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Variation in body and tooth size with island area in small mammals: a study of Scottish and Faroese house mice (*Mus musculus*)

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House mice from 24 Scottish and Faroese islands show positive correlation of skeletal size with island area, conforming to a model of resource limitation in very small islands. Molar size is not correlated with island size, suggesting greater genetic canalization; smaller individuals have larger tooth to body size ratio. The size variation may have a simple genetic basis or may be ecophenotypic. The offset between skeletal and molar size has potential use in the fossil record as a marker for these rapid effects, while longer-term evolutionary change reverts to approximate tooth–body size isometry. Collation of related studies indicates frequently deterministic relationships of small-mammal body size to island size. The parameters of the relationship (positive, negative or parabolic) vary widely with case study according to biotic and abiotic factors. In the present study there was no relationship of mouse size to any variable (e.g. presence of competitors) except island area.

Introduction

Variation in body size is the most ubiquitous observation when comparing populations of a mammalian species, whether living or fossil. While measurement of any element of the skeleton or dentition can in theory be used as a proxy for body size, they do not necessarily vary to the same degree, i.e. isometrically. In particular, it is frequently observed, at an intra-specific level, that body-size variation is accompanied by a lesser degree of tooth-size variation. This pattern is common among breeds of common domestic animals, for example, in contrast to the general isometry of tooth and body size across species (Fortelius 1985).

A fruitful arena in which to examine such patterns is in island populations since, as is well known, mammalian populations on islands are frequently subject to significant size change. According to the 'island rule' of mammalian biogeography (Van Valen 1973), small mammals on islands tend to gigantism, large mammals to dwarfism (Foster 1964), but this 'rule' has been the subject of much debate. Some authors (Lomolino 1985, 2005, Damuth 1993) show that, very generally, the larger the species' body size on the mainland, the greater its likely

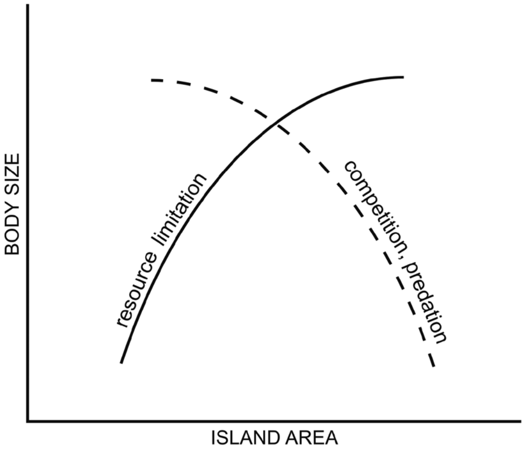

Fig. 1. Hypothetical relationship between island size and body size among populations of a small mammal species (based on Heaney 1978). In a given case, the resource limitation effect may be dominant, producing a positive relationship (solid line), or the competition/predation effect may be dominant, producing a negative relationship (dashed line), or the two may intersect, yielding a parabolic relationship; cf. Fig. 8.

relative dwarfing on an island, and the smaller its mainland body size, the greater its likely relative gigantism on an island. Others (e.g. Raia & Meiri 2006) stress the many exceptions, and consider the 'rule' to be an artefact of taxon-specific trends (e.g. artiodactyls larger, murid rodents smaller). Explanations for the trends usually invoke food limitation, and release from predator pressure and/or inter-specific competition (Foster 1964, Heaney 1978, Lomolino 1985, McNab 2010). It is now generally recognised that many patterns of body-size evolution have taken place on islands, and that the outcome in a given case will depend on the complex interplay of intrinsic and extrinsic biotic and abiotic factors (Lomolino *et al.* 2012).

A natural extension of the mainland *vs.* island comparison is to ask whether, within a species, there are observable trends in body size across islands of differing characteristics, such as latitude, distance from mainland, and area. Concerning area, a simplistic expectation might be that the smaller the island, the more pronounced the effect of dwarfing or gigantism. However, in a study of 39 subspecies of the squirrel *Callosciurus prevosti* in southeast Asia, Heaney (1978) found a parabolic curve of body size to island area: the squirrels became bigger as island size increased from 10^1–10^3 km^2, but then decreased again on islands from 10^4–10^6 km^2. Heaney suggested that food limitation on the smallest islands was responsible for the ascending part of the curve, but that above a certain island area, inter-specific competition became the dominant selective force, pushing down body size as a broad feeding niche became less tenable (Fig. 1). These ideas can be fruitfully considered alongside those of Lomolino (1985), who suggested that competition effects were most important for smaller species, resource limitation for larger ones. As predicted by Heaney (1978), it might be expected that the smaller the species, the smaller the islands that would be needed to show the domain of positive correlation of island size with body size (the ascending part of his parabolic curve).

Several studies of this nature have been undertaken since Heaney's (1978) work, but very few that have looked at the relative size changes across teeth and different parts of the skeleton. In this study we have made use of large samples of introduced house mouse from 24 islands of Orkney and Shetland (UK) and Faroe (Denmark). The islands cover a range of areas, distances from the mainland, habitats, and associated faunas. They therefore allow testing of various possible causal factors for observed size variation in the mice. In addition, the mice are preserved largely as associated skeletons, allowing us to compare the size response of different parts of the body, particularly teeth and the bony skeleton, and therefore to test for greater intraspecific conservatism of dental size suggested in studies of other taxa. Finally, study of dental wear enables us to assign relative ontogenetic ages to individuals, and therefore to examine the growth trajectories leading to any differences in adult skeletal size.

Material and methods

The Scottish and Faroe Island mice all fall within the western European *domesticus* clade of house mice (Jones *et al.* 2011, Bonhomme & Searle 2012). This is treated by most current authors as a subspecies of *Mus musculus* L. (Macholán *et al*. 2012), although its hybrid zone with *musculus* is narrow, and the two groups retain their integrity, so there are grounds for considering it a good species, *M. domesticus* Rutty, 1772 (R. J. Berry pers. comm.). In any event, the taxonomic consistency of the samples utilised in this study allows us to ignore taxon-specific differences, specifically the slightly lighter male body weight in *musculus* than in *domesticus* from the same geographical areas (Ganem 2012).

The Orkney, Shetland and Faroe archipelagos are situated (at their closest points) approximately 13 km, 170 km and 375 km from the Scottish mainland, respectively (Table 1 and Fig. 2). Orkney consists of about 75 islands and islets, of which 16 are inhabited by people. They are generally low-lying and treeless, but have fertile soils allowing for high agricultural activity. Situated to the north-east of Orkney, Shetland incorporates around 100 islands of which only 16 are inhabited. The Faroe Islands, colonised only around 800 AD, are rugged and mountainous. Finally, two of the studied populations came from islands in the Firth of Forth off the east coast of Scotland, only 4 and 8 km from the mainland. Areas were measured from a map using squared paper. Taken together, the islands selected in this study vary in size from 0.3–900 km^2.

