

On size and area: Patterns of mammalian body size extremes across landmasses

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Summary

We describe a biogeographic pattern in which mammalian body size extremes scale with landmass area. The relationship between the largest and the smallest mammal species found on different landbridge islands, mountaintops and continents shows that the size of the largest species increases, while that of the smallest species decreases, with increase in the area of the landmass. We offer two possible explanations: (1) that the pattern is the result of sampling artefacts, which we call the 'statistical artefact hypothesis', or (2) that the pattern is the result of processes related to the way body size affects the number of individuals that a particular species can pack in a given area, which we call the 'area-scaling hypothesis'. Our results point out that the pattern is not a statistical artefact resulting from random sampling, but can be explained by considering the scaling of individual space requirements and its effect on population survival on landmasses of different area.

Keywords: body size; islands; macroecology; mammals; population density; scaling

Introduction

A pressing challenge for ecologists and evolutionary biologists is to develop a conceptual and quantitative framework bringing together disciplines traditionally viewed as distinct, such as physiology, ecology, biogeography and macroevolution (e.g. Brown and Maurer, 1987, 1989; Ricklefs, 1987; Ricklefs and Schluter, 1993; Brown, 1995; Marquet *et al.*, 1995). Much of this quest for a synthetic framework has been based on empirical statistical patterns relating body size with physiological, ecological and evolutionary traits (e.g. Lawton, 1990; Blackburn *et al.*, 1993; Brown *et al.*, 1993; Brown, 1995). There are at least two reasons why body size has been so widely used. First, body size is an easy-to-measure trait for which there are large datasets available (e.g. Dunning, 1993; Silva and Downing, 1995a). Secondly, and more importantly, body size is known to be related to a variety of physiological, ecological and evolutionary characteristics of organisms (e.g. Peters, 1983; Calder, 1984; Schmidt-Neilsen, 1984; Bonner, 1988), hence body size patterns can in principle be explained by the interaction among processes acting at these three levels.

Body size patterns have usually been analysed as simple allometric relationships, fitting straight lines after appropriate transformation of variables. However, recent empirical analyses (Marquet *et al.*, 1995; Silva and Downing, 1995b) and theoretical models (Brown *et al.*, 1993) have pointed out that the allometric scaling of several ecological attributes of species, such as population density, may not be monotonically related to body size. Population density has been shown to be a peaked function of body mass (Marquet *et al.*, 1995; Silva and Downing, 1995b), with medium-sized species (of about 100 g) attaining on average high densities, which then decrease towards larger and smaller body sizes. Similar patterns have been found for other ecological variables, such as population energy use (Marquet *et al.*, 1995) and population variability (Pimm, 1992). In the latter

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case, medium-sized species are on average less variable in numbers. Population density and variability are two of the major determinants of extinction probability (e.g. MacArthur and Wilson, 1967; Leigh, 1981; Diamond, 1984a; Goodman, 1987; Pimm *et al.*, 1988). Since probability of extinction decreases with increasing population size and decreases with decreasing variability, it seems reasonable that medium-sized species would be less prone to go extinct. Indirect support for this hypothesis comes from the examination of body size frequency distributions made by Maurer *et al.* (1992). These authors hypothesize that the characteristic shape of these distributions, skewed towards large sizes and with a large number of medium-sized species, is the result of body size related biases in extinction probabilities.

In this paper, we present a new pattern, this time relating the presence of species in landmasses of different area to their body size, which provides a more direct test of the idea that intermediate-sized species are less prone to extinction. How would we expect this hypothesis to play itself out in the distribution of body sizes on islands? We would expect that both the largest and smallest species, given their low population densities and higher population variability, would be able to persist only on very large landmasses. On these areas, total population sizes would be sufficient to prevent extinction even though population density could still be low. On small landmasses, medium-sized species should predominate. Thus, the probability of a particular species being found on any given landmass will depend upon its body size and the size of the landmass. We investigate these ideas to try to expand the scope of body size related patterns and to place them into the framework of island biogeography theory (MacArthur and Wilson, 1967). We return to this in the Discussion.

