

# The animal species–body size distribution of Marion Island

Kevin J. Gaston<sup>\*†</sup>, Steven L. Chown<sup>‡</sup>, and Richard D. Mercer<sup>§</sup>

<sup>\*</sup>Biodiversity and Macroecology Group, Department of Animal and Plant Sciences, University of Sheffield, Sheffield S10 2TN, United Kingdom; <sup>‡</sup>Department of Zoology, University of Stellenbosch, Private Bag X1, Matieland 7602, South Africa; and <sup>§</sup>Department of Zoology and Entomology, University of Pretoria, Pretoria 0002, South Africa

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**Body size is one of the most significant features of animals. Not only is it correlated with many life history and ecological traits, but it also may influence the abundance of species within, and their membership of, assemblages. Understanding of the latter processes is frequently based on a comparison of model outcomes with the frequency of species of different body mass within natural assemblages. Consequently, the form of these frequency distributions has been much debated. Empirical data usually concern taxonomically delineated groups, such as classes or orders, whereas the processes ultimately apply to whole assemblages. Here, we report the most complete animal species–body size distribution to date for those free-living species breeding on sub-Antarctic Marion Island and using the terrestrial environment. Extending over 15 orders of magnitude of variation in body mass, this distribution is bimodal, with separate peaks for invertebrates and vertebrates. Under logarithmic transformation, the distribution for vertebrates is not significantly skewed, whereas that for invertebrates is right-skewed. Contrary to expectation based on a fractal or pseudofractal environmental structure, the decline in the richness of species at the smallest body sizes is a real effect and not a consequence of unrecorded species or of species introductions to the island. The scarcity of small species might well be a consequence of their large geographic ranges.**

**S**ystematic variation in the numbers of species of different body sizes is one of the most readily apparent features of the structure of animal assemblages. Indeed, species–body size distributions for such assemblages have been documented over a period of nearly 100 years, with more than 300 now in the literature. The rate at which they are produced continues to grow (1, 2). Nevertheless, understanding of the form taken by these distributions remains wanting. Perhaps foremost, this lack is because almost all documented examples of species–body size distributions are for selected higher taxa typically at the level of classes or orders (e.g., carabid beetles, birds, mammals), and not for all, or even the bulk, of the species that compose entire animal assemblages. The precise form of the distributions for such higher taxa varies, particularly with spatial scale (3–12). However, in terrestrial systems they are typically strongly right-skewed, with many more small-bodied than large-bodied species. Moreover, the smallest body-size class is seldom the most speciose, despite the argument that the fractal or pseudofractal nature of the environment provides progressively more opportunities for smaller organisms (12–16). The paucity of species in the smallest size class has been attributed to a variety of causes, including resource distributions, size-biases in speciation and extinction, and optimization of energy allocation (8, 12, 17–26). It has also been attributed to the influence of species in other taxonomic groups, where such body sizes are closer to being modal and which may thus be better exploiters of, or competitors for, the available resources (5, 27, 28).

The principal, and influential, exception to the preoccupation in the ecological literature with species–body size distributions for particular higher taxa has been May's (15, 29) estimate of the form of the species–body size distribution of all known terrestrial

animal species [see also ref. 30; Fenchel (31) conducted a similar exercise for aquatic species]. Although explicitly somewhat speculative, in that it involved significant approximation and extrapolation, this distribution was also strongly right-skewed and again revealed a paucity of species in the smallest size class. However, in common with many other species–body size distributions, a major concern in interpreting this one is the effect of the absence of a considerable proportion of extant species (29). Newly described species in higher taxa tend to be smaller-bodied, on average, than those already known (32–37), and some of the hyperdiverse and more poorly known taxa are small-bodied (e.g., nematodes, mites). Debate has thus persisted as to the overall richness of small-bodied species relative to those of larger body size (15, 29, 31, 38–40).

Given that the paucity of small-bodied species for individual higher taxa need not necessarily translate into such a paucity of species in the smallest body-size classes for entire terrestrial animal assemblages, it remains an open question what form species–body size distributions for the latter might actually take. In this paper, we report such a distribution for the free-living Animalia assemblage of Marion Island.

## Data

Marion Island is the larger of the two sub-Antarctic islands that make up the Prince Edward archipelago (46° 53' S, 37° 57' E), which lies ≈2300 km south-east of Cape Town. It has a surface area of ≈290 km<sup>2</sup> (2), a maximum elevation of 1230 m, a cool hyperoceanic climate (mean annual air temperature ≈5° C), and a tundra-type biome (for details see refs. 41 and 42). The flora and fauna of the island have been subject to prolonged and intensive study (41–47). This study has culminated in a 4-year (1996–1999) survey of the invertebrate assemblages associated with each of the broad land types, with replicated standardized field sampling conducted continuously for periods of a year or more in each type (48–50). This study has resulted in a remarkably full understanding of the composition of the fauna.

