‘On being the right size’* – Do aliens follow the rules?

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Abstract

Aim: To assess whether mammalian species introduced onto islands across the globe have evolved to exhibit body size patterns consistent with the ‘island rule,’ and to test an ecological explanation for body size evolution of insular mammals.

Location: Islands worldwide.

Methods: We assembled data on body mass, geographical characteristics (latitude, maximum elevation) and ecological communities (number of mammalian competitors, predators and prey) for 385 introduced populations across 285 islands, comprising 56 species of extant, non-volant mammals. We used linear regression, ANCOVA and regression tree analyses to test whether introduced populations of mammals exhibit the island rule pattern, whether the degree of body size change increased with time in isolation and whether residual variation about the general trend can be attributed to the geographical and ecological characteristics of the islands.

Results: Introduced populations follow the predicted island rule trend, with body size shifts more pronounced for populations with greater residence times on the islands. Small mammals evolved to larger body sizes in lower latitudes and on islands with limited topographic relief. Consistent with our hypothesis on the ecology of evolution, body size of insular introduced populations was influenced by co-occurring species of mammalian competitors, predators and prey.

Conclusion: The island rule is a pervasive pattern, exhibited across a broad span of geographical regions, taxa, time periods and, as evidenced here, for introduced as well as native mammals. Time in isolation impacts body size evolution profoundly. Body size shift of introduced mammals was much more pronounced with increasing residence times, yet far less than that exhibited by native, palaeo-insular mammals (residence times > 10,000 years). Given the antiquity of many species introductions, it appears that much of what we view as the natural character and ecological dynamics of recent insular communities may have been rendered artefacts of ancient colonizations by humans and commensals.

Keywords

Anthropocene, body size evolution, competition, Holocene, introduced species, invasive species, island biogeography, island rule, meta-analysis

*This title is, in part, homage to J. B. S. Haldane’s (1926) compelling essay published first in 1926.
1 | INTRODUCTION

Humans have been transporting vertebrates to islands worldwide since prehistoric times. The successful introduction of such exotic species has often led to the extinction of native species (Courchamp, Chapuis, & Pascal, 2003; Long, 2003), especially on isolated, small islands. Not only do they compete with native species, but these introduced populations often adapted and evolved in response to the local environments within short historical periods (Baker, 1980; Lister & Hall, 2014; Losos, Warheit, & Schoener, 1997; Michaux, Cucchi, Renaud, Garcia-Talavera, & Hutterer, 2007; Renaud, Hardouin, Pisani, & Chapuis, 2013; Rowe-Rowe & Cradraft, 1992). The time-scale and direction of evolution in introduced mammals are, however, insufficiently known, and relevant studies are largely limited to those on invasive rats and mice (e.g. Lister & Hall, 2014; Pergams, Byrn, Lee, & Jackson, 2015).

Perhaps the most compelling patterns of evolutionary transformations in native insular vertebrates are those in body mass, known as the 'island rule' which describes a graded trend from gigantism in small species to dwarfism in large species (Foster, 1964; Lomolino, 1985, 2005; Van Valen, 1973). Based on our earlier studies of native insular mammals (Lomolino, Sax, Palombo, & van der Geer, 2012; Lomolino et al., 2013; van der Geer, Lytras, Lomolino, Palombo, & Sax, 2013), we hypothesized that the island rule pattern results from reversals in selective pressures from ecological displacement in high diversity communities on the mainland (which drive diversification in fundamental traits – body size in particular) to ecological release and convergence in body size (gigantism in small-sized species and dwarfism in large-sized species) on species-poor islands, especially in the absence of other mammals.