The pattern

As we are interested in the relationship between extinction proneness, body size and area, we need to use data on landmasses that have been successfully colonized and whose actual fauna is mostly the result of subsequent extinctions. In this way, extinction processes as related to body size and landmass area are emphasized, while patterns resulting from lack of dispersal are minimized. These requirements are fulfilled by mammals found in landbridge islands, mountaintops and continents, whose actual species compositions are mainly the result of a selective extinction process associated with relaxation phenomena (e.g. Diamond, 1984a,b). The processes and theory discussed here are not restricted to the realm of 'true' islands, but to any landmass from isolated fragments of habitat up to continental landmasses. Continents have speciations as well as extinctions. Our arguments are based on extinctions and that is the reason why we selectively included relaxation faunas. Nonetheless, whether a species gets to its location by colonization, fractionation or speciation, it must still resist stochastic extinction, so our basic argument should hold. Furthermore, the absence of a particular body size species in a continental landmass is most likely to represent selective extinction rather than lack of colonization, thus fitting our criteria for including them in the analysis.

The relationship between the largest and the smallest mammal species in different landbridge and mountaintop islands and continents is shown in Table 1. Note that as the size of the largest species within an insular fauna increases, so does the landmass area. Furthermore, as the size of the smallest species decreases, the area of the landmass where it is found also increases. These patterns are highly significant within archipelagoes, across continental landmasses, and when all cases are analysed jointly in one general regression. A plot of both general regressions (Fig. 1) shows that the regression lines intersect at $\log_{10}(W) = 1.71 \pm 0.2$ (s.e. calculated using standard error propagation techniques; Taylor, 1982). There are other ways of representing the same pattern. One alternative is to use area as the independent variable. However, we use body size as the independent variable

Table 1. Statistics for the regressions between landmass area and species' maximum and minimum body size

Landmass type	<i>n</i>	Slope maximum size	Slope minimum size	Source
Mountaintop islands (American Southwest)	28	0.84 (0.49)***	-1.44 (0.29)**	Patterson (1984)
Mountaintop islands (American Southwest)	23	0.76 (0.51)***	-0.86 (0.49)***	Brown (1978)
Landbrige islands (Sea of Cortéz)	20	0.62 (0.66)***	-5.19 (0.34)***	Lawlor (1983)
Continents	7	0.68 (0.72)**	-1.73 (0.28) n.s.	Rusler (1987), Maurer <i>et al.</i> (1992)
Total (<i>I</i> = 1.71)	78	1.17 (0.62)***	-2.74 (0.47)***	
Subtotal ^a (<i>I</i> = 1.72)	71	0.79 (0.37)***	-1.73 (0.34)***	

^a Statistics computed after excluding data points for continents.

I = body size at the point of intersection of the two regression lines; the proportion of variance explained by the regression is given in parentheses.

