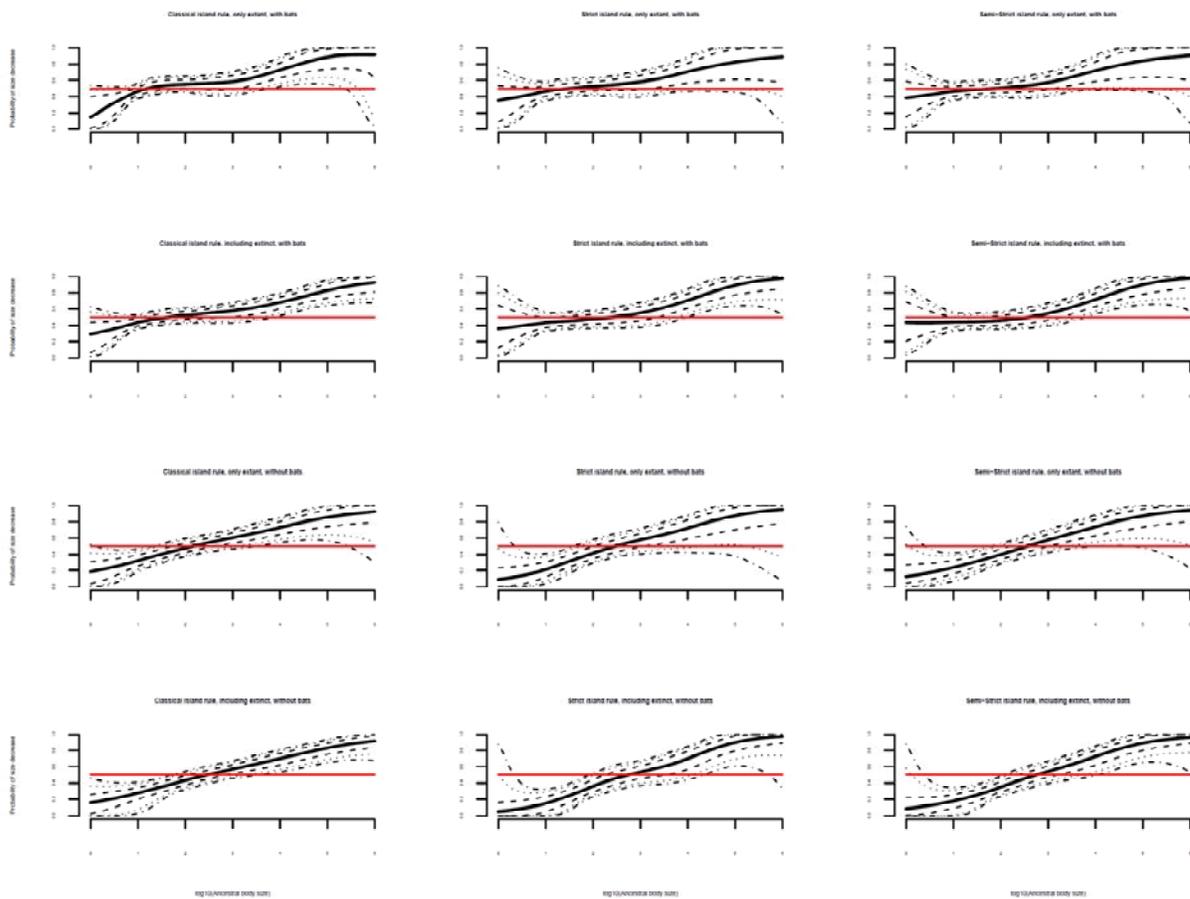
426

427

428

Figure S1. Relationships between ancestral body size and directionality of evolutionary size change after island invasion for the 12 separate analyses without any threshold for a minimum size difference between island and mainland clades.

The structure and meaning of the individual lines in each panel are identical to those in Figure 1.