Despite the pervasive nature and generality of the island rule pattern across a diversity of taxa, regions and time periods (e.g. Burns, 2016; Lomolino, Riddle, & Whittaker, 2017:503-513; Lomolino et al., 2012, 2013; Lytras, van der Geer, & Rook, 2010; McClain, Boyer, & Rosenberg, 2006; van der Geer et al., 2013, 2016), there exists much variation about the general trend for native insular mammals. This variation has sometimes led to rejection of the island rule pattern for mammals (e.g. Meiri, Cooper, & Purvis, 2008; Meiri, Dayan, & Simberloff, 2004; Raia, Carotenuto, & Meiri, 2010). However, our analysis of body size variation of 385 insular populations of mammals from 98 species across 248 islands indicated that this residual variation was attributable to differences in functional characteristics (e.g. diet, ‘bauplan’) among the species and to variation among islands in their geographical and ecological characteristics, in particular latitude, topographic and environmental diversity, and diversity of insular communities, especially co-occurring mammals (Lomolino et al., 2012). Insular relative body size ($) of small mammals increased with latitude, consistent with Bergmann’s rule (Bergmann, 1847), but as $ was standardized for body size of the mainland populations, this trend indicates that the Bergmann’s rule pattern may be more intensified on islands. This study on native insular mammals also indicated that, for small mammals, gigantism was more pronounced for populations inhabiting smaller and more isolated islands, and those of more limited topographic complexity. Insular body size of mammals (both small and large species) also tended to be larger on islands with fewer mammalian competitors.

Our complementary study on temporal shifts in body size of small mammals inhabiting Mediterranean islands from the late Miocene to the early Holocene provided further evidence for the influence of ecological interactions on body size evolution of native insular mammals (van der Geer et al., 2013). Small mammals (e.g. mice, shrews and pikas) tended to increase in body size following colonization of these islands, but these trends towards gigantism ceased or were reversed following colonization of the islands by mammalian competitors or predators. A study on palaeo-insular rodent populations from 58 species across 32 islands worldwide also indicated the influence of climate – with gigantism in rodents being much less pronounced during cold phases of the Pleistocene in the Mediterranean (van den Hoek Ostende, van der Geer, & Wijngaarden, 2017).

Here, we capitalize on the thousands of unplanned experiments of introductions of mammals onto islands to further investigate the generality and causality of body size evolution. Our purpose is to assess whether mammalian species introduced onto islands across the globe have evolved to exhibit body size patterns consistent with the island rule, and to test our ecological explanation for body size evolution of insular mammals; that is, body size evolution should be dependent on the presence of ecologically relevant competitors and predators (Lomolino et al., 2012). To evaluate this hypothesis on the ecology of evolution, we test its predictions that body size evolution of introduced mammals (1) is more pronounced (i.e. greater degree of gigantism and dwarfism) for populations with longer residence times on islands; (2) is influenced by characteristics of the islands, including latitude (with body size of small mammals increasing with latitude, consistent with Bergmann’s rule) and maximum elevation of the islands (with body size evolution being more pronounced on low elevation islands because of their lower habitat diversity); and (3) is more pronounced on ecologically simple islands, that is those with fewer mammalian predators, competitors or prey.

2 | MATERIALS AND METHODS

2.1 | Data collection

We compiled a data set containing information on mammals introduced onto islands worldwide (Figure 1) including their insular and mainland body mass, time of introduction, the latitude, longitude and maximum elevation of the island, and the number of co-occurring species of mammalian competitors, predators and prey (noting also whether they were native or alien species). A list of the data sources is found in Appendix 1.

Our data set is the most extensive compiled thus far for body size evolution of mammals introduced to islands, comprised of information on 385 populations introduced onto 285 islands, ranging in absolute latitude from 0.13° to 63.42°, and in maximum elevation from 1 to 5,030 m. The introduced populations belong to 56 species.
from seven orders – most of these being invasive species (pests), that is those that tend to spread rapidly after establishing their ranges. This is partly due to the nature of zoological collections that are often based on eradication campaigns. The five most frequently introduced species in our data set are commensal rats (Rattus exulans, Rattus norvegicus, R. rattus), house mice (Mus musculus) and rabbits (Oryctolagus cuniculus).

Based on introduction date, our data are divided into two broad temporal ranges: the Holocene for pre-modern introductions ($n = 269$) and the Anthropocene ($n = 100$) for introductions after 1610, following the definition of Lewis and Maslin (2015) (for 16 populations, no time of introduction was available) (for sources on introduction date, see Appendix S1 in Supporting Information). The year 1610 represents the onset of the European expansion, starting a new wave of species introductions.