The mice were collected by R. J. Berry in the 1960s and 1970s, principally by hand but also by the use of traps baited with maize and peanut butter. The skeletons had previously been defleshed using papain. From the total collection of around 6000 individuals, islands and samples for

Table 1. Data on the 24 sampled islands and their rodents. *n* = number of *Mus musculus* in age group 4. M1 = first upper molar; femur, mandible and molar dimensions are means ± SE of samples at age group 4; Presence of rodent species: A = *Apodemus sylvaticus*, M = *Microtus arvalis*, N = *Rattus norvegicus*, R = *Rattus rattus*.

Island	*n*	Distance to mainland (km)	Area (km^2)	Human population 1961		Mandible length (mm)	Femur length (mm)	M1 width (mm)	Presence of rodent species
				indiv.	indiv. km^{-2}				
Shetland									
Mainland	11	170	900	13282	14.76	12.38 ± 0.10	13.43 ± 0.20	0.99 ± 0.33	A,M,N
Yell	7	235	200	1155	5.78	12.01 ± 0.11	13.41 ± 0.21	1.03 ± 0.01	A
Fetlar	9	250	39	127	3.26	11.88 ± 0.08	12.57 ± 0.25	1.07 ± 0.02	A
Unst	6	260	110	1148	10.44	12.06 ± 0.14	12.36 ± 0.40	1.11 ± 0.03	N
Whalsay	7	225	18	764	42.44	11.86 ± 0.11	12.75 ± 0.18	1.01 ± 0.02	R
Foula	12	175	13	54	4.15	11.90 ± 0.09	12.95 ± 0.32	1.02 ± 0.02	–
Papa Stour	9	205	7	55	7.86	12.09 ± 0.14	13.00 ± 0.19	1.07 ± 0.02	–
Fair Isle	15	13	9	64	7.11	11.48 ± 0.08	12.36 ± 0.10	1.02 ± 0.02	A
Orkney									
Mainland	3	29	434	13495	31.09	11.71 ± 0.15	13.00 ± 0.38	1.07 ± 0.03	A,N,R
Papa Westray	6	78	11	139	12.64	11.92 ± 0.16	12.58 ± 0.33	1.08 ± 0.06	A,N
N Ronaldsay	6	86	12	161	13.42	11.42 ± 0.10	12.58 ± 0.16	1.12 ± 0.03	A
N Faray	1	370	1.5	5	3.33	11.75	12.50	1.20	–
Sanday	6	64	82	670	8.17	11.75 ± 0.16	12.73 ± 0.30	1.10 ± 0.02	A,M,N
Hoy	6	13	110	511	4.65	12.42 ± 0.11	13.46 ± 0.30	1.05 ± 0.02	A,N
Westray	7	65	54	872	16.15	12.07 ± 0.13	12.91 ± 0.20	1.12 ± 0.02	M,R
Stronsay	3	52	37	497	13.43	11.83 ± 0.21	12.92 ± 0.08	1.12 ± 0.02	A,N
Egilsay	1	55	6.5	54	8.31	11.88	12.13	1.10	N
S Ronaldsay	7	11	59	980	16.61	11.88 ± 0.14	13.25 ± 0.22	1.07 ± 0.02	M,N
Firth of Forth									
Isle of May	14	7.5	0.7	7	10.00	11.08 ± 0.13	11.96 ± 0.13	1.0 ± 0.003	–
Inchkeith	2	5	0.3	3	10.00	10.87 ± 0.37	11.50 ± 0.87	1.02 ± 0.07	–
Faroe									
Nolsoy	9	395	10	345	34.50	11.46 ± 0.13	12.86 ± 0.27	1.08 ± 0.02	–
Hestur	5	400	6	86	86.00	11.15 ± 0.17	11.50 ± 0.33	1.01 ± 0.02	N
Mykines	6	435	9.5	92	92.00	11.96 ± 0.30	12.15 ± 0.66	1.04 ± 0.02	–
Sandoy	6	375	111	1684	1684.00	11.91 ± 0.19	13.32 ± 0.33	1.08 ± 0.02	–

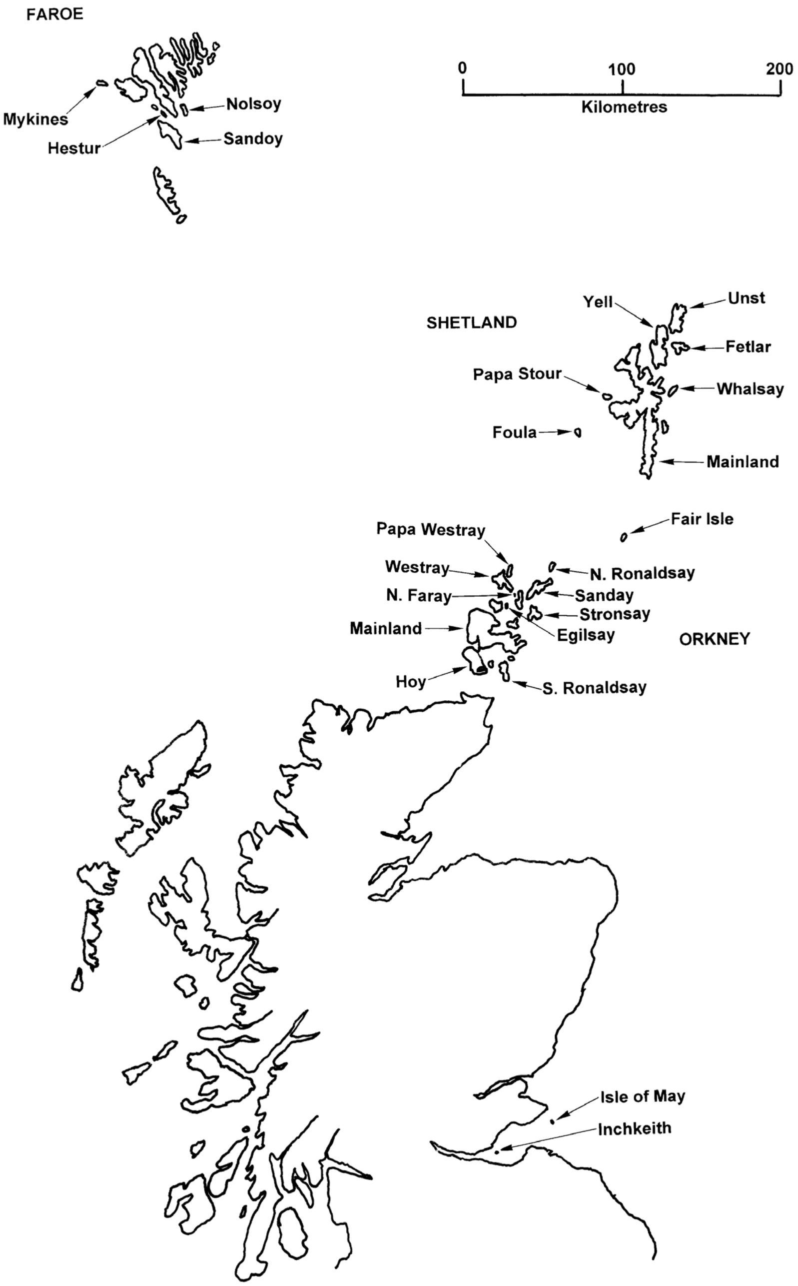

Fig. 2. A map showing the islands sampled in this study.

the present study were selected on the basis of available sample sizes, including the preservation of required dental and skeletal elements. Sample sizes (generally determined by the number of skulls in the collection containing at least M1 and M2 for ageing) ranged from 10 to 30.

