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CONTENTS

Volume 48(2) | 2024



Insects great and small: on the significance of size



Experiences and some early results in monitoring congregating fireflies using night photography on a boat



British & Irish insects: The first 408 million years

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 www.youtube.com/RoyalEntomologicalSociety


 www.linkedin.com/company/royentsoc

- 57 Editorial
- 58 Letter from the President
- 59 Correspondence
- 61 Article: Insects great and small: on the significance of size
- 70 Article: Experiences and some early results in monitoring congregating fireflies using night photography on a boat
- 76 Article: British & Irish Insects: The first 408 million years
- 84 Featured Insect: Greater Wax Moth *Galleria mellonella*
- 85 Insects in the News
- 86 Opinion Pieces: Focus on the Freelancers
- 93 Opinion Pieces: In praise of the scientific naming of nature
- 95 Society News
- 96 Journals and Library
- 98 RES Student Science Communication Award 2023
- 103 Meetings
- 108 Obituaries
- 110 Reviews
Events



Antenna

Index and online copies



Index

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Cover Picture: 'Incoming!', a Buff-tailed Bumblebee queen, *Bombus terrestris*, photographed by Raymond J Cannon.

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RESEARCH SPOTLIGHT



Insects great and small: on the significance of size

“Why are there so many more kinds of insects than other animals? ... Most of the explanation lies simply in the small size of insects”

Robert M. May (1978)

Size matters

The size of an insect, especially small size, is a topic that is of perennial interest to theoretical ecologists, who have repeatedly asserted that being small is one of the features that have permitted the numerical dominance by insects of terrestrial animal communities, as well as their extraordinary speciosity (see the quotes above and below). Perhaps their enthusiasm for the subject depends to some extent on the ease with which size, especially body length, can be measured! Here I will try to persuade you that they are right to be interested in both the smallness and bigness of insects.

How big is a ‘typical’ insect?

My interest in insect size was stimulated by discovering (after

only 46 years!) the Royal Entomological Society’s excellent ninth symposium volume, ‘Diversity of Insect Faunas’ (Mound *et al.*, 1978). One of the most original contributions to that meeting was that of the Australian-American-British mathematical ecologist Robert May, who produced a paper full of ideas that continue to motivate fresh research today. Noticing the overwhelming predominance of small insects in natural species assemblies, he illustrated this *inter alia* with two graphs that plotted UK beetle species numbers versus their size, using both linear and logarithmic axes (Fig. 1). While the linear plot shows well enough that most beetle species are small, the (inset) log-log plot is clearly superior in showing that the species-size data are distributed around a

modal length of about 3 mm.

An example with this ‘typical’ size is the carpet beetle, *Anthrenus verbasci* (Dermestidae). This ‘typical’ value is surprisingly small. Many, even entomologists, will think of ladybirds (Coccinellidae) as being average sized coleopterans, but the invasive Harlequin Ladybird, *Harmonia axyridis* (probably now the most frequently encountered of these insects) is at about 7–8 mm in length, more than twice as big as a carpet beetle. Another familiar species, the Wasp Beetle, *Clytus arietis* (Cerambycidae), is about 16 mm, twice as big again. Obviously, there must be a lot of coleopteran species that are much smaller than 3 mm! An example of such an insect is *Octotemnus glabriculus* (Ciidae), an insect well known to me

“[What] enabled the pterygote insects to monopolise the majority of the vast number of niches ... offered by the development of vegetation? ... The answer, I suggest, is ‘size, metamorphosis and wings’”