We searched various published sources (Appendix S2) to determine the number of mammalian symbionts on each focal island. We used the conventional approach of total number of relevant species instead of $\alpha$-diversity (sensu Whittaker, 1972), which is likely a better estimate of the level of competition and predation on large islands, because $\alpha$-diversity is not readily available yet for our focal islands. Species richness ranged from 0 to 73 (native competitors), six (predators) and 50 (prey) (12, 6 and 12, respectively, for alien species). Geographical data (latitude, longitude and maximum elevation) for the focal islands were taken from the Islands Website of the United Nations Environment Programme (http://islands.unep.ch/). For islands not included in this database, we used alternative sources (see Appendix S1). Isolation was not included as an independent variable because it was irrelevant for species introductions, except in terms of the effects of isolation on diversity of co-occurring species, which were recorded as independent variables in our analyses. Similarly, island area was not included in our analyses because species do not respond to area per se. Rather, the relevant drivers of body size evolution (correlated with island area) include the diversity of symbionts (numbers of competitors, predators and prey) and diversity of habitats (a correlate of maximum elevation); variables explicitly included in our analyses of factors influencing body size evolution of these mammals.

2.2 | Calculations of $S_i$

For each island, we calculated the average body size measurement of the focal, introduced population from the available museum specimens and then divided this by the average body size of the mainland population, preferably from the same geographical region (Appendix S1 and S2). The resulting ratio $S_i$ (relative insular body size) served as the dependent variable in our analyses. Body size measurements included total body length, tail and foot length, and body mass at death, and $S_i$ was expressed in mass equivalents or the ratio of cubed linear dimensions when measurements were of body, tail or foot length. For rats and mice, we measured as far as available only specimens with advanced dental wear (stages V and 5, respectively, in [King, 2006]), as rats and mice grow slightly after they reach maturity (Roach, Mehta, Oreffo, Clarke, & Cooper, 2003). A number of species display sexual size dimorphism (for reference per species, see Appendix S1). We separated the sexes for these taxa (all artiodactyl species, Herpestes, Macropus, Martes, Mustela, Mus, Oryctolagus, Phalanger, Suncus) and then either used only the measurements from one sex (the one with the most available specimens) or the average for both males and females, where $S_i = ((S_i \text{ male} + S_i \text{ female})/2)$. For species with significant sexual dimorphism (Acomys, Bandicota, Eliomys, Erinaceus, Glis, Lepus, Rattus, Sylvilagus, Trichosurus), we pooled data from males and females.

Feral domestic breeds were excluded, because either information on which specific breed was introduced was missing, or more than one breed were used to establish a local population. This is, for
example, the case with the Amsterdam Island feral cattle, which
derived from a mixture of several small-sized European breeds (Jer-
shey, Tarentaise, Grey Alpine, Breton Black Pied; see, however, for a
size change estimation Rozzi & Lomolino, 2017). It is especially valid
for ancient introduced species, such as the mouflons of Sardinia
and Cyprus (Ovis orientalis musimon and O. o. ophion) and the wild
goat of Crete (Capra aegagrus cretica). The respective ancestral sheep
and goat are unknown.

Body mass data for mainland populations were taken from Smith
et al. (2003), or from the Encyclopedia of Life (http://eol.org) for
those populations that were not included in the former study. For
mainland species with significant geographical size variation, we took
the body mass for the population that is geographically closest to the
area of origin for the insular population. For some islands, this
required the use of several mainland populations, for example in New
Zealand, where house mice from Auckland Islands and North Island
have haplotypes in common with M. m. domesticus of Britain (King
et al., 2016), those from antipodes, which include haplotypes
recorded in M. m. domesticus of Spain (Searle et al., 2009), while
the mice from the south part of the South Island belong to the M. m. cas-
taneus group (perhaps from India) (King et al., 2016). For the ancestral,
mainland reference for the Polynesian rat (R. exulans), we used popu-
lations from Indochina (Thomson et al., 2014) suggested that this spe-
cies originates from Flores, but material from that island was not
available for our measurements). See Appendix S1 for a detailed justi-
fication of mainland-island pair per introduced population.