Three measurements were taken on each skeleton: length of mandible, width of first upper molar, and length of femur. In this way, the cranium, dentition and postcranial skeleton were all represented. Molar width was measured using digital hand-held calipers, but femur and mandible lengths were determined using a small measuring board with squared paper on the base, the end-points being viewed with a travelling microscope (Festing 1973). The positions and points of measurement are shown in Fig. 3: mandible length excluded the symphysis, while the femur measurement is diaphysis length, excluding the proximal and distal epiphyses which were often lost. Where the distal epiphysis was still attached to the diaphysis, it was gently separated to allow measurement. Mean intra-specimen coefficients of variation (100 × SD/mean), averaged between five specimens each measured 10 times, were: mandible length 0.157; femur length 0.113; molar length 2.261. Sexual dimorphism appears not to be a confounding factor: Davis (1983), studying the same samples, most of which are sexed, found no significant differences in male and female dimensions. In the present analysis, therefore, samples were compared without regard to sexual composition.

To correct animal size for age variation, it was necessary to obtain at least a relative estimate of individual age. This was undertaken by scoring wear stage on the three molars of the upper jaw, using the scale developed by Lidicker (1966). A typical life-span for free-living house mice is approximately 14–18 months, and the eight wear stages defined by Lidicker range from stage 1 (little-worn teeth, aged 0–1 month) to stage 8 (teeth almost worn out, aged 14 months or more). The estimation of wear stage depends on the degree of expansion and fusion of dentine 'lakes' when the teeth are viewed occlusally (Fig. 3c). However, we were unable to age unstained teeth because of the difficulty of visualising the boundary between dentine and enamel. This problem was solved by staining the teeth using hot, strong tea, which darkens the more porous dentine preferentially to the enamel (S. Davis pers. comm.). Following trials, the best results were obtained by soaking 3 standard tea bags in 50 ml of water at 65 °C, dipping the teeth for 10 seconds, and allowing to dry. The absolute ages must, however, be treated with caution. Molar wear rate is influenced by diet, with laboratory mice showing dental stages a few months behind those of free-living animals at the same absolute ages (Lidicker 1966, Davis 1983). Like ours, Lidicker's results were based on free-living mice. Nonetheless, to avoid any danger of extrapolating the absolute age of wear stages from one population to another, we quote our results in terms of wear stages rather than absolute ages.

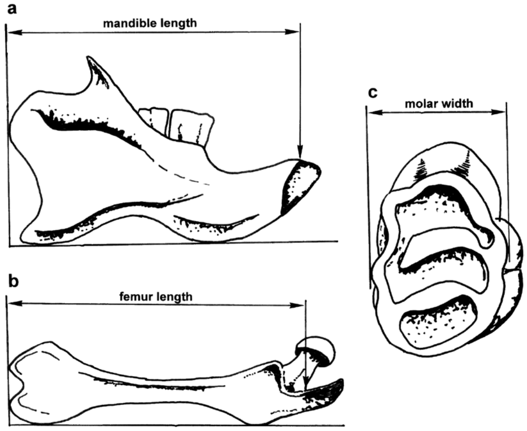

Fig. 3. Measurements taken. (**a**) mandible length, (**b**) femur length, and (**c**) molar width. The position of the measuring device is shown in **a** and **b**. In **b** the distal epiphysis has been removed. Not to scale.

Statistical procedures were carried out in STATISTICA ver. 10. A regression analysis was performed to test associations between *Mus* dimensions and metric attributes of islands. The presence or absence of other rodent species, however, is a non-parametric variable, hence Spearman's rank correlation analysis was performed to test the relationship between these and other variables. Because of the mixture of variable types, multiple regression analysis was not possible, so we performed Spearman's rank correlation on regression residuals. Growth curves were fitted using the von Bertalanffy function, as in Sukumar *et al.* (1988), Derocher and Stirling (1998), and others. The parameters were determined in STATISTICA using a non-linear least-squares method by an iterative procedure.

Results

The pattern of skeletal growth through life was first examined. Mean femur length was plotted against dental wear stage for six islands with the largest sample sizes over all age categories (Fig. 4), and von Bertalanffy equations fitted (Table 2). These show continuous growth, slowing with age in most samples. Nolsoy and Sandoy gave poorer fits than the other sites, partly due to the absence of data in the youngest

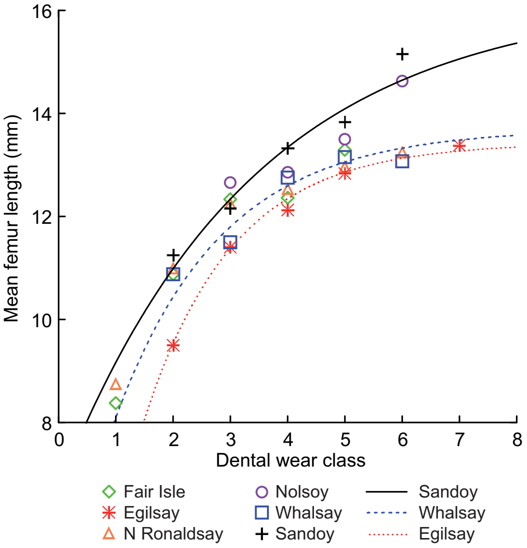

Fig. 4. Mean femur length (mm) plotted against dental wear stage (an index of age) for mice from six islands. Growth curves were fitted using the von Bertalanffy function (*see* text and Table 2).

and oldest age classes, partly because the curve does not flatten off so clearly, a high rate of growth appearing to continue longer. However, as far as our sample sizes allow, size differences between islands appear to be due both to lower birth size (e.g. Egilsay), and to more prolonged growth (e.g. Sandoy) (Fig. 4).

Table 2. Parameters of the von Bertalanffy function for mean femur length *versus* dental wear stage among six island populations of house mice. The fitted equation is $F = F_\infty\{1 - \exp[-k(A - A_0)]\}$ where F = mean femur length, F_∞ = asymptotic femur length, k = a constant, A = age (dental wear stage), A_0 = age at which $F = 0$ (an artificial construct).