T. R. E. Southwood (1978)

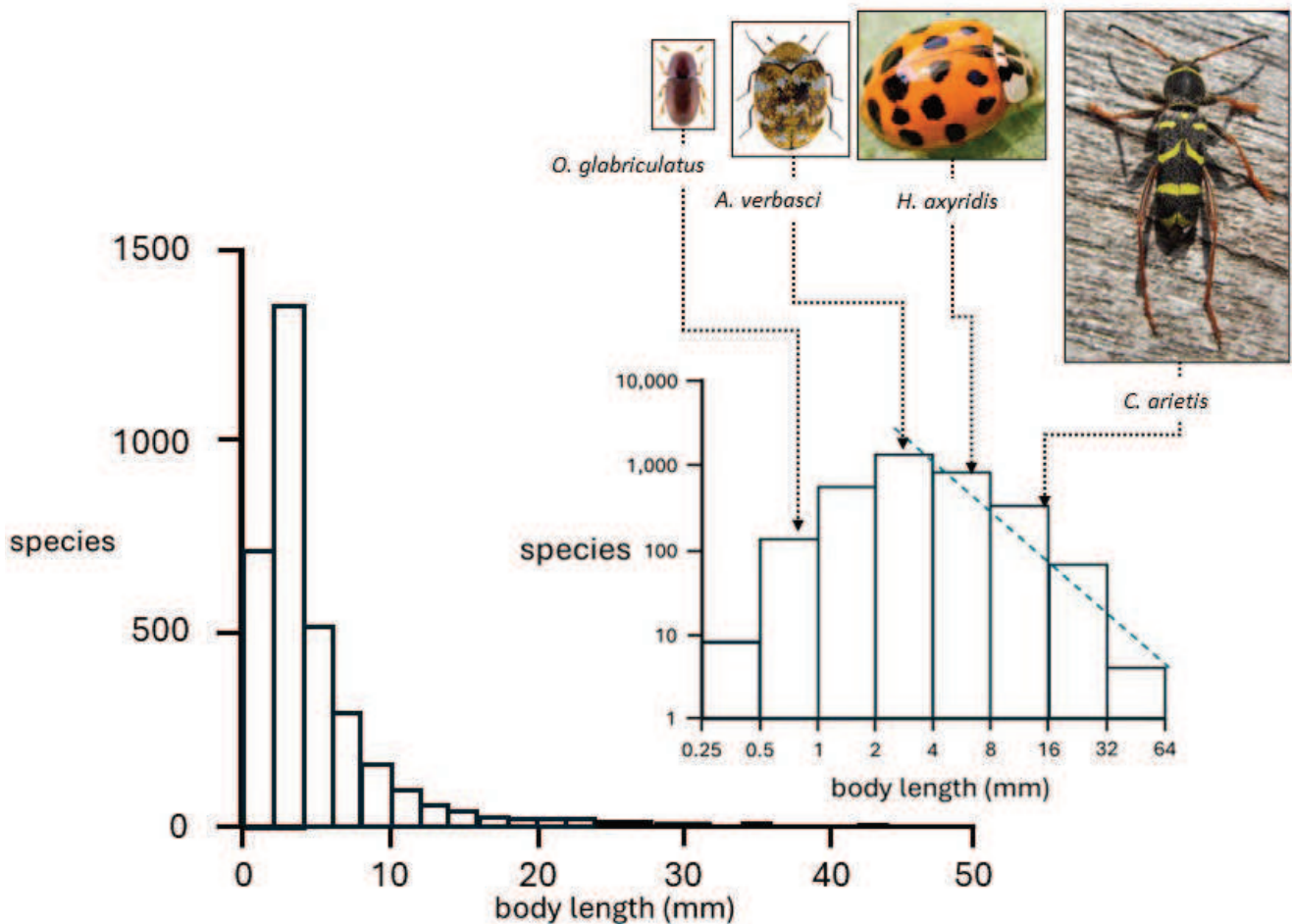


Figure 1. Species-size distribution for British Coleoptera, data taken from Fowler (1887). Main graph: Plotted on linearly scaled axes. Inset: Plotted on logarithmic axes to base 10 (vertical axis) and base 2 (horizontal axis). The dotted line in the inset graph represents the relation $S \propto L^{-2}$. Redrawn from May (1978). Credits for inset images of insects are: *Octotemnus glabriculatus* and *Anthrenus verbasci*, Udo Schmidt, CC BY-SA 2.0; *Harmonia axyridis*, entomart.be; *Clyto arietis*, Stuart Reynolds.

(Guevara *et al.*, 2000) that is only 1.5–2.0 mm long. It’s not well known because it is generally only found inside fungal fruiting bodies. There are indeed a lot of these tiny ciid beetles, with >100 spp. in the genus *Cis* alone.

Insect lengths are in fact distributed in what is termed a lognormal distribution. Statistical distributions of this type, first noted by Hemmingsen (1934), are commonly observed for species-size plots in many animal groups (a detailed paper on the subject of insect size is that of Schoener *et al.*, 1968). The key feature of this

distribution, as Fig. 1 makes clear, is that within the range of body lengths that occur among various different species of insect, there is a strong concentration of species at the smallest end of that range. This is what May meant when he remarked upon the importance of small size for the diversification of insects as a whole (see the quotation at the head of the article).

May’s theory-rich paper attempted to account for this insect species-size distribution, but suffered from the relatively small sample sizes that were then

available to him. To explore the question here, I have made use of a much larger dataset on the ‘typical’ adult lengths of 3,440 different species of hexapods relatively recently compiled for a different purpose by Ferns *et al.* (2016). In it, body length data were recorded without reference to sex from species in every extant order ($n=32$), as recorded in handbooks and species descriptions. I should make clear that Rainford *et al.* (2016) have also made an extensive inquiry into possible links between species size and the diversification of the hexapod

class, using a different dataset. Their statistical analysis is much more sophisticated than my own, but as we shall see comes to mostly similar conclusions.

Fig. 2 shows the frequency of occurrence of \log_{10} -transformed species-specific lengths for all 32 orders combined. As expected, the curve is well described by a lognormal distribution. The biological significance, if any, of the lognormal relationship remains uncertain; such a distribution is to be expected for any variable that is itself the multiplicatively combined product of other normally-distributed variables (Koch, 1966). In the present case, the fit is quite good; there appears to be a slight excess of insect species on the left-hand side of the graph (*i.e.*, there is more than the expected number of species which are smaller than the lognormal mean) but the

deviation is actually quite small. Distributions with a pronounced right-handed skew (*i.e.*, more large species than expected from the lognormal distribution) are commonly seen in species-size plots; a wide variety of evolutionary and ecological explanations for this skew has been considered (Novotny *et al.*, 1996; Kozłowski *et al.*, 2002) but there is no general explanation.

Simply averaging the lengths for all these hexapod orders isn't good enough because the bulk of species is contained within a relatively small number of highly diverse orders. To allow for this, I computed a weighted mean length for all hexapods which gave a value of 12.9 ± 1.73 mm (mean \pm S.D.). It's probably too big, because very small insects are almost certainly seriously under-represented in the database. According to a widely

used polynomial mass:length relationship derived for insects by Sage (1982), a hexapod of this length would be predicted to have a body mass (fresh weight) of about 54.5 mg.

The relative size of an insect

How does this 'average' insect size compare with that of other animals? This is interesting because size is an important factor in determining how many different kinds of animal can co-exist in any one ecosystem. This question was addressed in a classic paper by the ecologist G. Evelyn Hutchinson (1959), an important figure in developing the concept of ecological niche. Hutchinson maintained that animals using similar resources can avoid competition by partitioning a potentially broader niche through character displacement (Brown *et al.*, 1956),