2.3 Statistical analyses

We conducted all statistical analyses using XLSTAT (version 2012;
Addinsoft, New York, USA), which is a program that runs in the
EXCEL environment. First, we expressed body size variables as the
mean values of measurements for individuals of each insular popula-
tion, and we then conducted statistical analyses at this (i.e. the popu-
lation) level. Because each insular population was the product of a
distinct introduction, often at periods quite disparate in time, and with
genetic and geographical isolation to assure their independence, we
consider each insular population to be an evolutionary independent
unit. Our dependent variable (S) is a comparison of the means for a
particular insular population and its mainland source/reference popu-
lation and, thus, reflects the evolutionary independence of each spe-
cies population. Although we included taxonomic order as a covariate
in the analyses described below, we chose not to include species
identity of each insular population as a variable in the analyses
because it would have likely confounded any inferences and possibly
introduce a narcissus effect (as described above, the variable for body
size [M] was fixed for each species population, and thus, species identi-
ty is a surrogate for M). We did, however, conduct an initial analysis
of the island rule pattern (i.e. the relationship between S and M) after
pooling the data for insular populations to the species level; this yield-
ing results qualitatively identical to those for the entire data set. All
other analyses were conducted with the expanded data set (i.e. at the
level of insular populations), which enabled us to assess the influence
the full set of relevant independent variables, including M, taxonomic
order, latitude and maximum elevation of the islands, and diversity of
co-occurring mammalian competitors, predators and prey.

We used analysis of covariance (ANCOVA; significance level 5%) to
assess the relationship between relative insular body size (S) and
two independent variables – body size of the species on the mainland
(M) and taxonomic order (using log10 transformation of body size vari-
ables S and M; regression model LogS = b1(order) + b2(LogM) +
b3(order)*(LogM)). We first conducted these analyses with both vari-
ables (S, M) and an interaction term ((order)*(LogM)) to test whether the slopes of the relationship between S and M differed
among mammalian orders. When this was found not to be the case,
we conducted a second ANCOVA, this time without the interaction
term (assuming the same generalized slope across orders) to assess
differences in S–M relationships (i.e. island rule patterns) among
orders (as indicated by differences in the intercepts of these relation-
ships). This latter analysis also generated residuals, which are essen-
tially deviations above or below the island rule pattern after adjusting
for the influences of both body size and of taxonomic order.

Residuals from ANCOVAs for both Holocene and Anthropocene
introductions, taken separately, were then used as the dependent vari-
able in regression tree analyses (RTA) to assess the effects of the
remaining independent variables: latitude and maximum elevation of
the islands, and diversity of co-occurring mammalian competitors,
predators and prey. RTA parameters included the following:
method = CHAID, maximum tree depth = 5, significance level = 5%,
split threshold = 5%, authorize redivision, Bonferroni correction/merge
threshold = 5%, minimum parent size = 4, minimum son size = 2 and
number of intervals = 10. RTA is a recursive, binary machine-learning
nonparametric and distribution-free method that does not require
transformations. RTA is able to deal efficiently with missing variables,
which is not affected by outliers, non-normality or monotonic transfor-
mation of data (Bell, 1999; Breiman, Friedman, Olshen, & Stone, 1984;
Loh, 2011, 2014; Olden, Lawler, & Poff, 2008; Steinberg & Colla, 1997;
Steinberg & Golovnya, 2006). One especially important advantage of
machine-learning methods in ecological and evolutionary applications is
that they do not assume data independence, thus alleviating the need
for phylogenetic controls of such data (Davidson, Hamilton, Boyer,
Brown, & Ceballos, 2009; see also Westoby, Leishman, & Lord, 1995;
Melo, Rangel, & Diniz-Filho, 2009). Its principal product is a recursively
branching tree that describes the direct, interactive and contextual rela-
tionships between the response variable (here S) and a subset of the
predictor variables. The first branch is determined by first sorting the
entire data set by the values of each predictor variable and then deter-
mining which of those variables is best at splitting the data into two
subgroups that are most homogeneous with respect to values of the
response variable. This process is then repeated for each of the subse-
quent branches. The resulting ‘maximal trees’ are then pruned until an
optimal tree is selected, in our case the tree with the smallest relative
error rate for predicting test data based on models (trees) developed
from independent training data.
3 | RESULTS

The range in relative insular body size was greatest for the Holocene introductions \( n = 269; S_i \) ranging from 0.430 to 2.377 for Dasyprocta leporina of Guadeloupe Island and R. exulans of Tulagi Island, respectively), intermediate for Anthropocene introductions \( n = 100; S_i \) ranging from 0.515 and 1.889 for R. norvegicus of St. Agnes Island and M. musculus of Gough Island, respectively) and most restricted for those with uncertain periods of introductions \( n = 16; S_i \) ranging from 0.766 to 1.700 for Paradoxurus hermaphroditus of Bangka Island and Myodes glareolus of Skomer Island, respectively). Because the latter results are in line with those of Holocene and Anthropocene introductions and contain no outliers, we exclude them from further analyses. The practically horizontal trendline for Anthropocene populations (Figure 2) is a result of mutually neutralizing trends of individual orders, for the greater part driven by the counter-intuitive body mass decrease in most R. norvegicus populations.