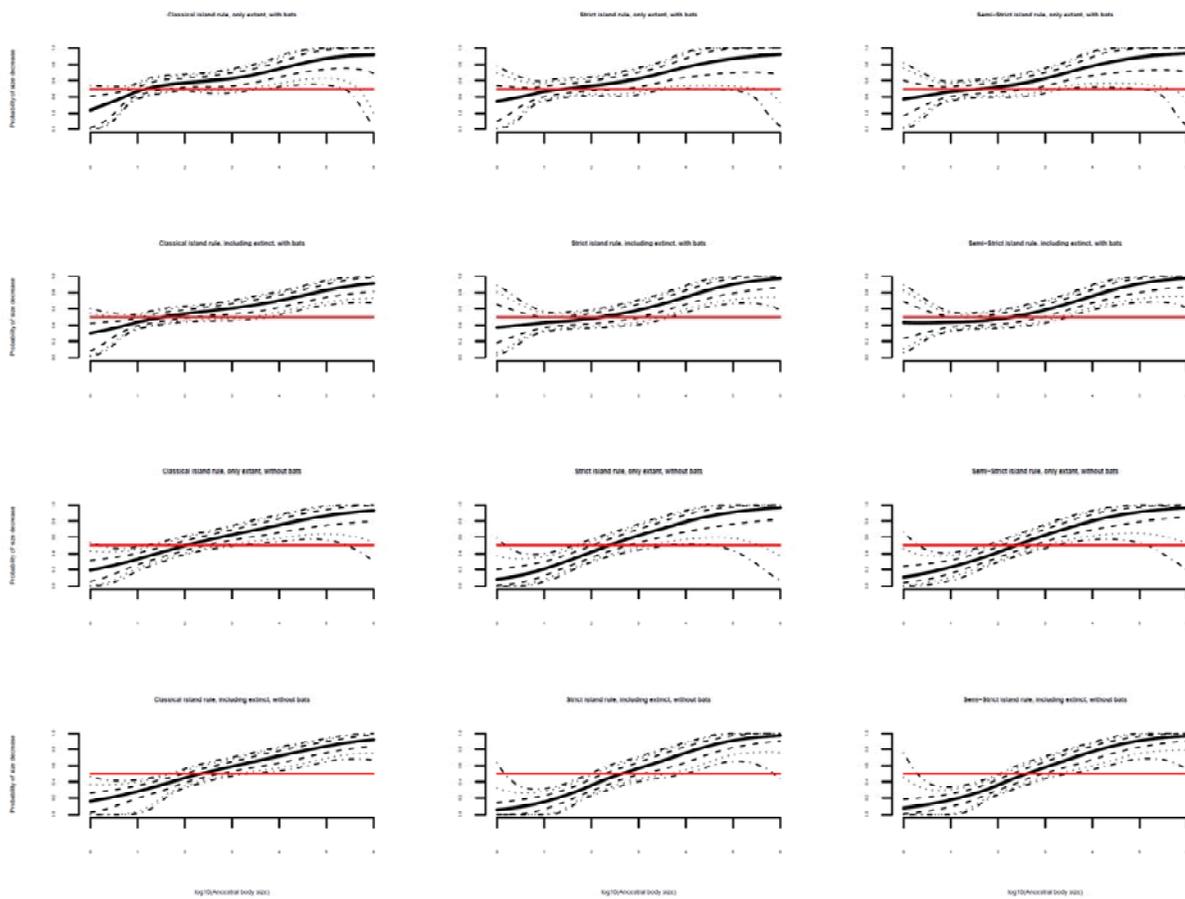


429

430

Figure S2. Relationships between ancestral body size and directionality of evolutionary size change after island invasion for the 12 separate analyses with a threshold for a minimum size difference between island and mainland clades of 5%.

The structure and meaning of the individual lines in each panel are identical to those in Figure 1.