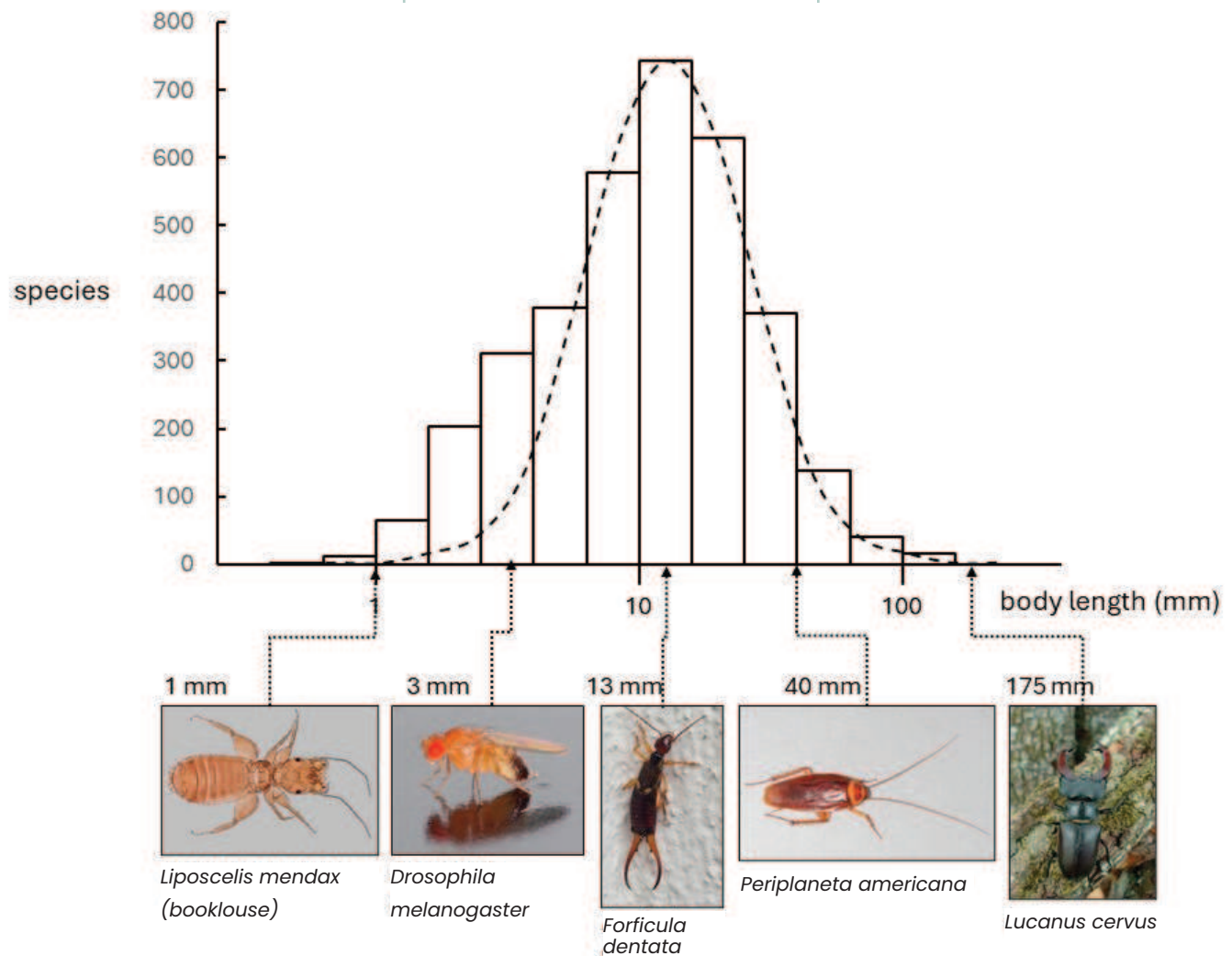


Figure 2. Species-size distribution for 3,440 species of insect from 32 orders. Columns show the number of species with described typical length in a range of 0.2 \log_{10} units. The horizontal axis is logarithmically scaled but is labelled to indicate actual body size. The dotted line shows a fitted lognormal distribution centred on the modal value for the whole set. There is evidence of an excess of (smaller) species on the left-hand side of the curve. Below the graph are shown portraits of insects of various indicated body lengths. Original figure, data computed from Ferns *et al.* (2016). Picture credits: *L. mendax*, Australian Plant Health and Environment Laboratory (CC BY 3.0 au); *D. melanogaster*, André Karwath (CC BY-SA 2.5); *F. dentata*, Nikola Szucsich (CC BY-NC); *P. americana*, Gary Alpert (CC BY 2.5); *L. cervus*, J.F.Gaffard (CC BY-SA 3.0).