** *P* < 0.02; *** *P* < 0.0001; n.s., *P* = 0.22.

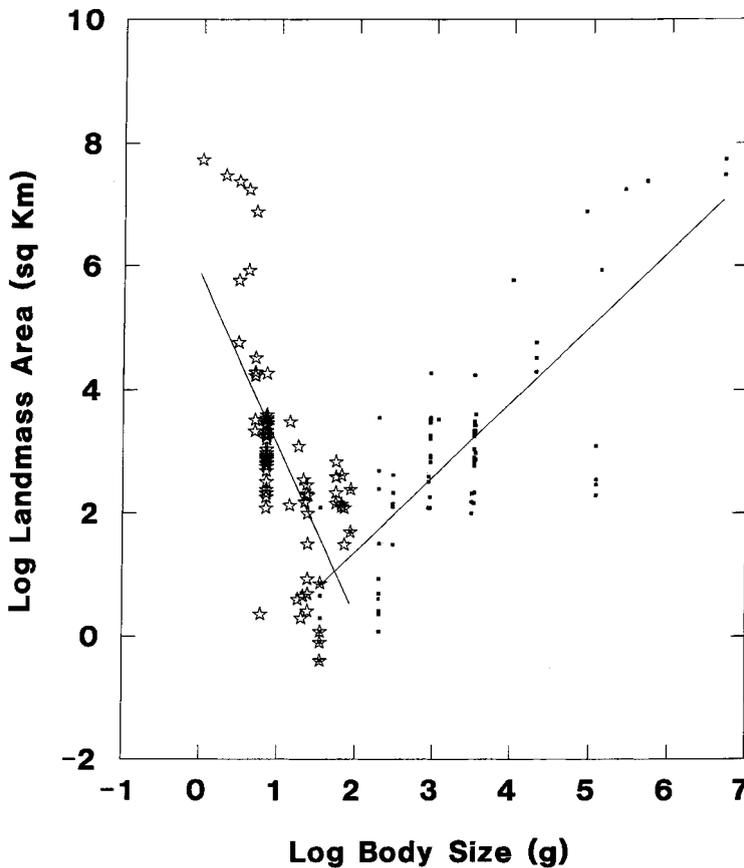


Figure 1. Relationship between landmass area and species' maximum (solid squares) and minimum (stars) body size. Sources of data provided in Table 1.

because one of the explanations for the pattern (see below) is framed in terms of the relationship between ecological traits – at the level of organisms and populations – and body size. Thus the use of body size as the independent variable in our analyses is justified to the extent that we are not looking at landmass area *per se*, but how body size affects the persistence or presence of a particular species in landmasses of different area.

The hypotheses

The pattern shown in Fig. 1 deserves explanation. We can offer two hypotheses regarding the processes underlying the observed distribution of body size extremes across landmasses. Our first hypothesis is that the pattern is the result of sampling artefacts, which we call the ‘statistical artefact hypothesis’. Our second hypothesis is that body size affects the number of individuals which a particular species can pack in a given area, and which leads to the pattern. We call this the ‘area-scaling hypothesis’.

The statistical artefact hypothesis

Because species richness and area are positively correlated (MacArthur and Wilson, 1967), larger landmasses have a higher probability of picking up species with extreme values of body size. In statistical terms, the pattern presented in Fig. 1 is qualitatively predicted by the theory of order statistics (Balakrishnan and Cohen, 1991). The smallest and largest body sizes present in a landmass with S species, is analogous to the first- and last-order statistic of a sample of size S coming from a particular distribution or pool of body sizes. In particular, when $S = 1$, the expected first-order statistic equals the expected last-order statistic and both correspond to the first moment of the distribution from where the samples were drawn (Balakrishnan and Cohen, 1991). In terms of the pattern presented in Fig. 1, this means that the intersection of the two regression lines is expected to be at the mean value of the pool.

Given that the appropriate pool for this worldwide relationship (the body size distribution of all species of mammals worldwide) is not well known, as an alternative test of this statistical effect, we redo the analysis including only the mountaintop islands of Southwestern North America and the landbridge islands in the Sea of Cortéz, California, excluding data from continents (see Table 1). For these archipelagoes, we assumed the North American mammalian biota, listed in Brown and Nicoletto (1991), to be the pool. For each landmass, we drew a random sample equal in size to the observed number of species for that landmass. Then, for each landmass we took the smallest and largest body sizes in our sample and subsequently regressed these values against the known area of each landmass. In this way, we obtained the slopes for the regression of landmass area versus the smallest and largest body sizes and the intersection point of both regression lines. This bootstrap procedure was repeated 1000 times; the results are shown in Fig. 2. In all cases, the observed values were outside the central 95% of the distribution derived by random sampling. This suggests that the pattern observed in Fig. 1 does not correspond to the passive effect of random sampling, thus rejecting the sampling artefact hypothesis.

The area-scaling hypothesis

As stated earlier, species of mammals of large and small body size are characterized by low population densities and high population variability. In turn, these effects imply that to persist these species will require large areas to sustain total population sizes, large enough to avoid extinction. Under this hypothesis, we believe that the observed pattern in body size extremes across landmasses of different size is the result of how minimum area requirements for species survival scales with body size. According to this hypothesis, medium-sized species require less area to