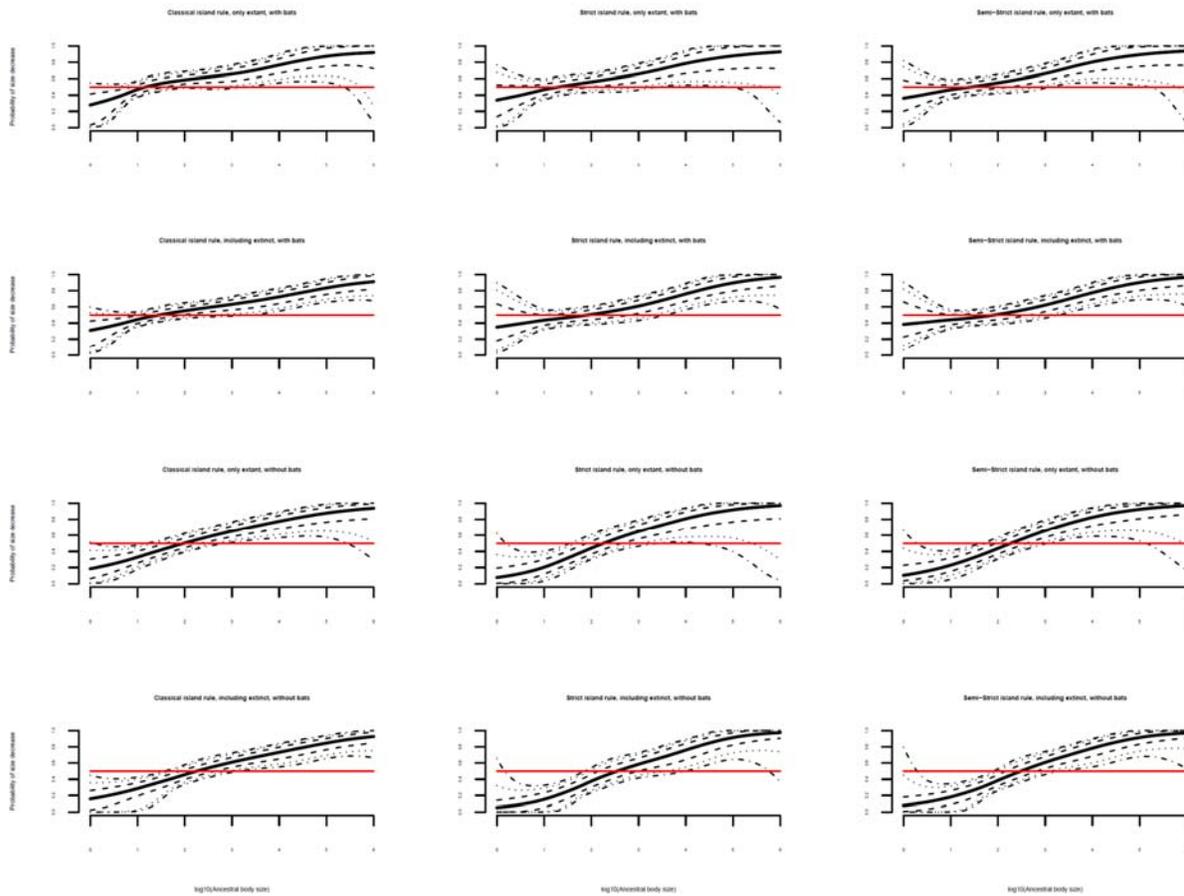


431

432

Figure S3. Relationships between ancestral body size and directionality of evolutionary size change after island invasion for the 12 separate analyses with a threshold for a minimum size difference between island and mainland clades of 10%.

The structure and meaning of the individual lines in each panel are identical to those in Figure 1.