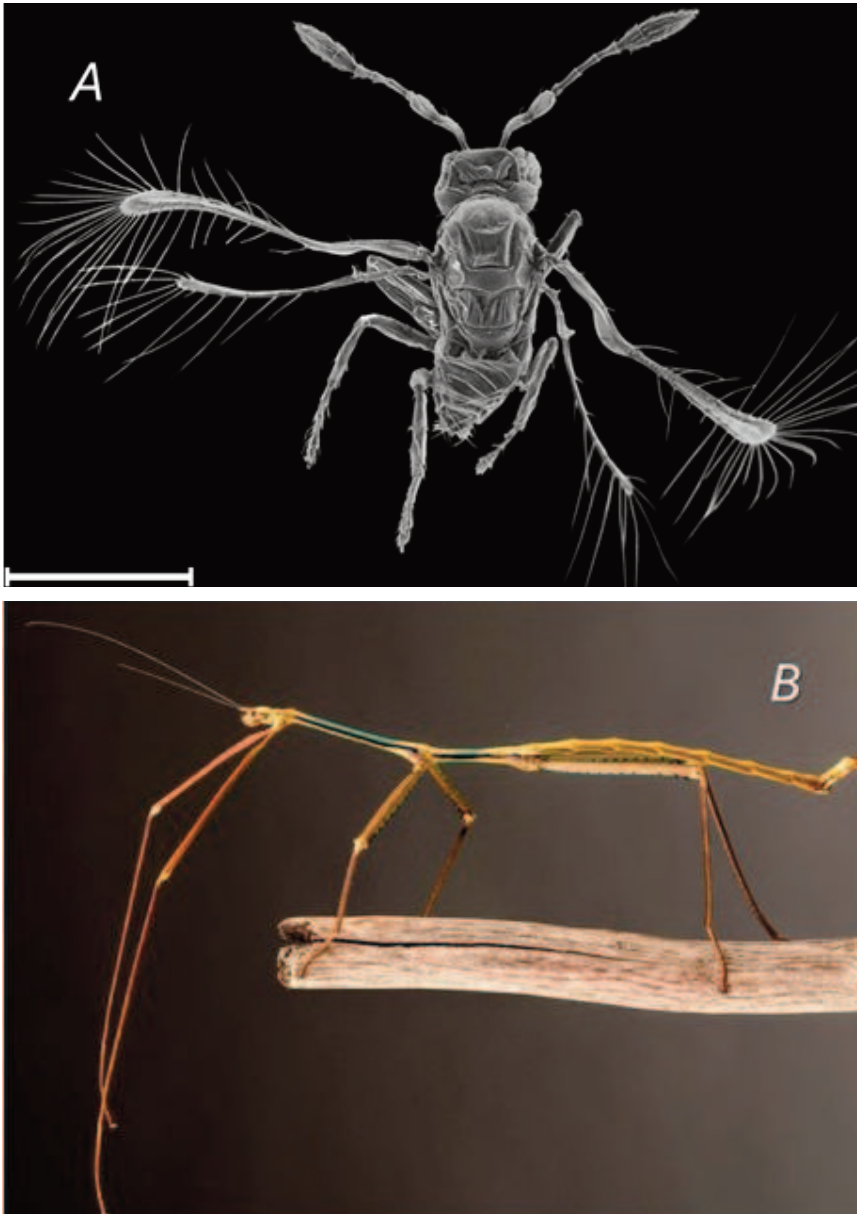


Figure 3. A very small and a very large insect. **A.** *Kikiki huna* (Hymenoptera, Mymaridae), the smallest recorded winged insect. Adult female, habitus dorsal, scale bar = 100 μm . body lengths for females of this species were measured at 158–190 μm ($n=10$). Photo: John T. Huber and John S. Noyes, CC BY-SA 3.0. (Huber *et al.*, 2013). **B.** *Phryganistria tamdaoensis* (Phasmatodea, Phasmatidae). Adult male, body length 190.6 mm (female can reach 228.7 mm). Photo: Joachim Bresseel and Jérôme Constant, CC BY-SA 3.0. (Bresseel *et al.*, 2014).

where the occupying animal's size is the character that is evolutionarily displaced.

The size range of insects does overlap with that of other animals. The smallest insects are generally either apterygotes, tiny feather-winged ptiliid beetles (Grebennikov, 2008), or parasitic wasps, 'fairyflies' (Mymaridae), all less than 1 mm long. The smallest insect is said to be the wingless male of the mymarid wasp *Dicopomorpha echmepterygis* (Mockford, 1997), which can be as small as 139 μm in length, but the winged female of this species is significantly bigger; the record for the smallest winged insect

appears to go to another mymarid, *Kikiki huna* (Fig 3A), one of which was measured at 158 μm long (Huber *et al.*, 2013). At the other end of the size scale, giant phasmids in the genus *Phryganistria* (Fig. 3B) are strong contenders for the biggest insects in linear dimensions, some having been reported to reach body lengths of up to 640 mm (Hennemann *et al.*, 2008). Other giant phasmids *e.g.*, *Heteropteryx dilatata*, are not so long but heavier, with an adult weight of up to 65 g (Bank *et al.*, 2021). It is frequently asserted that Goliath beetles (*Goliathus* spp., family Scarabaeidae, subfamily Cetoniinae) are the biggest insects

on the basis that they are the heaviest; their fully fed larvae can weigh up to 100 g, but the adult itself is generally only about half that weight (Vendl *et al.*, 2016). Among other very large insects are the orthopteran giant wētā, *Deinacrida rugosa* (Anostostomatoidae), adult females of which can attain weights of 20 g (Kelly *et al.*, 2016), and the hemipteran giant toe-biter *Lethocerus maximus* (Belostomatidae), which can reach a length of 100 mm (Ribeiro *et al.*, 2018).

For comparison, the smallest vertebrate is a terrestrial frog from Brazil, *Brachycephalus pulex*, adult males of which have a snout-to-vent length (SVL) of just 7.10 ± 0.47 mm (Bolaños *et al.*, 2024). Although a number of other tiny amphibians have been discovered, it is evident that the extent of the competitive overlap between the smallest vertebrates and the average insect is actually very limited.

On the other hand, insects aren't by any means the world's smallest animals, with many of which they almost always co-occur in terrestrial habitats, especially in the soil. Perhaps the most numerous and diverse of these other invertebrates are Acari (mites); the smallest apterygotes overlap in size with both parasitic and free-living mite species, in which size distributions peak in the \log_{10} size class of -0.5 to 0.0 units (*i.e.*, about 0.3–1.0 mm) (Walter, 1999). Other invertebrates also overlap in size with the smallest insects.

Although most insects are significantly bigger than most rotifers (length 400–500 μm , maximum about 2 mm; Hyman, 1951) and tardigrades (length 100–500 μm , maximum about 1.7 mm; Brusca *et al.*, 2003), there is clearly overlap with both of these taxa at lengths of < 1 mm. The same is true of the largest single-celled protists, ciliates (Ciliophora), which range in length from 20–600 μm (Lynn, 2008). The long, thin highly flexible bodies of several other invertebrate groups (*e.g.*, annelids, nematodes, *etc.*) are so different from those of insects that it does not seem sensible to compare them. The smallest insects must frequently compete for niche space with other non-insect invertebrates. As