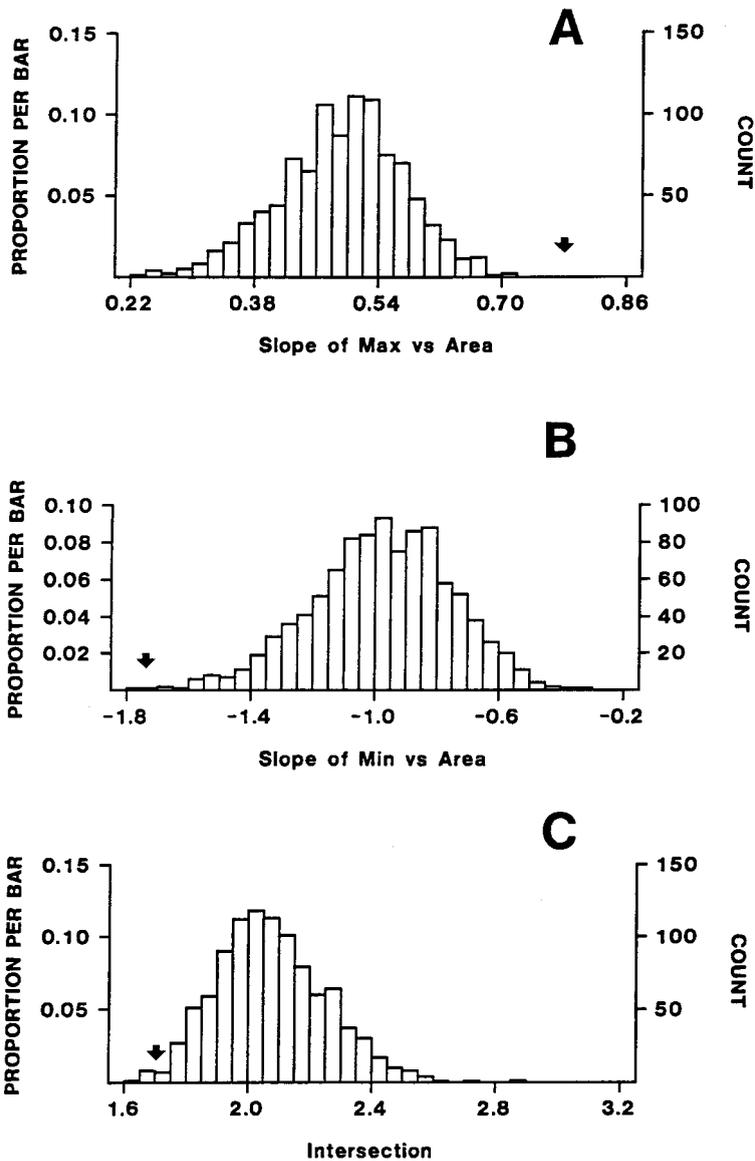


Figure 2. Results of the bootstrap analysis. Frequency histograms show the distribution of values for (A) the slope of the regression between the largest species in a biota and landmass area, (B) the slope of the regression between the smallest species in a biota and landmass area, and (C) the body size at the interception point of both the smallest and largest regression curves. Arrows indicate observed values.

sustain a viable population, and this increases towards larger and smaller species. We hypothesize that this is correlated with medium-sized species being able to sustain a higher number of individuals per unit area (i.e. higher population densities), with population density decreasing as species get larger or smaller (Marquet *et al.*, 1995; Silva and Downing, 1995b). Because population size is one of the major determinants of population extinction risk, we hypothesize that medium-

sized species have, on average, lower extinction rates than their larger or smaller relatives. This results in medium-sized species being able to sustain viable populations on very small islands. A very simple idea is at the core of this hypothesis. If the number of individuals per unit area that a species can pack is low (as is the case for large and small species), then their extinction risks should increase as available area (i.e. landmass area) decreases. Furthermore, each species can be characterized by a threshold area (minimum area) below which it will be unable to persist. This threshold area will depend on the species' body size. The net result of this process is that only large landmasses will have the whole range of body masses for a particular taxa, from the very small to the very large species. Lack of empirical data on population extinction risks on islands precludes a direct test of this hypothesis. However, known scaling relationships relating body size with individual spatial requirements and density allow us to attempt a preliminary test.

For the sake of clarity, we will first derive an explanation for the scaling of the largest body sizes found on islands. To perform the basic processes of self-maintenance, reproduction and interaction with other organisms and with the physical environment, organisms must take in energy as an increasing function of body mass (Peters, 1983; Calder, 1984; Schmidt-Nielsen, 1984). Furthermore, since resources (energy) are distributed in space, body mass also affects an individual's space requirements (McNab, 1963; Clutton-Brock and Harvey, 1978; Brown and Maurer, 1989). This is reflected in a positive relationship between home range area (A_i) and body mass (McNab, 1963; Harestad and Bunnell, 1979; Damuth, 1981a; Swihart *et al.*, 1988). This relationship has been empirically documented for mammals as:

$$A_i \propto W^{1.0} \quad (1)$$

where the subscript i indicates that this is the area required per average individual within a species of a particular size.