Island	F_∞	k	A_0	Explained variation (%)
Fair Isle	13.368	0.700	–0.410	98.3
N Ronaldsay	13.309	0.677	–0.587	99.6
Egilsay	13.538	0.584	–0.086	99.4
Nolsoy	16.238	0.225	–3.403	84.3
Sandoy	17.194	0.234	–2.431	96.8
Whalsay	13.714	0.456	–1.364	93.9

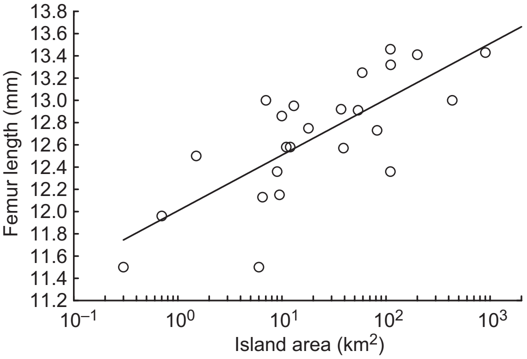

Fig. 5. Mean femur length plotted against island area for Scottish and Faroese *Mus musculus* of age group 4. A least-squares linear regression line is fitted (Femur length = 0.5013log(island area) + 12.006).

To further explore size differences among islands, it was essential to remove the variable of individual age, so subsequent analyses were restricted to age group 4, as this provided the largest combined sample sizes. However, it is first necessary to exclude the possibility that size differences, even within a single age class, might be an artefact of differential tooth wear. If dietary variation occurs among the island populations, mice subsisting on a coarser diet would wear their teeth more rapidly, so that at an equivalent dental wear (e.g. stage 4), two populations could be of different ontogenetic ages and differ in body size for this reason alone. Dietary differences and dental wear rates are unknown for the study populations. However, the body-size differential among the islands is seen throughout life, including the youngest age classes (Fig. 4), suggesting that this effect is not important. If the differences were an artefact of differential tooth wear, size would be expected to be very similar among populations at birth, the curves diverging gradually thereafter as tooth wear increases.

Across the 24 islands, mean femur length at wear stage 4 was correlated with island area ($r = 0.456$, $p < 0.025$). Similarly, mean mandible length was positively correlated with island area ($r = 0.408$, $p < 0.05$). These data indicate that, among the island mice, there is a positive relationship between body size and island area. The correlations were stronger when femur and mandible lengths were regressed against log(island area): $r = 0.756$ ($p < 0.001$), and $r = 0.710$ ($p < 0.001$); respectively (*see* Figs. 5 and 6).

An idea of the magnitude of the effect is given by the percentage differences between the sample with the largest mean femur length (Hoy), and one of the smallest (Isle of May) (cf.

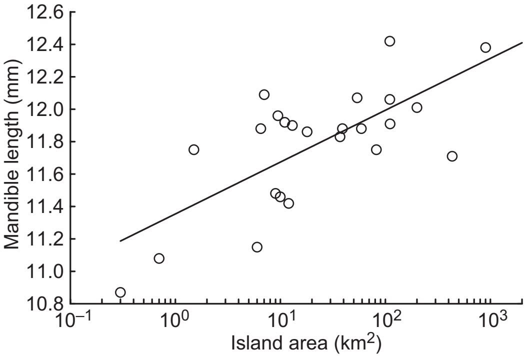

Fig. 6. Mean mandible length plotted against island area for Scottish and Faroese *Mus musculus* of age group 4. A least-squares regression line is fitted (Mandible length = 0.1389log(island area) + 11.3541).

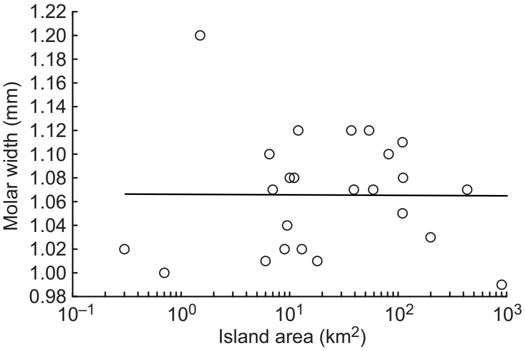

Fig. 7. Mean width of first upper molar plotted against island area for Scottish and Faroese *Mus musculus* of age group 4. A least-squares regression line is fitted (Molar width = 0.0005log(island area) + 1.0665).

Table 1). For mean femur and mandible lengths in age category 4, these two populations differed by 12.5% and 12.1%, respectively. Taking femur length as a rough estimator of body size, and applying a simple cube law, the Hoy and Isle of May mice differ by around 33% in body weight.

Interestingly, and in contrast to skeletal dimensions, molar size showed no correlation with island area or log(island area) (Fig. 7 and Table 3).

Berry and Jakobson (1975) tabulated live body weights and head-and-body lengths for samples of mice from many of the islands studied here. Analysis of their data for 14 islands indicates no statistically significant correlations of either size measure with island area (data not shown). Nor are head-and-body length or body weight correlated with our data on femur or mandible length, where data from the same islands were available (11 islands). It is not considered, however, that these findings undermine the correlation of island area with femur and mandible lengths found in the present study. The live animals measured by Berry and Jakobson (1975) were trapped in various seasons of the year,

Table 3. Correlations between house mouse dimensions and environmental variables for 24 islands of Scotland and Faroe. r is Pearson's correlation coefficient for linear regression, and r_S is Spearman's rank-correlation coefficient. Emboldened values are statistically significant (* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$, two-tailed test). '*Apodemus* + *Microtus*' is the presence of either *Microtus*, or *Apodemus*, or both. '*Rattus*' is the presence of either *R. rattus*, or *R. norvegicus*, or both. 'No. of rodent species' covers all the above but excludes *M. musculus*. 'Residuals' are the residuals from a regression analysis of island area on *Mus* femur length. 'Log(residuals)' are the residuals from a regression analysis of log(island area) on *Mus* femur length.

	Femur length	Mandible length	Molar width	Island area	Residuals*	Log(residuals)*
Island area (r)	**0.456***	**0.408***	–0.278	–	–	–
Log(island area) (r)	**0.756*****	**0.710*****	0.008	–	–	–
Island distance (r)	–0.067	0.073	0.080	–0.09	0.040	0.086
Human population (r)	0.368	0.264	–0.205	**0.917*****	0.056	0.150
Human density (r)	0.122	–0.113	–0.136	0.150	0.060	0.011
Apodemus (r_S)	**0.417***	0.079	0.043	**0.470***	0.147	–0.061
Microtus (r_S)	**0.454***	0.251	0.065	**0.404***	0.145	0
Apodemus + *Microtus* (r_S)	**0.511***	0.187	0.157	**0.560****	0.301	0.036
Rattus (r_S)	0.169	0.247	0.121	**0.397***	–0.012	–0.241
No. of rodent species (r_S)	0.362	0.190	0.079	**0.609****	0.100	–0.201

* *see* text.

and included animals of all age classes. Skeletal dimensions are likely to be much less prone to seasonal variation than body weight, and the skeletons selected in the present study are from a single adult age-class to avoid ontogenetic bias.