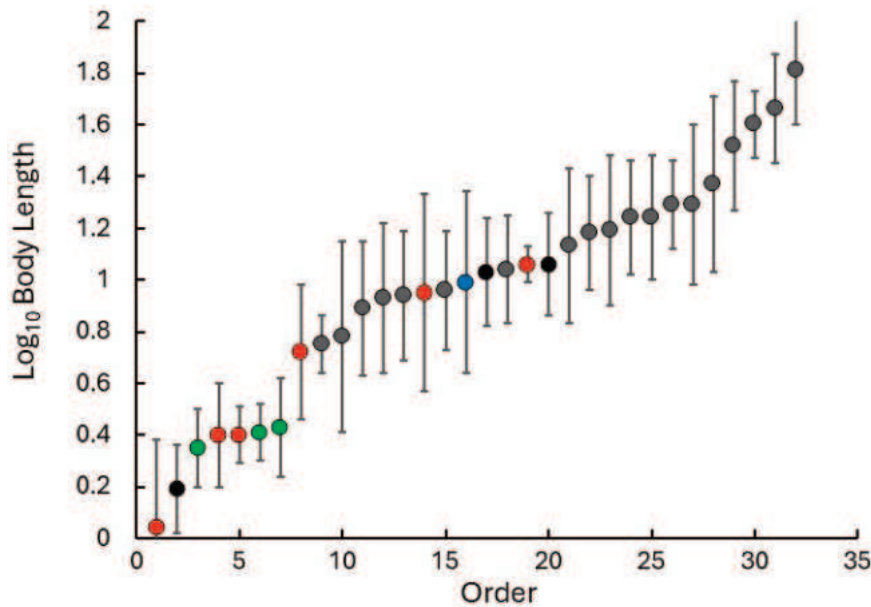


Figure 4. Log-transformed body length values (mean \pm S.D.) for 35 hexapod orders are presented along the x-axis in order of their mean size; those orders that are entirely or mostly apterous are coloured red, while entirely parasitic orders are coloured green. Hymenoptera, an order in which many species are parasitic, is coloured blue (see text). The sequence in which the orders are presented is: *Protura*, *Thysanoptera*, *Strepsiptera*, *Collembola*, *Zoraptera*, *Siphonaptera*, *Psocodea*, *Diplura*, *Isoptera*, *Coleoptera*, *Embioptera*, *Hemiptera*, *Diptera*, *Zygentoma*, *Ephemeroptera*, *Hymenoptera*, *Mecoptera*, *Dermaptera*, *Archaeognatha*, *Raphidioptera*, *Neuroptera*, *Plecoptera*, *Blattodea*, *Trichoptera*, *Mantophasmatodea*, *Grylloblattodea*, *Lepidoptera*, *Megaloptera*, *Orthoptera*, *Odonata*, *Mantodea*, *Phasmatodea*. Original figure, data taken from Ferns *et al.* (2016).

we will see later, it's possible that the very existence of these similarly-sized invertebrates may have effectively limited the proliferation of insect species into the smallest size categories.

Different orders of insect have different mean body lengths

Of course, not all insect orders are the same, and this is emphasised by a graphic representation of data from the study of Ferns *et al.* (2016) (Fig. 4). Beetles (*Coleoptera*) as noted above are on average considerably smaller than members of other orders. My value for the weighted mean length of *Coleoptera* is at 6.03 ± 2.34 mm, considerably bigger than the value proposed by May (1978), presumably because his sample was restricted to UK beetles, which appear to be smaller than those occurring elsewhere in the world, but is nevertheless still only about half as long as the weighted mean for all insects (12.9 ± 1.73 mm). Other insect orders appear to be considerably larger with *Odonata* (40.2 ± 2.35 mm), *Orthoptera* (33.2 ± 1.78 mm), *Phasmatodea* (64.0 ± 1.62 mm) and *Mantodea* (45.5 ± 1.62 mm) all being markedly longer than the average insect.

Have these between-order differences in the body size of insects evolved as the result of natural selection, or have they arisen by chance? Having analysed a different hexapod species-size dataset to the one used here, Rainford *et al.* (2016) concluded that there is little or no phylogenetic component to the evolution of body length within the class; they also found only weak evidence that body size variation is associated with species richness. Mayhew (2007) had previously found no evidence that body length has influenced either cladogenesis or extinction rates among insects, and Rainford *et al.* (2016) again found no evidence for an inverse relationship between diversification rate and body length.

I agree with these conclusions. Looking at the mean order-specific body lengths from the Ferns *et al.* (2016) dataset as a whole, the whole set of average body lengths according to order is a pretty good fit to the lognormal distribution, suggesting that size is indeed randomly allocated among the orders. This is possible because the orders with most species are also the orders with mean lengths closest to the

overall mean for the whole dataset.

Body length is also clearly uncorrelated with position in the phylogenetic age of the order, indicating that body size evolution among hexapods does not follow Cope's Rule, according to which, body size increases progressively during the lifetime of a taxon (Roy *et al.*, 2024). Length is also obviously unrelated to the number of species in the order, which could conceivably indicate that on divergence from its ancestral order, the first member of the new order would radiate to produce descendent taxa whose sizes become again distributed at random over the entire possible size range.

But I think that Rainford *et al.* (2016) may have been premature to conclude that "hexapod body size evolution is ... dominated by neutral processes". To me, 'neutral processes' means that the character in question is invisible to selection because it carries no adaptive significance. Failure to detect differences in body length between today's superorders doesn't mean that selection on size has never been important, and it seems to me perfectly feasible to imagine a situation in which species packing according to size is indeed determined through evolutionary character displacement according to a general rule that applies in all or most insect orders. Moreover, some hexapod groups may be exceptions to this general rule, and display deviant species-size relationships, but are too small in species number to perturb the statistical picture for the whole class.