Taken together, most introduced species populations exhibited the graded trend in relative insular body size consistent with the island rule (Figure 2). Results were qualitatively identical when data for insular populations were pooled to the species level (linear regression indicating the relationship between \( S_i \) or \( \log_{10}S_i \) and \( \log_{10}M \) was not significant for species during the Anthropocene, but was highly significant for species during the Holocene; \( p > .90 \) and \( p < .003 \), respectively, see Figure S1 in Appendix S1). However, there was much variation about the island rule trend for insular populations, indicating (as predicted) the influence of other factors on body size evolution, including

1. time in isolation (Figure 2), with populations with a longer residence time on the islands exhibiting more pronounced body size evolution (i.e. greater degrees of gigantism and dwarfism exhibited by populations introduced during the Holocene than by those introduced during the Anthropocene). The latter group fails to exhibit the trend when taken as a whole (Figure 2), but exhibits the trend when analysed per order (Figure 3), with rodents exhibiting the opposite trend and thus causing the discrepancy between Figures 2 and 3.

2. functional characteristics of the species associated with their taxonomic order (in particular metabolism, ‘bauplan’, diet and generation time), as indicated by differences in the intercepts of the island rule trend lines among orders (Figure 3),

3. geographical characteristics of the islands, including latitude (a correlate of or proxy for environmental temperatures and primary productivity) and maximum elevation (a measure of topographic relief, habitat diversity and the influence of anthropogenic activities, which tend to dominate lower elevations). Regression tree analyses indicated that species evolved to larger body sizes (after adjusting for body mass of ancestors and for taxonomic order) on islands located in the lower latitudes and on those of lower maximum elevation (Figures 4–6), and

4. the ecology of evolution, with introduced species exhibiting ecological character release and displacement – evolving to larger size on islands with fewer mammalian predators (Figures 4, 5a, 6a,b), alien prey (Figure 6c), and competitors (Figure 6a,b). Consistent with these results among species, inspection of relative insular body size values for two of the most commonly introduced species, M. musculus and R. rattus, combined revealed that they tend towards gigantism in allopatry (\( S_i > 1.0 \) for 19 of 27 allopatric populations), but dwarfism in sympatry (\( S_i < 1.0 \) for 16 of 23 sympatric populations; \( p < .005 \), chi-square test of independence that body size of these populations is responding in the same fashion in allopatry and sympatry).

**FIGURE 2** The effects of time on body size evolution of insular mammals are evident in comparisons of patterns among populations differing in residence times on islands. Mammal populations introduced onto islands during the Anthropocene (within the last 400 years) failed to exhibit the island rule (a graded trend from gigantism in small species to dwarfism in large species), those with longer residence times (i.e. introduced during the Holocene) exhibited the predicted pattern, albeit not as pronounced as that exhibited by palaeo-insular mammals (residence times > 10,000 years). Anthropocene: \( R^2 < .001 \); Holocene: \( R^2 = .293 \); Uncertain period: \( R^2 = .076 \); Palaeo-insulars: Lomolino et al. (2012) [Color figure can be viewed at wileyonlinelibrary.com]
DISCUSSION

Although introduced species exhibited patterns consistent with the island rule and with our findings for native insular mammals, there were some important differences and some genuinely anomalous patterns observed. These additional patterns provided important insights with regard to the influence of time in isolation, environmental factors associated with latitudinal gradients (e.g. climate and primary productivity), and the combined and possible cascading effects of interactions among native and alien competitors, predators and prey.

