Size and supersize

Some years ago a physicist colleague expressed doubts to me that there could ever be any kind of deep theory of biology — that is, nothing that might match the routine success of physics in explaining things such as the detailed flow pattern of a fluid starting from simple assumptions. Given the pervasive influence of chance in evolution, she suggested, mathematics probably would never be nearly as useful in biology.

I was more optimistic, although I'm not sure I had good reason to be. Years later, I now think we were both, in a sense, partially right. Biology, much like geology or human history, has an inescapably contingent character, as chance events send history down one channel or another. There's no law-like explanation for why a creature as strange as the duck-billed platypus simply had to exist.

But broad patterns do emerge all the same, and in recent years we've seen many examples. The interactions among proteins in the cell, for example, conform to network patterns we would expect on mathematical principles; they can be explained as the natural outcome of a simple evolutionary process. Likewise, distributions of species lifetimes or fluctuations in ecological populations also follow quite simple patterns explicable by simple processes.

Of course, statistical patterns feel a little abstract. Could mathematical theory explain some of the more 'living' features of biological reality? The blue whale, for instance, is the largest of all mammals, and seemingly anomalous in its size. It weighs in at 175,000 kg, around 30 times the weight of the African elephant. Is this size a freak of nature, the consequence of a rare accident? Or might it actually be unsurprising in the light of other facts and basic physical principles? Recent work suggests that mathematics may indeed be able to resolve such questions.

Biologists have long noted a striking pattern in the distribution of animal species by size (considering species within a 'clade' or family descended from a common ancestor). For example, species of mammals, birds, fish and insects all follow a simple distribution, showing a strong right skew about the mean size. Take terrestrial mammals: the most common size here is about 40 g, roughly the mass of a common rat. This is a little higher than the smallest — the pygmy shrew at 2 g — but far less than the largest, with the now-extinct Columbian mammoth having a mass of about 10 million g.

At least one species of enormous sea monster is just what we should expect.

This regularity co-exists — not too peacefully, it would at first seem — with another pattern known as Cope's rule, named after the American palaeontologist Edward Drinker Cope. This describes the tendency for the body size of organisms within any lineage to increase through evolutionary history. The rule finds particularly strong support in mammals, and it makes some good sense. Larger organisms have an advantage in fighting off predators and capturing prey, and perhaps also in surviving temporary environmental challenges. Once a species is established in a niche, bigger seems to be better; species drift toward higher masses.

Clearly, Cope's rule would drive species to ever larger sizes. So the observed stable distribution of sizes implies the action of some countervailing influence. And there is one — extinction. Indeed, biologists believe that extinction actually tends to become more likely as species grow larger, as bigger organisms face higher demands for energy and their populations tend to have lower overall numbers, among other effects.

So, we have evolutionary drift to bigger sizes, held in check by eventual extinction of the larger species. A few years ago, for terrestrial mammals at least, Aaron Clauset and Doug Erwin showed that this is almost, but not quite, enough to explain the observed size distribution (A. Clauset and D. Erwin, *Science* **321,** 399–401; 2008). There is one further element: a fundamental lower bound on organism size that is directly linked to thermal regulation.

In mammals and birds, it is well understood why no species is smaller than the pygmy shrew. It's mass of 2 g represents the boundary beyond which a warm-blooded organism's ability to generate heat internally (dependent on body volume) cannot match up with convective heat loss to the air (dependent on surface area). No organism can be smaller than this. Hence, the balance between the two processes of growth, as captured in Cope's rule, and increasing likelihood of extinction at high mass, has to play out in the presence of this hard lower boundary.

Impressively, these three factors together appear to give a more or less complete explanation. Clauset and Erwin showed that a mathematical balance of this sort gives rise to a strongly skewed size distribution that is very close to what is observed empirically for terrestrial mammals. Intriguingly, the hard boundary at lower sizes — as opposed to the softer boundary at higher masses (due to gradually increasingly likelihood for extinction) — accounts for the observed asymmetry of the distribution around the mean.

The story goes further too. If this explanation is correct, then one should expect it to apply to mammals in water as well as on land. The cetaceans — species including whales, dolphins and porpoises — do indeed exhibit the canonical right-skewed pattern, with the median size of about 360 kg being close to the smallest (37 kg) but far from the largest (175,000 kg). This suggests that the theory could hold for them, although obviously something must be very different given the huge upper range of sizes. The crucial change turns out to be the lower limit.

As Clauset now points out, the much higher thermal conductivity of water implies that the lower size limit in water is more like 7 kg, several thousand times higher than in air (A. Clauset, Preprint at http://arxiv.org/abs/1207.1478; 2012). This effectively shifts the resulting distribution upwards in size dramatically, and, again, the result fits very closely to the observed distribution of pelagic mammals.

And what about that whale? It is in the nature of any single species that the chancy character of history shows up most clearly. There is no way to explain why the blue whale has its size without making some long historical analysis of all the quirky pressures that created the species in the first place. But a less specific question is whether the size of the blue whale fits with what we should expect, or is instead an outlier, an anomaly.

And as Clauset shows, it seems to be the former. Indeed, his calculation of the chance that some oceanic species would be at least as large as the blue whale, given the opposing influences on size, is close to 90%. The chance of there having been a species considerably larger, even 5 times as large, is still appreciable. In our world, at least one species of enormous sea monster is just what we should expect. ❐

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