There are two notable features of the taxonomic distribution of insect body length that don't look like 'neutral processes' to me. First, apterygote hexapods (those orders in which no member species has wings), *i.e.*, the three non-insect orders *Protura*, *Collembola*, *Diplura*, and the primitively wingless insect orders, *Archaeognatha* and *Zygentoma*, as well as the pterygote order *Siphonaptera* (fleas), in which wings are now entirely absent, but which have presumably been lost, as well as the almost apterous order *Zoraptera*, are as a group mostly smaller than insects with wings (Fig. 3). The weighted mean

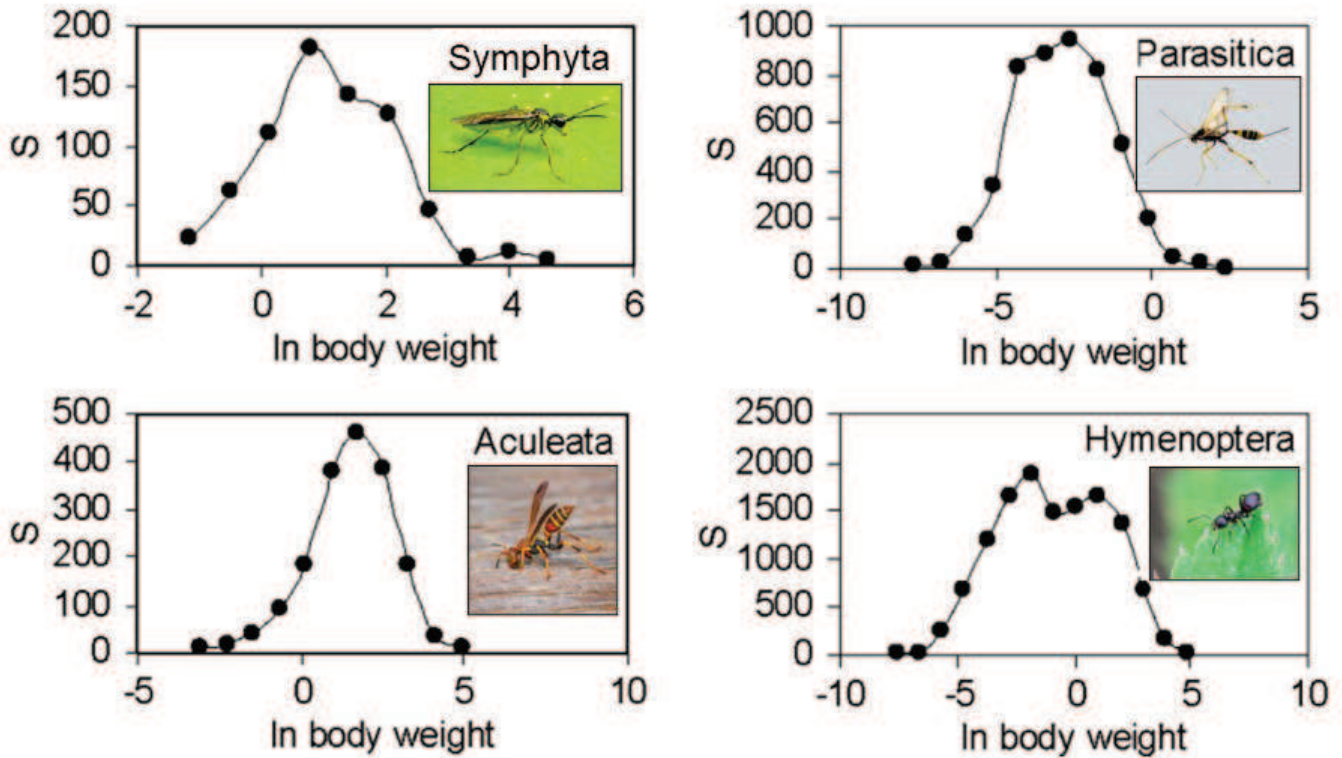


Figure 5. Natural log-transformed mean body lengths for individual species of Hymenoptera. Notice that the plot for Hymenoptera as a whole is bimodal, whereas plots for Symphyta, Aculeata and Parasitica are monomodal. S, species number. Data are from Ulrich (2006). The lines connecting the points in the graphs do not represent fitted curves. I have added inset panels to show representative species. Symphyta: *Tenthredo mesomela*, image by Guido Gerding, CC BY-SA 3.0; Aculeata: *Polistes dorsalis*, image by Fitz Clarke, CC BY-NC; Parasitica: *Acrorichnus* sp., image by Katya, Moscow, CC BY-SA 2.0; Hymenoptera: *Lasius niger*, image by AfroBrazilian, CC BY-SA 4.0.

length of the wingless orders is 3.16 ± 1.74 mm, as opposed to 13.11 ± 1.72 mm for those with wings. This implies that regardless of their respective evolutionary histories, apterygote insects are smaller than pterygotes.

Second, as is apparent from Fig. 4, within the Pterygota, parasitic species are in general smaller than non-parasitic species. The body lengths of two entirely parasitic orders, Siphonaptera (2.57 ± 1.29 mm) and Strepsiptera (2.24 ± 1.41 mm), as well as a third order, Psocodea (2.69 ± 1.55 mm), in which there is a strong representation of parasitic species, are all obviously considerably smaller than the general run of insects. Rainford *et al.* (2016) also noted that these fully or mainly parasitic orders appear to be significantly smaller than the rest.

The order Hymenoptera (ants, bees and wasps), well-known to have a high content of parasitic species, is particularly revealing. Examining a very large (12,601 spp.) and complete (88% of described spp.) dataset of European Hymenoptera, Ulrich (2006) found that this order has a clearly bimodal distribution of body size (Fig. 5). When its component species are classified

by suborder as Symphyta (sawflies), Aculeata (ants, bees and stinging wasps), or Parasitica (parasitic wasps; strictly all Apocrita except Aculeata), however, all three suborders display more or less monomodal weight distributions. Whereas dry body weight values for the non-parasitic species have modal values of about 10 mg (Symphyta) and 100 mg (Aculeata), dry weights of those species with parasitic life histories (Parasitica) are distributed around a value about four orders of magnitude lower in value, with a modal dry weight of only about 0.001 mg. If you look carefully at the species numbers in Fig. 5, you'll see that parasitic species actually dominate the Order as a whole. The small overall body size of this group of hymenopterans is therefore not due to lack of wings but is most likely a direct consequence of their parasitic habit.