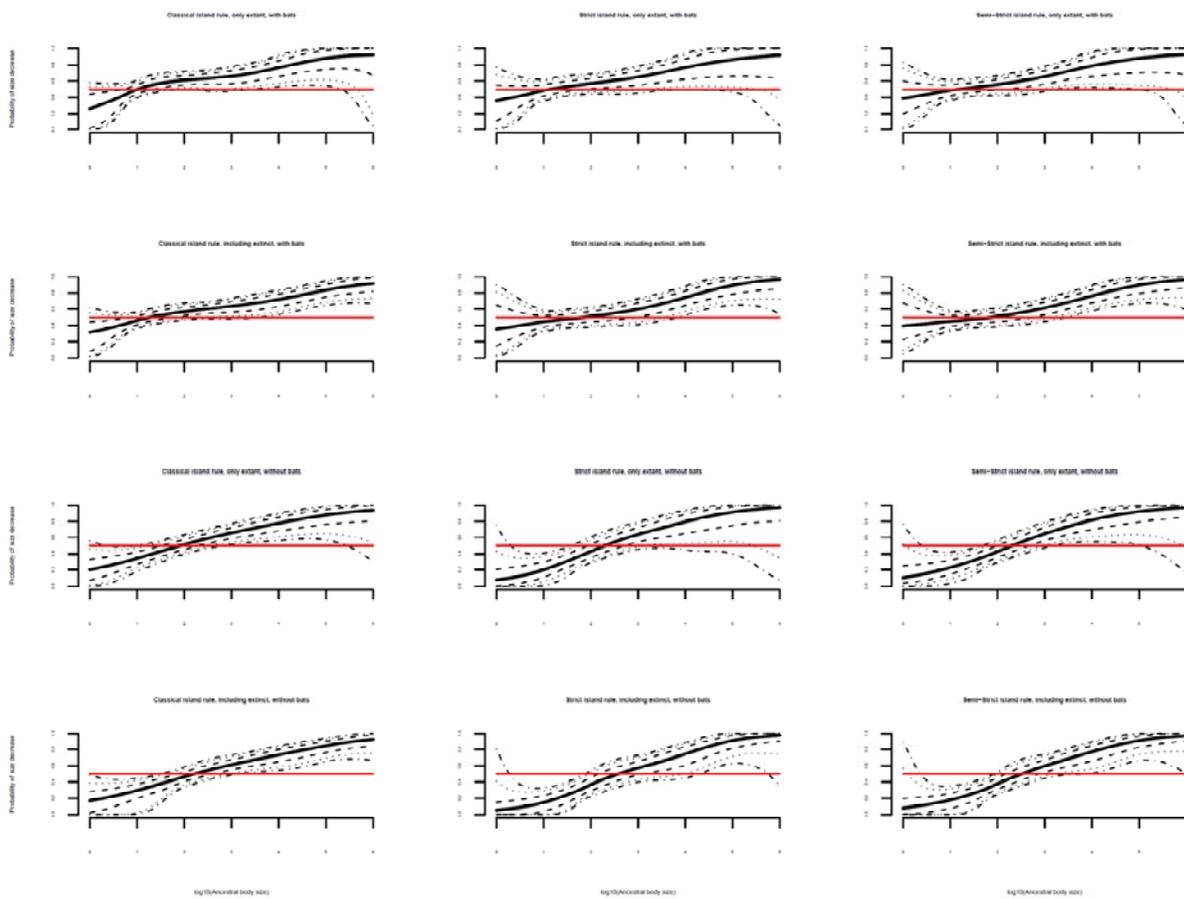
433

434

435

Figure S4. Relationships between ancestral body size and directionality of evolutionary size change after island invasion for the 12 separate analyses with a threshold for a minimum size difference between island and mainland clades of 15%.

The structure and meaning of the individual lines in each panel are identical to those in Figure 1.



436

437

438

Figure S5. Relationships between ancestral body size and directionality of evolutionary size change after island invasion for the 12 separate analyses with a threshold for a minimum size difference between island and mainland clades of 20%.

The structure and meaning of the individual lines in each panel are identical to those in Figure 1.