We also looked for correlations between mouse size and the presence or absence of possible competitor species. The terrestrial mammal faunas of Shetland, Orkney and the Faroe Islands are limited (Harris & Yalden 2008, Berry 2009), but four species (which, like the house mouse, are almost certainly introduced: Corbet 1961) can be considered possible competitors: the wood mouse *Apodemus sylvaticus* the Orkney vole *Microtus arvalis orcadensis*, the brown rat *Rattus rattus* and the Norwegian rat *Rattus norvegicus*. The latter two species are also potential predators of the mice. The occurrence of these species on the study islands is shown in Table 1. The smaller-sized *Mus* populations tend to be on islands lacking the other species, and Spearman's rank correlation coefficient (r_S) indicated a weak, positive association between mean size of house mouse (indicated by femur length) and the presence of the smaller rodent species, whether treated separately or combined (Table 3). For the presence of rats (either species), Spearman's rank correlation coefficient is non-significant. To test whether the presence of *Apodemus* or *Microtus* has an effect on *Mus* size independent of island area, we first evaluated Spearman rank correlations between the presence of either species and island area, and found that the presence of each species (and also the presence of rats) is positively correlated with island area, i.e. larger islands are more likely to contain potential competitor species. Since the presence or absence of these species could not be entered into a multiple regression analysis along with island area due to non-normal distribution, we calculated Spearman' rank correlations between rodent presence/absence and the regression residuals of *Mus* size *versus* island area and log(island area). No correlation between any pair of variables was found.

We further regressed all house mouse dimensions separately against distance of the island from the Scottish mainland, and found that none is correlated with this variable (Table 3).

We finally tested for association between mouse size and human population density, in view of the frequently commensal nature of the island house mouse populations. Human population figures were taken from the 1961 UK census and from 1966 data given by West (1972) for the Faroe Islands, the closest available years to the collection dates of the mouse samples. We regressed mouse dimensions separately against total human population of each island, and population density per square kilometre (Table 1). No correlations were detected (Table 3).

Discussion

Explanations for the observed trend

Since the 'island rule' predicts that small mammals increase in size on islands relative to their mainland conspecifics, a simplistic expectation might be that as island size decreases, so might this effect be enhanced. This prediction is not borne out by our data for the Scottish and Faroese mice.

However, the observed changes could correspond to the ascending limb of Heaney's (1978) more sophisticated parabolic curve for the relationship of body size to island area (Fig. 1). According to Heaney's model, at small island areas, body size is positively correlated with area, as a result of food limitation being the dominant selective force even for small mammals. In the squirrels studied by Heaney, the curve flattened and then turned downward (negative correlation of body size to island area) at island areas of approximately 10^4 km^2 and above. House mice are considerably smaller in body mass than *Callosciurus prevosti* studied by Heaney, but the Scottish islands studied here also have a much smaller upper size limit than his southeast Asian ones — the largest is less than 1000 km^2 in area. It is therefore not unexpected that they should all fall within the region of positive correlation with mouse size.

Resource limitation

In a theoretical study, Case (1978) showed that, in general, reduction in the mean amount of available food should lead to evolutionary reduction in body size, and this could account for size reduction on islands. McNab (2010) has championed resource availability as the chief determinant of mammalian body size on islands and elsewhere. If resource limitation is the chief cause of body size variation among the mouse populations, we need to examine in more detail the feeding niche of the mice. Despite the fact that the house mouse is commensal with humans on most of these islands, we found no correlation of mouse size with either human population size (beyond the effect of island area) or density on the islands.

Although the commensal populations may be living in a relatively protected, high-nutrient habitat for much of the year, this does not exclude episodes of natural selection during which resource limitation may shape the body size distribution of the mice. First, studies of stomach contents and droppings make clear that even in commensal populations, agricultural grain or other products is by no means the sole food of the house mouse. Various arthropods appear to be the preferred food, although wild and crop plants are important, especially in winter (Berry 1968, Berry & Tricker 1969, Ward 1981, Berry & Bronson 1992, and studies reported therein).

Second, the corn ricks in which most of our mice were captured do not give a fully reliable winter environment for the mice — they may be threshed at any time of year, forcing out the mice, or may not even be built in a particular year (Berry & Jakobson 1975). Finally, even on inhabited islands, many mice are not commensal (e.g. observations on Fair Isle: Berry & Tricker 1969), so selection under 'wild' conditions will affect the overall island gene pool.

Mortality in the island mouse populations is high, especially during the winter months. Among wild-living mice on the island of Skokholm (Wales), for example, 40% of adults die during each two-month period in the summer, and an average of 55% every two months in the winter (Berry & Jakobson 1975). These authors conclude: 'this implies that individuals must live close to their physiological limit at all times of year'. In a bad winter, up to 90% of the total population can die (Berry 1968). Berry (1981) indicates that exposure to cold is the commonest cause of death, rather than starvation *per se*, although food shortage is likely to cause periodic problems. In fact, these two factors are linked, in that death from the cold implies a physiological inability to maintain a positive energy balance.

It is therefore likely that even on inhabited islands where commensalism is a major element of house mouse ecology, there is a sufficient element of wild living, both in the long-term history of mainly commensal populations, and in populations living away from human habitation, for resource limitation to influence mouse size in the island as a whole. In addition, although human density is not correlated with island size, it may nonetheless be the case that commensal mice on small islands with low human population, are more likely to suffer resource limitation than those on larger, more heavily populated islands. Resource limitation therefore seems a plausible explanation for the observed reduction of mouse size on smaller islands.

Inter-specific competition and predation

Schoener's (1969) models provided a theoretical expectation that the body size of species on islands should be inversely related to the intensity of interspecific competition. In Heaney's (1978) proposed domain of negative correlation of intraspecific body size with island area, predicted among larger islands, he postulated interspecific competition and/or predation as the major forces reducing body size in small mammals as biotic diversity increased (Fig. 1). For competition, this is based on the idea that a generalist species should reduce in size when sympatric with more specialist competitors; small mammals tend to be larger on islands where the absence of competitors allows them to occupy a broader feeding niche. Several empirical studies have found an inverse correlation between small mammal body size on islands, and the presence or diversity of competitors (Lawlor 1982, Yom-Tov *et al*. 1999, Lomolino *et al*. 2012). However, the response of individual species may differ. Angerbjörn (1986) found that the body size of *Apodemus sylvaticus* on European islands is lower if competitor rodent species are present, suggesting competitive displacement, but the competitor species themselves become larger. White and Searle (2007) found that common shrews (*Sorex araneus*) were greatly reduced in body size on the one Scottish island where the smaller pygmy shrew (*S. minutus*) was absent.