4.1 The role of time

Although body size evolution of Holocene introductions (those prior to 1610) was comparable to that for Holocene native species, it was much less pronounced than that of palaeo-insular mammals (i.e. residence times > 10,000 years; Figure 2; see also Lomolino et al., 2013; fig. 5). This of course is entirely consistent with the predicted effects of time in isolation, but it also provides a measure of the rate of body size shift in these mammals. The commensal rats illustrate the effect of time perhaps best: all insular populations of the Polynesian rat, *R. exulans* (n = 94) and the Asian house rat, *R. tanezumi* (n = 12), both Holocene introductions, evolve larger body sizes (except *R. exulans* on Fergusson Island where *S*~i~ ~ 1). Almost all Anthropocene populations of the brown rat, *R. norvegicus* (n = 21), on the other hand evolved smaller body sizes. Likely, it is not the relatively short time in isolation that causes this aberrant pattern, but rather a combination of factors including the unnatural, modified ecosystems in which these rats have to survive. We refrain here from further speculation, as too many factors can be thought of (e.g. drought, population size, stress, biased database).

Individual taxa, however, varied substantially in their rate of body size evolution, with numerous populations of some species exhibiting significant change in body size during the Anthropocene (i.e. within < 400 years), for example house mice on several islands (see also below). The rate as well as the magnitude of body size evolution was especially rapid for populations of small mammals introduced to isolated islands lacking other mammals, but dominated by alternative prey in the form of dense colonies of seabirds. Our results are consistent with observations of a fast change in other introduced populations, for example the Orkney vole (Cucchi et al., 2014) and tiger snakes on southern Australian islands (Aubret, 2015).
4.2 | The effect of latitude

That populations of mammals introduced onto tropical islands evolved to larger size than those introduced onto islands of the higher latitudes is counter to our previous findings and counter to Bergmann’s rule (Lomolino et al., 2012; see also Yom-Tov, Green, & Coleman, 1986; Yom-Tov, Yom-Tov, & Moller, 1999 for reports of Bergmann’s latitudinal gradient in common brushtail possums, *Trichosurus vulpecula*, and Polynesian rat, *R. exulans*, of New Zealand). Our anomalous findings for mammals introduced onto tropical islands may be explained, at least in part, by the relatively high temperature, low seasonality and high primary productivity of tropical ecosystems which seem optimal for the particular species that dominate the record of introduced species we studied. The nine most commonly introduced species include, in decreasing frequency of island introductions (in parentheses), *R. exulans* (95), *M. musculus* (51), *O. cuniculus* (23), *R. norvegicus* (22), *R. rattus* (20), *Phalanger orientalis* (16), *Suncus murinus* (14), *R. tanezumi* (12) and *Herpestes auropunctatus* (10).

For rodents, which form the greater part of our database, Alhajeri and Steppan (2016) reported a positive association between body mass and precipitation variables, especially those that are associated with primary productivity, whereas they found no association between body size and temperature. While still speculative, we may infer that the set of species we studied, dominated by commensals, is far from representative of the character of native mammals – both in their responses to environmental characteristics and their close association with anthropogenic environments. We admit, however, that more rigorous studies are required to investigate why introduced species are larger on tropical islands; or, alternatively, why body size of these commensals is lower on islands in the higher latitudes.

4.3 | The ecology of evolution

Although body size of introduced species evidenced the influence of co-occurring species of mammals, consistent with our previous findings and our hypothesis on the ecology of evolution, evidence for the effects of competitors was not pervasive – limited to the effects of alien competitors on body size of rodents introduced during the Anthropocene. Again, we can only speculate at this point, but submit that the differences in the influence of competition on natives versus introduced species may be a function of the atypical nature of commensal species. A review of the list of the most commonly introduced species, above, reveals that they are not only commensal, but also highly invasive – spreading rapidly, especially across anthropogenic habitats, once introduced onto islands. In the Philippines, for example, the three commensals – *R. tanezumi*, *R. exulans* and *S. murinus* – only become established in disturbed forests where there are few native competitors (Rickart, Balete, & Heaney, 2007; see also de Guia & Quibod, 2014). This may also help explain the larger body size of introduced mammals on low elevations islands, where human populations often dominate and transform most insular habitats, thus favouring the invasive commensals.