Small size may be a general characteristic of endoparasites that results from strong limitation on maximum size. Poulin *et al.* (1997) analysed the body lengths of a wide range of animal parasites and found that log-right-skewed body species-size

distributions (*i.e.*, more large species than predicted by the lognormal distribution) are less frequent in parasitic species than expected. Size limitation on parasitoids imposed by the size of the host is known to occur in host-parasite relationships, as has been shown for aphids and their hymenopteran parasitoids by Cohen *et al.* (2005). One might well observe that since the number of hymenopteran parasitoids is so very large (Forbes *et al.*, 2018), parasitism itself must have been one of the strong drivers of diversification in insects as a whole; this might well lead us to conclude that it is actually parasitism that has driven the proliferation of very small insects rather than the other way around.

It's not about metamorphosis!

On the other hand, when I compare the weighted mean body lengths of those insect orders that undertake complete metamorphosis (Holometabola) (12.73 ± 1.89 mm) and those that don't (Hemimetabola) (14.82 ± 1.62 mm), I find that the two superorders do not differ. In agreement with this, although Rainford *et al.* (2014) had previously found that complete

metamorphosis was a key innovation in the phylogeny of the class that has driven the subsequent hyper-diversification of insects, Rainford *et al.* (2016) could uncover no evidence of a link between complete metamorphosis and the size of extant insects.

I think this result is very interesting. Since their phylogenetic divergence approximately 350 Mya, the extent of holometabolan species diversity has increased remarkably compared to that of hemimetabolans, so that today around 80% of extant insect species belong to one of the 5 holometabolan orders (Rolff *et al.*, 2019). It is scarcely conceivable that such radiation could have taken place in the absence of any selection on body size. I suppose that what this means is that there is now no evidence of *maintained directional selection* on size, even if it had once been important in getting to where we are today. But there might still be pockets of species-space (*i.e.*, among the Apterygota and also among parasitic species, especially in the Hymenoptera) in which maintained downward selection on size did indeed occur over long periods of time.

Smaller insects have larger populations

In attempting to explain the slope of the fitted line on the right-hand side of typical species-size plots, May (1978) drew attention to the already well-known fact that in any one environment it is not only the number of species, but also the total number of individual insects of a particular size that is approximately inversely related to L^2 (where L is the insect's body length). Some 7 years later, work by Morse *et al.* (1985), confirmed this and showed that this size distribution can be modelled by utilising the then newly-proposed theory of 'fractal space' in the ecosystem that supports them.

A fractal is an iterated self-similar pattern that presents a larger and larger linear dimension to the observer when measured by steps of decreasing size (Mandelbrot, 1982). It was argued by Morse *et al.* that the population size of consumers that can be supported by any ecosystem is

ultimately limited by resources (*i.e.*, nutrient flow). These resources originate from the primary producers (plants) distributed on and over surfaces that are clearly more extensive than the land area below. For this reason (just as Hutchinson *et al.*, 1959, had supposed) the larger the 'mosaic' plant surface on which an insect lives, the greater the supply of resources. Morse *et al.* proposed that this surface is fractally structured, and that when any particular dimension of the environment (effectively a transect) is probed by an insect with length L , the trophic resource available to it will be proportional to $L^{(1-D)}$, where D is the fractal dimension. A higher value of D leads to a steeper increase in resource availability with decreasing insect size, supporting a larger population of these smaller insects.

Morse *et al.* (1985) determined the value of D empirically for a range of different temperate and tropical vegetation types. Its value varied between 1.28 and 1.79 (mean = 1.44). Assuming that population size is determined by the availability of food, this led them to predict that the population size of insects depending on such an environment should be negatively related to insect length, the relationship having a negative slope of about -0.44 . In habitats such as these, then, small insects should greatly outnumber large ones. Censuses of insect populations from several radically different terrestrial ecosystems, one of which is illustrated in Fig. 6, confirmed that insect population sizes were indeed negatively correlated with length. The fitted slope of the relationship indicated that the fractal dimension D of such environments had a typical