Among the Scottish house mice there appears to be no correlation between residuals of body size and the presence of competitor species when the effect of island area on rodent diversity is removed. This suggests that either competition between the other species and *M. musculus* is minimal, or else perhaps that the rodents have not been on the islands long enough for competitive displacement to have taken place. Not only feeding-niche separation may drive such displacement, but also selection for success in agonistic interactions. It has been found that successful reproduction in house mice is disrupted by the presence of competitor rodents (Lidicker 1966, Berry & Tricker 1969). Large body size could be selected for in such circumstances. Smirin and Smirin (1999) showed that house mice (*M. musculus*) are extremely aggressive towards wood mice (*A. sylvaticus*), and that larger individuals are the most successful in agonistic encounters. Since *A. sylvaticus* is the main competitor to *M. musculus* on the Scottish islands, this could drive size increase in the latter species, though it is already larger on islands where *A. sylvaticus* is most likely to be present, because of the common causality of island area.

Concerning predation, it is generally considered that for small mammals, smaller body size is advantageous as it enhances crypsis and the ability to escape into small hiding-places. Angerbjörn (1986) found that the body size of *A. sylvaticus* on European islands was reduced in the presence of predators. On the other hand, Lomolino (1985) challenged the general assumption that small mammals avoid predation by being small, or that they increase in size in response to predator release. Amori and Massetti (1996), reviewing body size of various Mediterranean island small mammal species, found no relationship to the presence or absence of ground or avian predators.

For the Scottish mice, we have insufficient data reliably to determine the magnitude or selective impact of predation. Birds of prey are the most likely predators of small mammals on islands. However, Berry (1981) and Berry and Bronson (1992) indicated that house mice are rarely taken by avian predators on the islands under study, so this is unlikely to be a significant selective force. None of islands sampled in this study support wild mammalian carnivores. The impact of domestic cats, or of rats, is uncertain. Cristaldi and Amori (1988) indicated that rats are significant predators of smaller mammals on Mediterranean islands, and attributed the exclusion of *Mus musculus* from the island of Filicudi to the presence of rats. Rats (mainly *Rattus norvegicus*) occur on some of the study islands (Table 3), and the mouse population of Bordoy (Faroe) became extinct between 1915 and 1920 after rats colonised the island (Berry *et al*. 1978). It is therefore theoretically possible that on islands where rats and mice co-exist, rat predation could impose a selective force on the body size of the mice. However, no correlation with mouse size is evident (Table 3). For house mouse in particular, Smirin and Smirin (1999) made the interesting observation that nomadic individuals of house mice (the most likely to be predated) contribute little to reproduction, so body-size selection resulting from predation may be limited.

Climate

The possibility that the body size variation in the mice is thermoregulatory in origin should be considered. This would predict that mice living in colder habitats would have larger body size, reducing heat loss because of smaller surface area to volume ratio. However, there has been much dispute about the validity or otherwise of ‘Bergmann’s Rule’ (positive correlation of size to latitude) and the proposed thermoregulatory explanation for it where it exists (Geist 1987, Lister 1992, McNab 2010). Berry and Jakobson (1975) found an ‘approximate fit to Bergmann’s Rule’ among four widely-separated wild-living populations of house mouse [N Faray, May, Skokholm (Wales) and Macquarie (Australian sub-Antarctic)], while tropical populations are generally of smaller body size than temperate and high latitude ones (Berry & Jackson 1979). However, there was no correlation with climate among commensal populations (Berry & Jakobson 1975). White and Searle (2007) found an effect of latitude, in a 'Bergmannian' direction, on body size of common shrews on Scottish islands, as did Yom-Tov *et al.* (1999) on *Rattus exulans* in the Pacific. Conversely, Renault and Michaux (2007) found an anti-Bergmannian trend among mainland European wood mice (*Apodemus sylvaticus*) — smaller individuals to the north. Laboratory experiments have demonstrated selection for increased body size over several generations of cold-reared mice, apparently because of its correlation to fecundity (Barnett & Dickson 1989). There is also the possibility that body form may be directly affected by the influence of temperature: Harrison (1959), for example, showed that body weight and tail length in house mice are to some extent influenced by temperature during ontogeny.

Climatological data for all of the sampled islands were not available in the current study, and in any case, as pointed out by Berry and Jakobson (1975), local climatological data do not necessarily give a good idea of the temperatures experienced by mice in their microhabitats. Nonetheless, it seems unlikely that temperature variation among the islands is sufficient or sufficiently regular to account for the changes in size. In data given by Berry and Jakobson (1975), the mean temperature of the coldest month at stations on each of the four main island groups in the present study differed by less than 1 °C: Torshavn (Faroe) 4.1 °C, Baltasound (Shetland) 3.5 °C, Kirkwall (Orkney) 3.8 °C and Isle of May (Firth of Forth) 3.3 °C. In each case also, the annual duration of mean temperature below 5 °C was similar at three to four months. Nor is there any reason to suppose that the larger islands within each group (with the larger mice) are generally colder than the smaller ones, as would be required by this model.

Genotypic/ecophenotypic basis

A genetic basis for adaptive body-size differences among the island mice is quite plausible. Although founder effect has played an important role in determining the genetic composition of the island populations, strong natural selection has been shown to rapidly modify the island gene pool, especially under conditions of extreme physiological stress (particularly by cold) (Berry *et al.* 1987). On Skokholm (Wales), the genetic constitution of the mice was shown by these authors to change significantly over a period of just a few months. Therefore, the relatively short period of evolutionary time (perhaps only a few tens of years in most cases) since the mice colonised the islands is no bar to adaptive genetic modification, especially in relatively simple, multigenic characters like body size, for which house mouse populations contain a great deal of variance (Crowcroft & Rowe 1961). The Skokholm mice were about 25% heavier than their mainland ancestors after ca. 60 generations of isolation, and this increase could have occurred much earlier (Berry 1964). Moreover, body size in *Mus musculus* has been shown to be strongly heritable (Roberts 1981).

Even so, a non-genetic, ecophenotypic component is also plausible as a contributing or major factor for the body size variation among some or all of the populations. Resource limitation can cause developmental dwarfing, and the mean body size of house mice has been shown to be rapidly adjustable ecophenotypically as well as genetically (Berry & Jakobson 1975).

The correlation of mandible and femur length with island size in our mouse populations contrasts with the lack of correlation in molar width. Molar size, in other words, is more stable among these populations than skeletal size. It is a common observation in many mammalian species that tooth size varies less among populations than postcranial size, so that 'dwarfed' populations tend to have a higher ratio of tooth size to postcranial size (Gould 1975, Fortelius 1985). Between-species variation, on the other hand, tends to revert to isometry between tooth and body size (Lister 1996).