The observed positive allometric exponent indicates that the larger the species, the larger the amount of area it requires per individual, hence the lower the density per unit area that it can attain. For example, imagine a species whose average individual requires 1 km² to complete its life-cycle. Furthermore, let us assume that there is little overlap between individuals in their use of this area. If this is the case, this species will attain densities close to one individual per km² and will probably not be found in landmasses of less than 1 km², since no individual could survive there. It is unlikely to be found in moderately larger areas either (e.g. 1 to 50 km²), since the number of individuals such an area would be able to sustain would probably not be enough to ensure the species' long-term persistence (i.e. its minimum viable population density). Thus, this species will only be likely to be found on landmasses whose area is above a threshold or minimum area needed for assuring its persistence. The point of this example is that the area that the average individual of a species requires, by affecting the species population density, affects the minimum area of the landmass required (A_m) for the persistence of the species.

Continuing with the development of our hypothesis, we can approximate the minimum landmass area required (A_m) for a species of a given size (W) as:

$$A_i \propto N_m A_i \quad (2)$$

where N_m is the minimum number of individuals required to avoid extinction in the absence of immigration (see also McNab, 1994a, for a similar allometric argument). Thus, if N_m is equal to 500 (individuals) and A_i is equal to 0.1 (km² per individual), then the minimum area required for the persistence of this species (A_m) would be 50 km². Substituting Equation (1) into Equation (2), we arrive at:

$$A_i \propto N_m W^{1.0} \quad (3)$$

The final step in the development of this hypothesis entails the approximation of the scaling of N_m . Unfortunately, there are not enough data in the literature to provide reliable empirical estimates of the total number of individuals needed for the long-term persistence of a particular species, especially since this number is, at present, difficult to estimate (e.g. Lawton, 1990; Meffe and Carroll, 1994). However, we can still represent N_m as an unknown allometric function of the following form:

$$N_m \propto W^x \quad (4)$$

Substituting this equation into Equation (3), we can estimate A_m as:

$$A_m \propto W^{(1+x)} \quad (5)$$

Although the value of x is unknown, this does not preclude us from exploring the potential implications of different values of x . If x is close to -1 , then A_m would be independent of size for the largest species found on landmasses ($A_m \propto W^0$). This is probably not accurate, since it is well known that large species require large landmasses for persistence (Brown, 1971, 1978; Diamond, 1984a). However, if x is close to 0 (i.e. N_m is independent of body size), the scaling of A_m is:

$$A_m \propto W^{1.0} \quad (6)$$

This value for the allometric exponent of A_m is in good agreement with the reported slopes for the scaling of the area of the landmass required for the persistence of species of the largest body size (Table 1). In fact, the slope for the general regression of landmass area versus the species of largest body size (Table 1, Fig. 1) is 1.17 ± 0.1 (s.e.), which is not significantly different from 1.0 (two-tailed t -test, $t = 0.18$, d.f. = 77; $P > 0.5$).

The next step in the development of the area-scaling hypothesis is to explain the relationship between body size and landmass area for species of smallest body size (stars in Fig. 1). According to the area-scaling hypothesis, the observed negative scaling relationship for small species would imply that the area required per individual (A_i) of small species (below about 100 g) increases as body size decreases (i.e. a negative allometric exponent in Equation 1), thus implying that the smaller the species, the larger the area it requires for survival. This entails a change in the allometric exponent of A_i from positive (for large species) to negative (for small species). So far as we know, the only empirical evidence for this comes from two studies, one by Brown and Maurer (1989) and the other by Kelt and Van Vuren (unpublished data). Brown and Maurer (1989) showed that species below a threshold size of about 100 g require larger areas than predicted by Equation (1). Because these authors did not report the allometric slope of this relationship, we estimated it from their data (published by Brown and Zeng, 1989) on body size and the calculated median lifetime dispersal distance for adult individuals of species weighing less than 125 g. We regressed \log_{10} body mass against a measure of individual space requirements (\log_{10} of the squared median lifetime dispersal distance). The result of this analysis yielded a slope of $b = -2.4$ (s.e. = 0.43; $r^2 = 0.79$, $n = 10$, $P < 0.05$). Since lifetime dispersal distance squared provides an estimate of the amount of space that a particular individual requires to complete its life-cycle, we assume it is proportional to the area required by an individual A_i . Using the allometric exponent in Equations (1) to (3) and substituting this into Equation (6), we have:

$$A_m \propto W^{-2.4} \quad (7)$$

This implies that minimum area requirements scale negatively for small species below a threshold size of about 100 g. The observed slope for the general regression of \log_{10} landmass area versus \log_{10} smallest body size is -2.74 ± 0.34 (s.e.); this value is not significantly different from -2.4 (two-tailed t -test, $t = 0.103$, d.f. = 86; $P = 0.92$). Working with a dataset of 48 species and

subspecies of mammals, Kelt and Van Vuren (unpublished data) also showed that the slope of \log_2 minimum home range with \log_2 body size changes sign near 100 g. Below 100 g their slope is significantly negative, whereas above 100 g it is significantly positive.

Discussion

As with most hypotheses based on empirical allometric relationships, the validity of the area-scaling hypothesis depends on the generality of the assumed scaling relationships used in its development. We recognize that the negative scaling of A_i with body size for small species is controversial, based as it is on two datasets and the biogeographic patterns reported in this paper. We hope that this report as well as the theoretical developments of Brown *et al.* (1993) will spur empirical work on the energetic allometry of small organisms. Interestingly, the relationship between body size and other ecological variables, such as population density, have been shown to be more complicated than previously thought, with allometric slopes that may change sign at a particular threshold body size, emphasizing that small organisms do not behave as predicted by simple linear regression equations.

Most studies on the scaling of population density report simple linear relationships (Damuth, 1981b, 1987; Peters and Wassenberg, 1983; Peters and Raelson, 1984; Marquet *et al.*, 1990; Currie and Fritz, 1993), in which both variables are significantly and negatively correlated, with the scatter concentrated along a narrow region surrounding the best-fit line. However, using independent datasets, Brown and Maurer (1987), Morse *et al.* (1988), Lawton (1989, 1990) and Blackburn *et al.* (1993) found that the negative relationship between density and body size is either weak or absent, and that the best descriptor of this scaling pattern is a surface or polygonal region enclosing observed combinations of both variables (see review in Cotgreave, 1993). Typically, this polygon will have a well-defined upper boundary with opposite slopes on either side of a maximum value of population density occurring at intermediate body sizes (e.g. Marquet *et al.*, 1995). More recently, Silva and Downing (1995b) have shown that the allometric scaling of population density for mammals changes slope at a threshold body size of about 100 g, which is in agreement with the scaling pattern of body size extremes across landmasses reported in Fig. 1.

Landmass area, species extinction and body size evolution

The pattern shown in Table 1 and Fig. 1 warrants further comment. The area-scaling hypothesis we propose stresses the influence of individual constraints on minimum area requirements and species extinction probability, emphasizing a bottom-up causation across hierarchical levels (Vrba and Eldredge, 1984; Eldredge, 1985; Vrba and Gould, 1986). However, it is important to realize that the implications at the ecological and evolutionary levels are different, although not independent. While at the ecological level the space requirements of individuals set an upper limit to the number of individuals per unit area, hence affecting local population density, at the evolutionary level this is translated into the differential extinction of species within biotas (see also Brown, 1995).

The effect of area on population density was recognized by MacArthur and Wilson (1967) to be relevant in accounting for the species–area relationship on islands. This has been demonstrated with both correlational analysis (Williamson, 1981) and experimental studies (e.g. Crowell, 1973). However, its connection with the body size of species has received little attention. Although a number of studies have assessed the relationship between body size, population density and extinction risk for species inhabiting archipelagoes (e.g. Pimm *et al.*, 1988, 1993; Pimm, 1992; Tracy and George, 1992; Schoener and Spiller, 1992), they have not explicitly looked at the interaction between body size and island area as affecting extinction and persistence. An important exception is the study of Schoener and Schoener (1983) on lizards on small Bahamian islands, who found