Our results for the differential responses of two commonly introduced species (*M. musculus* and *R. rattus*) in sympatry versus in allopatry are consistent with those reported for black rats in New Zealand, which are larger in the absence of mice (Yom-Tov et al., 1999), and for those reported for a variety of small mammals of the Mediterranean palaeo-islands, where body size evolution trends reversed after introductions of competitors (van der Geer et al., 2013). It likely is no coincidence that the world’s largest wild house mice live on Gough Island, South Atlantic Ocean (Rowe-Rowe & Crafford, 1992), where they are the only mammalian inhabitants and feast heavily on chicks of two dozen species of seabirds that breed...
in dense populations on these islands (Cuthbert et al., 2016; Gray et al., 2014). This super-normal abundance of food and lack of predators and competitors allowed the mice to grow almost twice as large as their ancestors ($S_1 = 1.89$). A similar condition may be present on many other, low elevation islands where mice grow to relatively large size: many of these low elevation islands are covered by colonies of breeding birds that are released from predation by terrestrial mammals, in turn providing a bumper crop of atypical prey for rodents and other mammals introduced onto these islands (see terrestrial mammals, in turn providing a bumper crop of atypical prey for carnivores by limiting productivity of seabird colonies on these islands. This is indeed the case for the two islands with the relatively largest carnivores (Bering and Mednyi, with $S_1 = 1.306$ and $S_1 = 1.397$, respectively), where these foxes exclusively feed on sea birds and seals (Mednyi) or on these atypical prey plus small voles (Bering) (Zagrebelnyi, 2000).

### 5 CONCLUSION

The hundreds of unplanned experiments of species introductions to islands across the globe provide important insights on the generality and pervasive nature of the island rule, with introduced populations of mammals exhibiting the predicted, graded trend from gigantism to dwarfism. As observed for native populations of insular mammals, there remained much variation in their body size evolution, with populations on tropical islands and those with lower maximum elevation and, for the rodents, fewer co-occurring species of native predators. Numbers in parentheses indicate range for each split (branch) of the regression tree for this independent variable [Color figure can be viewed at wileyonlinelibrary.com]

![Regression tree analyses indicated that residual variation about the island rule trend for (a) rodents, (b) carnivores and (c) lagomorphs introduced onto islands during the Holocene (after controlling for the effects of taxonomic order and body size of the ancestral, mainland species; Figure 3a) was higher (larger than expected body size) for populations on tropical islands and those with lower maximum elevation and, for the rodents, fewer co-occurring species of native predators. Numbers in parentheses indicate range for each split (branch) of the regression tree for this independent variable [Color figure can be viewed at wileyonlinelibrary.com]
insular communities – in particular, mammalian species which tend to have a dominant influence on community structure.

Taken together, our studies on native and introduced populations of insular mammals across a broad span of geographical regions, taxa and time periods (this study, and see Introduction) provide strong support for the above explanations for insular body size and, in particular, our hypothesis on the ecology of evolution. The island rule pattern appears to be the result of reversals in selection pressures (sensu Lomolino, 2009) from those associated with ecological displacement and evolutionary diversification in high diversity and ecologically (and taxonomically) balanced communities on the mainland, to ecological release along with displacement from the particular inhabitants of species-poor, unbalanced insular communities (where mammals are typically only a minor component).

Our research on the ecological and evolutionary dynamics of mammals introduced onto the world’s islands also provides important insights for those attempting to conserve the integrity of native insular biotas. It is now clear that alien species can strongly impact one of the most fundamental characteristics of native species – their body size, which strongly influences all physiological, demographic and ecological characteristics of mammals. Equally important, these impacts of alien species are likely to be either directly or indirectly mediated, amplified or otherwise modified by human activities. Beyond the initial introduction of a particular alien species, anthropogenic activities often favour the expansion of that species by transforming native habitats to those more favourable to the commensals they transport (especially across low elevation islands). In addition, the effect of subsequent introductions of additional alien species may cascade across trophic levels – alien predators, competitors and prey affecting the body sizes of not only native mammals, but other alien species as well. These dynamics in body size, and those in population levels of native and alien populations of mammals, along with concurrent shifts in diets of these species, likely have significant impacts on native seabirds and other vertebrates and invertebrates that evolved in isolation on what were
typically mammal-free islands. Finally, given the antiquity of many of these species introductions, which often predate the onset of the Anthropocene by many centuries if not millennia, it appears that much of what we now view as the natural character, composition and ecological dynamics of recent insular communities may have been rendered artefacts of ancient colonizations by humans and our commensals (see van der Geer, Lolomino, & Lyras, 2017; Lolomino et al., 2017:592–594).

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**APPENDIX 1**

**DATA SOURCES**