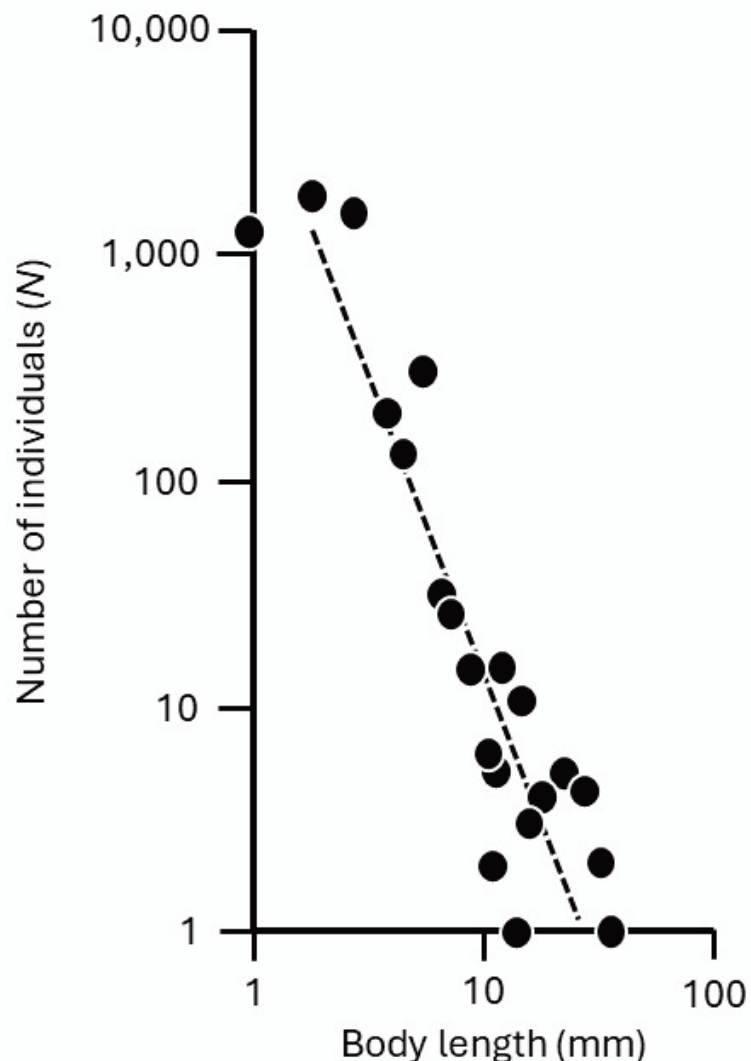


Figure 6. Number of individual arthropods (mainly insects) collected by sweep net from understory foliage in primary forest, Costa Rica, plotted against their size. The dashed line indicates a relationship in which $N \propto L^{(1-D)}$, where the fractal dimension D of the environment is about 1.4. Redrawn from Morse *et al.* (1985).

value of about 2.8. Thus, from the point of view of the insects, these ecosystems were even more ‘fractal’ than they had appeared to the researchers.

Species packing and the ‘slippery slope’

But if there are more individual small insects than large ones in the ecosystem, then surely there should also be more small species? To a considerable extent, the implications for species numbers of Morse *et al.*'s fractal paper had already been prefigured by May (1978), in trying to explain the negative value of the slope on the right-hand side of his species-size curves (Fig. 1). Noting that it was well-known that larger populations of individual insects contain more species, he asked whether it was possible that the greater number of insect species with small body dimensions could be a natural consequence of the larger numbers of small individual insects. I won't go through the argument in detail, but after making some back-of-envelope calculations, May plausibly concluded that the predicted dependence of species number on species abundance was “nowhere near enough” to explain the observed increase in species number with decreasing insect size. Even if May had in 1978 known the results of Morse *et al.*'s field work, published seven years later, his conclusion would almost certainly have been the same.

Instead, May opted to explain the relationship between species number and insect size by revisiting a classic paper by Hutchinson (1959), which directly addressed the question of how many species can co-exist; this has since been dubbed the ‘species packing problem’ (MacArthur, 1969). Hutchinson proposed that any terrestrial environment has a granular or ‘mosaic’ character based on its physical structure, and that this granularity offers a greater variety of niches suitable for occupation by small species than is available to larger species. In other words, as insects get smaller, we can expect there to be more insect species packed into the environment, because it ‘has more room for them’. This rather vague idea was worked out in more detail in a

mathematical paper co-authored with Robert MacArthur (Hutchinson *et al.* 1959), which even Robert May described as “difficult” (I can only agree!). That paper proposed that the number of species S of length L present in any ecosystem should be inversely proportional to L^2 but there was no good explanation for why the number of species should reach a peak and then fall away on the left hand side of the species-size graph at very small sizes. Nineteen years later, May himself revisited the same idea, this time arguing that in the right-hand region of the species-size curve the observed slope is due to the environment's granular nature as a 2 – 3-dimensional surface. Although this sounds very like the fractal dimension explored by Morse *et al.* (1985), May's publication didn't mention the term ‘fractal’. Remember too that here May was looking at species number, not the number of individual insects. May (1978) proposed that $S \propto L^{-\gamma}$ where $\gamma = 2-3$, and showed that this relationship appears to hold for British Coleoptera (Fig. 1B) as well as for British and Australian Lepidoptera, although in every case there was the usual deficit of the smallest species.

Loder *et al.* (1997) later pointed out that although a lot of effort had by then been devoted to looking at the slopes of the right-hand sides of such species-size curves, the biological significance of what they now dubbed the ‘slippery slope’ is unclear. Moreover, there is no theory that enables us either to predict the modal value of the distribution, nor to explain why there appears to be a cut-off point for small species. May's (1978) proposal, still the most plausible, is that at such small dimensions, occupancy of the niche by any particular kind of animal must be shared with similar-sized animals of kinds other than those being analysed. He says “for any one group (e.g., beetles), ecological aspects of the species-size relation tend to be masked by the group blending into ecologically similar, but taxonomically different, groups at both low and high ends of its size range”. Very small beetles, for example, may face competition from smaller but unrelated animals such as mites,

as I mentioned above.

What May *didn't* consider was that there may actually be a minimum physical size for any particular kind of insect, or even for any kind of animal at all. Such a limit might operate only in those orders that contain very small or very large species, and so there would be little evidence for it when examining size distributions within the Hexapoda as a whole. If there were indeed minimum and maximum sizes for insects, then they would constitute an entirely different kind of mechanism for determining the species-size modal value and explaining the prevalence of right-skew in lognormal species-size curves. Such limits would depend on anatomical and physiological considerations rather than ecological-evolutionary processes. I'll consider this subject in a future *Research Spotlight* article.

Little things that run the world

Famously, one of the twentieth century's most eminent entomologists, E.O. Wilson (1987), pointed out that insects and other terrestrial arthropods are “the little things that run the world”. Why ‘little’? I suppose Wilson must have meant that insects are very much smaller than humans. Since the average adult human is 1.66 m tall (mean of both sexes, whole world: <https://ourworldindata.org/>), this means that the average insect is 129 times smaller in linear dimension than the average human. A hexapod of ‘average’ length would be predicted (on average) to have a body mass (fresh weight) of about 54.5 mg (Sage, 1982). Since the mean weight of single human is 62.0 kg (world data, average of men and women: Walpole *et al.*, 2012), the average human is more than a million times heavier (to be exact, 1,137,615 x) than the average insect.

So just as Wilson said, insects are indeed very small compared to humans, and it is appropriate to reflect on how little they need us. But perhaps Wilson had more in mind than that? As we have seen, the smaller they are, the more individual insects, and the more different kinds of insect there are. Perhaps what Wilson meant was that it is the smallest insects that really dominate ecosystem processes in the places where they live.



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