that, for small islands, larger lizards have higher extinction rates than small lizards. In this study, we showed that body size affects the persistence of species in landmasses of different areas. In particular, for mammals we showed (Fig. 1) the existence of a threshold body size of about 100 g, such that increasingly large and small species persist only on landmasses of progressively larger areas. The results presented here concur with the view that island and continental area exert a high degree of control on species diversity (MacArthur and Wilson, 1967; Flessa, 1975); however, this is apparently mediated by organismal size. Our area-scaling hypothesis contributes an explicit mechanism for this process and suggests a way of merging allometric models with models of species diversity in insular habitats. Of great interest would be to study very small landmasses which, according to Fig. 1, show the largest deviations from expected values. We hypothesize that this may be associated with the greater turnover shown by small islands.

For the sake of simplicity, the area-scaling hypothesis implicitly assumes that species are not able to change their body sizes. However, microevolutionary change in body size of insular populations is a well-known phenomenon (e.g. Lomolino, 1985). In this regard, the area-scaling hypothesis suggests that body size changes should be linked to landmass area; the smaller the island and the farther the mass of a species is from 100 g, the larger the expected change in body mass necessary for species survival. This pattern has recently been reported by Maurer *et al.* (1992) and Brown *et al.* (1993). This change in body size would permit a species to reduce its energetic requirements with a consequent decrease in the per individual area needed to satisfy them, allowing for more individuals to be packed per island unit area (i.e. larger population sizes), thus reducing the extinction risks. A similar argument has recently been developed by McNab (1994a,b), who suggests the existence of a positive intraspecific correlation between resource use (estimated through basal metabolism) and island area. According to McNab (1994a,b), reduced resource requirements by individuals permit larger populations, which in turn increases the probability of population survival on small landmasses. This is essentially the same mechanism postulated by us, but arrived at by considering the relationship between basal metabolic rate and island area, with some important twists. On the one hand, we assume that a change in energetic requirements is associated with a change in body mass; however, as pointed out by McNab (1994a,b), this is not necessarily so. Changes in diet (increasing frugivory) and/or habit (e.g. evolution of flightlessness in birds) can contribute in varying degrees to the same process, although these changes are usually coupled to a reduction in size, which is apparently the most important mechanism (McNab, 1994a). The pattern presented in Fig. 1 reinforces McNab's suggestion that a reduction in size is the most common mechanism associated with reduced resource requirements. On the other hand, McNab (1994a) considers home range to be an increasing allometric function of body size. However, we have shown that this may not be the case. We suggest that the scaling exponent changes sign and magnitude at a particular threshold size (about 100 g in mammals). Thus, species progressively smaller than 100 g require increasingly larger landmasses to survive. This implies that species of mammals weighing less than 100 g should also decrease their resource requirements on small islands by a reduction in their basal metabolic rates. Partial support for this prediction comes from the observed reduction in metabolic rate observed in *Microtus breweri* (c. 70 g) on Muskeget Island (2.6 km²) (McNab, 1994a).

The approach outlined in this paper envisages the range of body sizes for a particular group of organisms to be constrained by the interaction between the size of the largest landmass available for colonization and evolution, and constraints operating on the energetic and spatial requirements of individuals belonging to each group. However, it is also important to point out that, although the actual distribution of the largest and smallest species of mammals across landmasses follows the pattern shown in Fig. 1, it would be unlikely that species of mammals smaller than those presently known could ever evolve given the steep physiological constraints on small body size

(Peters, 1983; Calder, 1984). However, the fossil record shows that species larger than those currently extant have existed. Interestingly, the occurrence of these species apparently coincides with geological epochs characterized by the existence of larger landmasses (Behrensmeyer *et al.*, 1992).