Although clearly very isolated, the animal assemblage of Marion Island is far from being a closed one (42, 51, 52). Here, we limit attention to those free-living (i.e., nonparasitic) species that breed on the island and use the terrestrial environment, thus excluding those that solely exploit freshwater and littoral habitats. This assemblage constitutes a well-defined one using a common spatial resource, and thus is potentially subject to any constraints on the frequency of species of different body sizes that might be posed by the fractal or pseudofractal nature of the terrestrial environment (12–16). The assemblage includes species of birds and mammals that breed on the island but may forage largely or exclusively at sea; these species have particularly important terrestrial ecosystem functions on the island (e.g., in

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<sup>†</sup>To whom reprint requests should be addressed. E-mail: k.j.gaston@sheffield.ac.uk.

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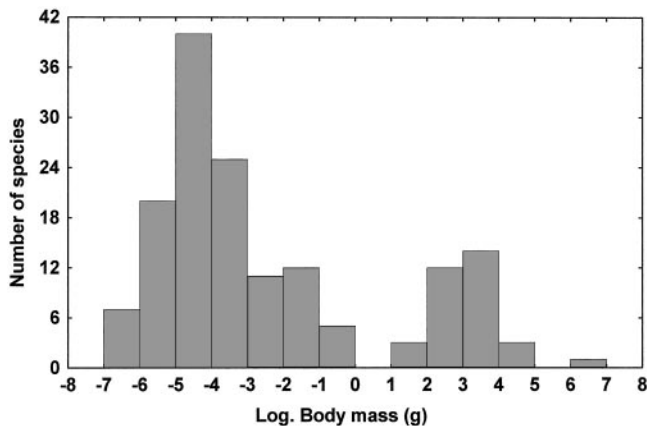


Fig. 1. Frequency distribution of logarithmically transformed body masses of free-living animal species using Marion Island to breed; the distribution excludes those that solely exploit freshwater and littoral habitats.

nutrient cycling, ecosystem engineering; refs. 51, 53, and 54). Significantly, the only major taxonomic component of the assemblage for which the number of species on the island has not been well characterized is the nematodes (see below). The precise taxonomic identities of some of the species in some other invertebrate groups (especially the mites) are yet to be resolved (some may be new to science; refs. 55 and 56), but the species-level composition is well understood, and it is very unlikely that significant numbers of species remain to be discovered.

Defined as above, the entire animal assemblage comprises 153 recorded species, including representatives of many groups that are commonly ignored in studies of community ecology and biodiversity (e.g., Collembola, Acari). The body mass of adults of each species that has been distinguished was determined in one of the following ways: by direct measurement, where possible averaging over multiple individuals [Collembola, Psocoptera, Hemiptera (in part), Thysanoptera, Coleoptera, Diptera, Lepidoptera, Hymenoptera, Mesostigmata (in part), Prostigmata (in part), Cryptostigmata (in part), Astigmata (in part), Araneae (in part), Mollusca], by using appropriate regressions to estimate body mass from body-length measurements [Mesostigmata (in part), Prostigmata (in part), Cryptostigmata (in part), Araneae (in part)], from the literature [Ixodoidea (in part), Aves (in part)], from the unpublished records of appropriate experts [Aves (in part), Mammalia], and by extrapolation from the body masses of related species of similar dimensions [Hemiptera (in part), Siphonaptera, Cryptostigmata (in part), Astigmata (in part), Ixodoidea (in part), Tardigrada, Annelida].

## Results and Discussion

The animal species recorded from Marion Island vary in body mass by over 15 orders of magnitude, from 0.00000045 to 1,350,000 g. The species–body size distribution based on logarithmically transformed body masses is approximately bimodal, with the second mode comprising vertebrates and the first mode comprising invertebrates (Fig. 1). We are not aware of such a marked size discontinuity having previously been documented for animal assemblages, although it may be influenced by the limited number of species in this particular case.

The logarithmically transformed body-size distribution for vertebrates is not significantly skewed [ $g_1 = 0.792$ ,  $n = 33$ ; using the test given by Sokal & Rohlf (57)  $t = 1.936$ , not significant (NS)]. The logarithmically transformed body-size distribution for invertebrates is significantly right-skewed ( $g_1 = 0.558$ ,  $n = 120$ ;  $t = 2.525$ ,  $P < 0.05$ ), and such a pattern can be interpreted in two different ways (12). It could be taken to mean that there

are relatively few very large invertebrate species in this assemblage, in comparison to a log-normal distribution covering the same range of body-mass values. Alternatively, the right skew could be interpreted as a consequence of more very large species in comparison to a log-normal distribution with the same mode and maximum.