A simple explanation for lesser intraspecific variation in tooth size is the tighter genetic and developmental control of teeth as compared with that of the bony skeleton. Although teeth may take a significant length of time to complete their formation, their size (especially their length and width) is fixed relatively early in their development, whereas bony skeletal elements grow over a longer period, and are therefore more susceptible to influence by environmental factors. Although there are simple allelic changes known to influence molar size in house mice (Grüneberg 1965), molar size in free-living populations appears in general to be more strongly canalized (Waddington 1942) than skeletal size. It has therefore been suggested (Lister 1995) that body size change with lesser or no tooth size change can be used with caution as a marker for ecophenotypic, as opposed to genetic, change in fossil samples. The variation in skeletal size, but not molar size, among our house mouse populations is consistent with this idea, which could be experimentally tested by examining the effect of different feeding regimes on tooth and body size. It may be more realistic, however, to suggest that in cases without direct information of this kind (e.g. the fossil record), body size change without dental size change could imply *either* an ecophenotypic effect, *or* selection on simple gene frequencies; in any case a rapid effect. But the adaptive re-equilibration of skeletal and dental proportion implies a longer-term, more entrenched genetic and developmental adjustment. This would explain why an offset between dental and skeletal size is commonly found between populations (or domestic breeds) of a species, while between species they are isometric.

Similar patterns have been encountered in other studies of island rodents. Yom-Tov *et al.* (1999) found that in *Rattus exulans* from various Pacific islands (*see* below), skull length is correlated to body size, but tooth measurements are not. A latitudinal gradient, seen in skull length, is also not seen in molar dimensions. In a study of wood mouse (*Apodemus sylvaticus*), Renault and Michaux (2007) found that across mainland Europe (where mice have been established for at least 16 000 years), the mandibles and molars provide very congruent patterns of size variation. On islands, however, a 'mosaic' pattern is frequently encountered. For example, on Ibiza, where body and mandible size were most greatly enlarged, molar size remained unaltered; mice colonised the island only 5000 years ago. Renault and Michaux (2007) also related morphology to mtDNA clade membership and found a stronger genetic effect on molar shape than on mandible shape. Within populations of the mice, also, mandible size appeared to be correlated with body length whereas molar size is not. The authors conclude that the possibility of change during growth may make mandible shape more prone to change in response to environmental factors than molar shape. Like us, they suppose that response time for molars should be slower than for mandibles, which could vary rapidly due to various environmental factors.

This conclusion appears to be in opposition to that of Pergams and Ashley (2001), who suggested that the very magnitude and rapidity of size change in introduced island rodent populations indicated a genetic rather than an ecophenotypic basis. Rapidity of change, however, should favour an ecophenotypic explanation, or at least does not distinguish between it and very rapid genetic change. Concerning magnitude of the effect, the observed or likely degree of phenotypic flexibility among individuals of the parent species can provide a yardstick: extremes of size beyond the norm are indeed likely to have a genetic underpinning (as suggested for extreme dwarfing of large mammal species: Lister 1995).

Changes more complex than size, if not merely the allometric consequences of size change, also point to a genetic basis (Lister 1992). Thus Renault and Michaux (2007) noted significant shape change in molars of *Apodemus sylvaticus* on Sicily. The Sicilian wood mice belong to a distinct mitochondrial subclade which diverged from the mainland Italian lineage at least 800 kyr ago. The species studied by Pergams and Ashley (2001) (*Rattus rattus* and *Peromyscus maniculatus* from the California Channel Islands) also showed cranial changes in the island populations that did not appear to be allometric in origin, indicating a genetic basis.

Comparison with other studies

The above discussion suggests that resource limitation on the smaller islands is responsible for the positive correlation of house mouse body size to island area observed in this study. This corresponds to the ascending (resource limited) limb of Heaney's parabolic model (Figs. 1 and 8a), and suggests that the descending (competition/predation-limited) limb, observed by him in southeast Asian tricoloured squirrels, is not realized in all cases.

Heaney's (1978) model, together with the results of Lomolino (1985), also predicts that the smaller the mammalian species, the smaller the islands needed to show the domain of positive correlation resulting from food limitation. In an attempt to test this prediction, available datasets for island area and small-mammal body size were collated (*see* Fig. 8). Several of the studies are on species of similar body size: *Peromyscus maniculatus* on islands of western Canada (Melton 1982); *Apodemus sylvaticus* on islands of the Mediterranean (Sara & Casimento 1995, Renault & Michaux 2007, Angebjörn 1986); and *Mus musculus* in Scotland and Faroe (present study). Each of these species in life is of similar size, typically 7–10 cm in head and body length (excluding tail). The fourth species, *Callosciurus prevosti* from southeast Asia (Heaney 1978) is considerably larger at ca. 25 cm head and body length. In addition, there are studies on common shrew (*Sorex araneus*) of the Scottish islands (White & Searle 2007), and *Rattus exulans* in the Pacific (Yom-Tov *et al*. 1999), which are discussed but not shown in Fig. 8 because raw data are not available. Further examples of trends in relation to island size are given by Lawlor (1982) and Lomolino (2005: table 3).

Heaney's *Callosciurus* study produced the most convincing parabolic curve, inflected at island sizes of around 10^4 km^2 (Fig. 8a). For Mediterranean *A. sylvaticus*, the largest single data set is that of Renault and Michaux (2007)