Ecological implications

The dynamics of extinction and origination occurring at the level of species within faunal assemblages, influences community-level processes by determining those species potentially available for colonization and interaction at the local level (Brown and Maurer, 1987; Ricklefs, 1987; Ricklefs and Schluter, 1993). Thus, landmasses of different size are expected to have qualitatively and quantitatively different communities. In particular, mammalian communities on small landmasses are expected (1) to be depauperate in large predators and herbivores (Diamond, 1984a) and thus (2) to be characterized by shorter food chains (Schoener, 1989; Cohen and Newman, 1991; Holt, 1993), and (3) to show less positively skewed body size distributions (Maurer *et al.*, 1992). Furthermore, larger species are present in a greater number of biomes within continents and exhibit less turnover across habitats and spatial scales (Brown and Nicoletto, 1991), coupling the dynamics of otherwise loosely coupled, spatially separated communities. Their selective loss from biotas, as landmass area decreases, can potentially cause a cascade of effects on local communities (Owen-Smith, 1987, 1989; Holt, 1993). Although we cannot predict the structure of communities in landmasses of different sizes, we certainly expect them to be different in both trophic structure and body size distributions. This topic requires further study.

But how general is this pattern? We would expect to find a pattern similar to that reported in Fig. 1 in insular settings and in fragmented habitats, especially where inter-island (habitat fragment) migration is low and rescue-effects (Brown and Kodric-Brown, 1977) are potentially unimportant. So far, we have explored two additional datasets. The first corresponds to records of 100 species of British land birds on 16 islands off the coast of Britain (Pimm *et al.*, 1988), and the second corresponds to a compilation of 113 Finnish and 51 Wisconsin lakes containing 20 and 23 species of fish, respectively (Tonn *et al.*, 1990). Although the range of areas sampled in the birds

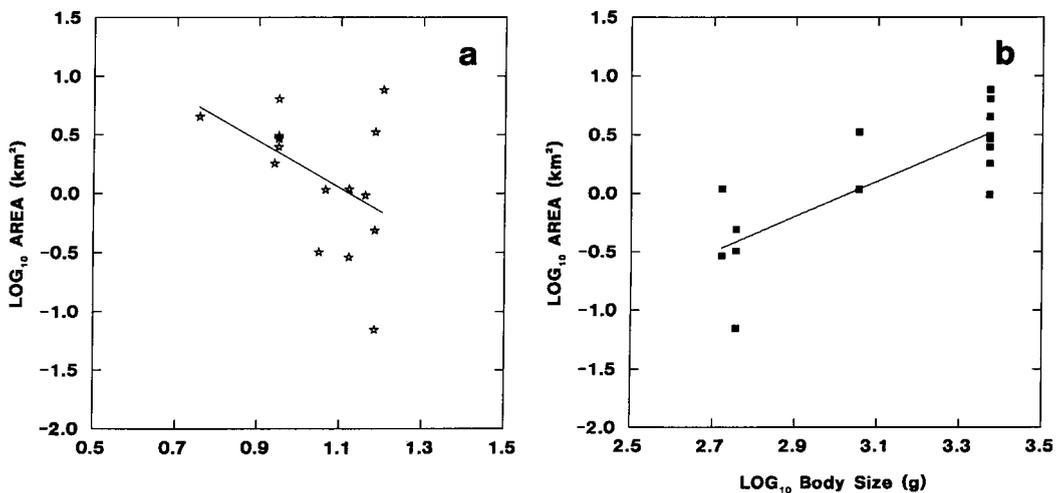


Figure 3. Relationship between minimum (a) and maximum (b) body sizes and island area for birds species on islands off the coast of Britain.

dataset is small (0.07–7.65 km²), both systems show a similar trend to that shown for mammals (Fig. 1). For birds, we found a negative relationship between the size of the smallest species found in a particular insular fauna and the size of the island (Fig. 3a; slope = -2.0, $r^2 = 0.22$, $P = 0.069$, $n = 16$), whereas it was positive for the largest species (Fig. 3b; slope = 1.5, $r^2 = 0.64$, $P < 0.001$, $n = 16$). A similar pattern was found for species of fish versus lake area (slope = -0.07, $r^2 = 0.037$, $P = 0.013$, $n = 164$ for the smallest species and slope = 0.07, $r^2 = 0.029$, $P = 0.031$, $n = 164$ for the largest species). Lake area was used in this analysis instead of lake volume because lake productivity is proportional to lake area. Fish biomass is generally modelled as a function of lake area (Kitchell *et al.*, 1974). These results underscore the generality of the pattern shown in Fig. 1. Furthermore, the slope values are remarkably close to the predicted values (especially for birds), which is significant when one considers that both systems are only partially isolated.

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