If, for the Marion Island species–body size distribution (as depicted in Fig. 1), the two size classes to the left of the modal class were to contain the same numbers of species as that class (i.e., there were to be no paucity of species in the smallest size classes), then at least 53 terrestrial animal species would have to be missing from the faunal inventory for this assemblage. If these classes were to contain more species than the modal class (in line with the decrease in richness to the right of the mode), then  $\approx 100$  species would have to be missing. The only plausible contributor to these numbers of species would be the nematodes. As previously mentioned, there are no data for nematodes for Marion Island. However, on the climatically similar Macquarie Island, 26 nematode species have been recorded (58), whereas on the more extreme, maritime Antarctic Signy Island, 27 species have been found (59). Boag & Yeates (60) also have recently compiled available information on the species richness of soil nematodes in terrestrial ecosystems. They estimate conservative average values for local or  $\alpha$ -diversity of 49 species in grassland vegetation, 53 in cultivated soil, and 23 in polar vegetation. The numbers of species to be found in samples from Marion Island seem likely to be in the region of 20 to 30 species. Collections that may be regarded as reflecting regional diversity give figures of 80 species in the entire sub-Antarctic/Antarctic region (59, 61), 36 species from fen vegetation (Wicken Fen, England), 41 from maritime turf (Orkney Island), 70 from tussock grasslands (New Zealand), 75 from alpine vegetation (Austria), 75 from Ellesmere Island (Canada), and 89 species from sites in Spitzbergen (60). Given the generally depauperate state of the biota of Southern Ocean islands, a figure of substantially less than 100 species thus seems probable for the whole of Marion Island.

The extent to which nematodes will offset the otherwise low numbers of very small species in the Marion Island assemblage obviously depends on their body masses. Information here is limited. However, such data are available for the 27 species found on Signy Island (59), spanning the size range 0.00000004 to 0.00002164 g. Of these species, 3 would fall within the invertebrate modal size class in Fig. 1, 9 within the size class to its left, a further 10 species within the size class to the left of the previous one, and 5 would occupy the vacant size class to the extreme left. Similarly, Yeates (62) gives data on the live body masses of eight species of soil nematodes in New Zealand. These body masses range from 0.0000000711 to 0.000009112 g and span the three extreme left-hand size classes in Fig. 1, including the one that is otherwise unoccupied. Yeates (63) gives data on the body masses (averaged over all stages) of the 29 most common species of litter and soil nematodes in a beech forest. These body masses span 0.000000025 to 0.000005441 g (median 0.000000132 g), and nearly half (13/28) would fall in a more extreme size class than the most left-hand occupied one in Fig. 1. Thus, it seems highly unlikely that the nematodes of Marion Island will remove the pattern of decline in species richness of the smallest bodied species observed in the overall animal assemblage.

Given their high global species richness, and the relatively poor state of their taxonomy in most regions, the possible role of mites in determining the shape of animal assemblage species–body size distributions has been highlighted (29, 40); of an estimated global total of at least some hundreds of thousands, less than 50,000 species of mites have been described (40, 64), and samples from some habitats support the notion that mites are a hyperdiverse group (40, 65, 66; but see also ref. 67). The detailed knowledge of the mite fauna of Marion Island provides an opportunity to examine their influence on animal species–

body size distributions. As defined here, mites comprise 50 of the species (33%; 42% of the invertebrates) in the Marion Island assemblage. These are significantly smaller-bodied than the other invertebrates; the average body size of the mite species was smaller than the average in each of 100,000 random draws of 50 from the 120 invertebrate species. Although additional cryptic species of mites yet may be discovered on Marion Island, these are likely to be very few and would most probably be found in the genus *Algophagus* (D. J. Marshall, unpublished work). The known species in this genus fall within the  $-4$  to  $-5$ , or modal, size class (log-transformed mass) for the Marion Island assemblage, and so any such additions will not significantly alter these results. Thus, mites make a substantial contribution to the overall shape of the invertebrate component of the species–body size distribution for the Marion Island assemblage.

In common with many faunas (particularly on islands), a significant proportion of those on Marion Island have been introduced by human activities (68). For 21 (14%) of the species presently on the island, the probability of introduction is sufficient to regard them as alien (some past introductions have since been removed or eradicated; ref. 68 and references therein). Although some of these species are having a marked, and arguably escalating, impact on components of the native biota, there is no evidence that, as yet, they have caused extinctions on the island (69–73).

Only one of the introductions (the mouse *Mus musculus*) is a vertebrate, and it is the smallest-bodied of those vertebrates in the Marion Island assemblage. Ignoring this species, the smallest bodied vertebrate is the indigenous gray-backed stormpetrel *Garrodia nereis* (38 g), which is close to the lower observed size limit for pelagic foraging seabirds (although the Least Petrel *Halocryptena microsoma* is somewhat smaller at 20 g; ref. 74) and perhaps close to the functional limit that is possible (75, 76).