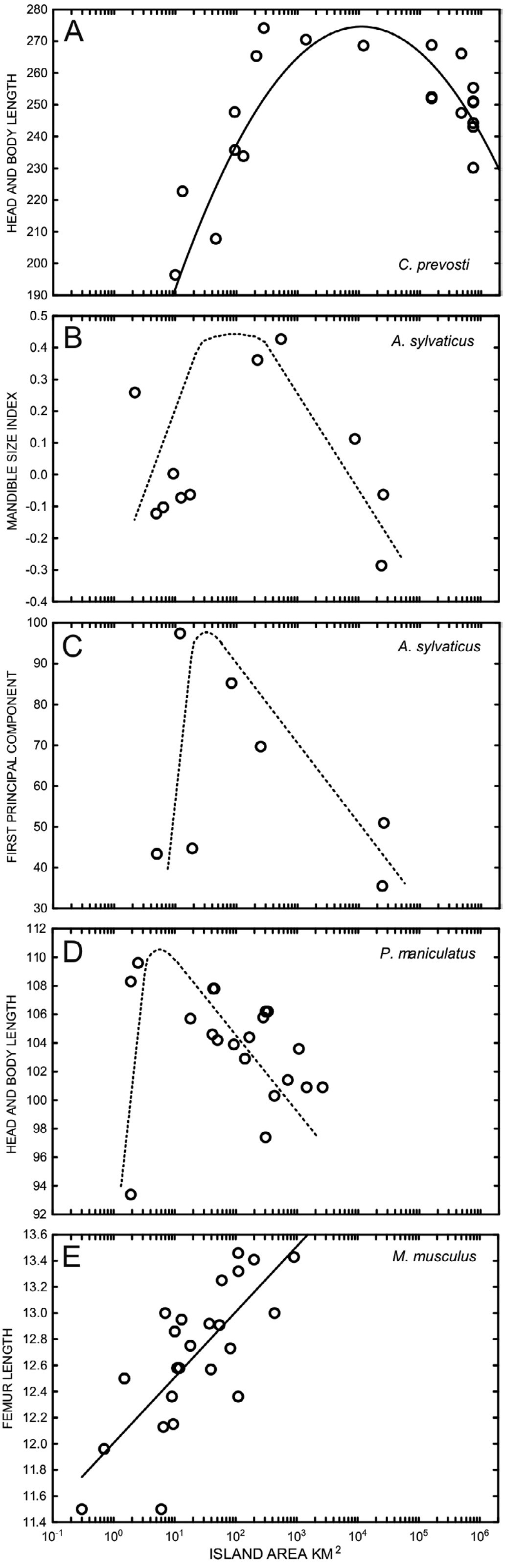

Fig. 8 [on the right]**.** Body size in published studies of different rodent species across various island groups. (**A**) Squirrels, *Callosciurus prevosti,* in SE Asia (quadratic fit obtained by Heaney 1978); (**B**–**C**) wood mice, *Apodemus sylvaticus*, in the Mediterranean (**B**: Renault & Michaux 2007; **C**: Sara & Casimento 1995); (**D**) deer mice, *Peromyscus maniculatus* in western Canada (Melton 1982); (**E**) house mice, *Mus musculus,* in Scotland and Faroe (this study, the least-squares regression of Fig. 5 is shown). In **B**–**D** hypothetical inflected curves have been drawn by eye. The studies of Sala and Casimento (1995) and Renault and Michaux (2007) are not entirely independent as the two largest islands (Sicily and Sardinia) are in common between the studies (of 7 and 12 islands respectively). The two papers do not use commensurate variables that would allow the studies to be pooled.

(Fig. 8b), not tested statistically but suggestive of a parabolic relationship with an inflexion around 10^2 km^2. Sara and Casimento's (1995) data set of the same species (Fig. 8c) shows a negative slope but with outliers of very small size on two of the smallest islands, around 10^1 km^2. Angerbjörn (1986) also regressed *A. sylvaticus* size against island area for a (different) group of Mediterranean islands, but although a line of negative slope was obtained, the relationship was not significant, probably because sample size of islands was small (7), and the range of island sizes restricted (ca. 10^2–10^4 km^2). Taken together, however, these three studies are strongly suggestive of a parabolic relationship in Mediterranean *A. sylvaticus* with an inflexion at island sizes of around 10^1–10^2 km^2.

The *P. maniculatus* study (Fig. 8d) reveals a negative correlation of body size with island area, but there is an outlier of small size at small island area. This is too limited for statistical interpretation, but could hint at the beginnings of the ascending (resource limited) limb of the Heaney model, with an inflexion around 10 km^2. Indeed, Melton (1982) described the *P. maniculatus* trend as a negative correlation, but with the very small mice of the smallest island (Table Island, 1.9 km^2) regarded as anomalous and resulting from 'food scarcity'.

The study of White and Searle (2007: fig. 5) on Scottish *Sorex araneus* shows negative correlation of body size with island size over an island size range of around 4–1600 km^2, but with an outlier of very small body size on an island of 4.5 km^2 (Shuna), although the authors suggest this may be due to competitive release due to the absence of the smaller *S. minutus*, rather than food limitation.

If the parabolic curve proves common to these examples, the domain of positive correlation would appear to be shifted toward smaller island sizes the smaller the mammal species: from *S. araneus*, to *A. sylvaticus* and *P. maniculatus*, to *C. prevosti*, corresponding to the prediction of the resource-limitation model.

However, this pattern is sharply contradicted by that of *Rattus exulans* (ca. 12–15 cm head and body length) in the Pacific. Yom-Tov *et al.* (1999) found an inverse relationship of body to island size in each of three island groups in the Pacific, statistically significant for the Solomon Islands and almost so (p = 0.06–0.07) for New Zealand and Hawaii. The range of island sizes for the Solomons and Hawaii extended down to 600 km^2 and 4 km^2 respectively, but for New Zealand down to 0.1 km^2, effectively excluding the possibility of a missing 'ascending limb' of positive correlation, despite a larger body size than *A. sylvaticus* and *P. maniculatus*.

The Scottish and Faroese *M. musculus*, conversely, are shifted in the opposite direction (Fig. 8e). Despite being of similar body size to *A. sylvaticus* and *P. maniculatus*, they show a domain of positive correlation extending to much larger island sizes, up to the limit of the study at 900 km^2. Two possible explanations, not mutually exclusive, are as follows. First, in these exposed northern islands, biotically depauperate compared with those of the other case studies, resource limitation remains a potent selective force up to larger island sizes, shifting the curve rightward in Fig. 8e.

Second, competition may have varying effects in different situations. Angebjörn (1986) showed that for *A. sylvaticus*, competition is a particularly potent size-depressing factor, apparently outweighing resource availability in several European island groups. This effect may therefore have pushed down body size of *Apodemus*, *Peromyscus* and *Callosciurus* in the studies cited here (Fig. 8a–d). Conversely, competition appears not to have influenced the body weight of *M. musculus*, or else took the form of agonistic interaction which tended to preserve large size.

Conclusion

The positive correlation of mouse size with island size, found in this study, is unusual among examples of island small mammals. Inverse correlations are common (Lomolino 2012), with a parabolic relationship occasionally seen. Thus, although small mammal species "show no consistent tendency to either dwarf or grow larger on islands" (Raia *et al* 2010), it is striking that so many of these studies do show a relationship of some kind: within a species and island group, size variation is rarely if ever stochastic, and usually varies deterministically with island area. In contrast, clear relationships to island area are not seen in the size variation (commonly dwarfing) of large mammals (Lomolino *et al*. 2012).

The differing patterns presumably result from the varying biotic and abiotic characteristics of different islands and island groups, the biology of the species in question, and possibly an element of contingency (Meiri *et al* 2011). In addition to potential causal factors discussed above, many taxon-specific factors have been suggested by different authors, such as resource clumping (Lawlor 1982) and aridity (Ganem *et al*. 1995), and the outcome in a given case will result from a complex interaction of these factors.

Further case studies, incorporating different combinations of these variables, should enable us to elucidate and quantify the contribution of various intrinsic and extrinsic factors to determining the body size of island mammals.

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