Lawton and Brown (77) reported a positive relationship across a wide variety of organisms between the probability of establishment of an invader accidentally or intentionally introduced to the British Isles and its body size, and the opposite trend for data for various insect orders. The 20 species of invertebrates that are alien to Marion Island are on average larger-bodied than the other invertebrate species; the average body size of the alien species was larger than the average in 97,276 of 100,000 random draws of 20 from the 120 invertebrate species (one-tailed test,  $P < 0.05$ ). However, this difference was not significant with a two-tailed test, suggesting either that there is no significant body-size difference in the introduced and indigenous species, or that there are differences that are the consequence of specific species or groups of species. Indeed, the large-bodied slug and calliphorid fly (see ref. 46) are likely to have contributed substantially to the significance of the one-tailed test. Nevertheless, following Lawton & Brown's (77) example of separating the species into higher taxa provides an indication that the second explanation is also appropriate. In this case, the 10 alien insect species were, on average, smaller than the other insect species (smaller on 95,258 of 100,000 random draws; one-tailed test,  $P < 0.05$ ). On the contrary, the single alien mite species has a larger body mass than the average mass of all mite species on the island, but not significantly so (larger on 35,973 of 100,000 random draws; NS), and the six alien collembolan species are likewise on average larger-bodied than the average of all Collembola, but again not significantly so (larger on 71,900 of 100,000 random draws, NS). This result suggests that for alien invertebrate species, there may be a threshold body size on either side of which the relationship between body size and successful establishment differs. One explanation for this possibility may be that for very small invertebrates, such as mites and spring-tails, physiological characteristics that allow individuals to

endure an oceanic crossing by ship in a dry hold (e.g., lipid content and desiccation resistance), and which are often positively related to body size (78), are likely to be most significant. For the larger insects, on the other hand, body size may already be large enough to ensure survival. In this case, the higher abundances (12) and the decline in probability of detection and subsequent eradication by humans associated with small body size are likely to be most significant.

Irrespective of whether this hypothesis is correct, the removal of these alien invertebrate species makes no marked difference to the estimated numbers of species that would have to be missing from the faunal inventory of the Marion Island assemblage if the two size classes to the left of the modal size class were to contain the same number of species as that modal class (47 rather than 53). However, if these classes were to contain more species than the modal class in line with the decrease in richness to the right of the mode, then, in the absence of the introduced species, rather more species would have to be missing.

In short, it seems that there is a genuine paucity of species in the smallest body-size classes in the animal assemblage that exploits the land of Marion Island, supporting the notion that such a pattern is not solely a feature of the species–body size distributions of individual higher taxonomic groups. The shape of the distribution thus cannot result from any fractal or pseudo-fractal structure of the terrestrial environment. Why should it take the form that it does? Most discussion of the determinants of the shapes of species–body size distributions has centered on individual classes or orders, and increasingly on the tradeoff between, and size dependence of, reproductive rate (production) and mortality (21, 23, 25). It is, however, questionable how readily such mechanisms will extrapolate to whole assemblage body-size distributions, comprising groups with fundamentally different patterns of physiology and life history.

One possibility that has been suggested is that species in taxa that are particularly small-bodied tend to be widely distributed, abundant, and good at dispersal, and that these characteristics effectively depresses their species richness (by limiting the opportunities for speciation). Such an argument has been used to explain why the global species richness of protists is not as great as their small body sizes might have suggested (31, 39, 79, 80; see also discussion of ref. 11 with regard to mites). Some support for this notion derives from the observation that of the indigenous collembolan species from Marion Island, 3 are endemic and 7 are widely distributed across the sub-Antarctic (the alien species are typically quite cosmopolitan; ref. 81), and that of 49 indigenous mite species, only 14 are endemic to the island, although this figure may be inflated because of poor sampling elsewhere (55, 56, 82). Likewise, of the 40 nematode species recorded in the maritime Antarctic, only 5 are endemic to single islands (61).

This argument rests on several assumptions, most notably that widely distributed species have the lowest probability of speciation, and that there are straightforward relationships between body size, range size, abundance, and dispersal ability. In the former case, the evidence is inconclusive (83), whereas in the latter, the relationships are complex and scale-dependent (12, 84). Thus, in this case, and like most other explanations for the species–body size distribution, there is some way to go before all of the links in the causal chain of reasoning are empirically verified. In so doing, recognition should be given to the fact that different processes may be important at different scales, and that no single explanation is likely to account for patterns at intraspecific, interspecific, and whole-assemblage scales.

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