

# The evolution of large size: how does Cope's Rule work?

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**Cope's Rule is the tendency for organisms in evolving lineages to increase in size over time. The concept is detailed in many textbooks, but has rarely been demonstrated. Many suggestions of the benefits of large body size exist, but none has yet been confirmed empirically. Using a large-scale analysis of recent studies, Kingsolver and Pfennig have now shown how size benefits survival, mating success and fecundity, and they provide convincing arguments for a mechanism that is capable of driving Cope's Rule.**

Cope's Rule is the tendency for evolutionary lineages to increase in size over time [1] and, in spite of being over a century old [2], is still poorly understood. Studies across a wide range of taxa have supported [3,4], and rejected [5–7] it, with one recent study suggesting that previous analyses had been tested at too high a taxonomic level to be effective [3]. Cope's Rule has also been explained as a statistical artefact of increasing variance in size in a clade that arises from small ancestors [8]. For Cope's Rule to operate, large body size must provide an increase in fitness (Box 1). A new study by Kingsolver and Pfennig [9] appears to demonstrate this for the first time.

Using a recent study of data assembled from natural populations [10], Kingsolver and Pfennig [9] assessed information about the effects of size change on fitness. Requirements for data to be included in this new study were: (i) natural variation of quantitative traits; (ii) measurements of fitness; and (iii) estimation of selection differentials or gradients (providing a standardized measure of directional selection, enabling cross-study comparisons).

The authors split characteristic traits into 'overall size traits' (e.g. total length, mass, etc.), or 'other morphological traits'. This 'other trait' category included size-dependent characteristics, such as wingspan, flower size, and so on, and therefore the new results are likely to be conservative as many of these traits will be tied to body mass. This splitting of traits gave a total of 854 trait estimates: 91 for size, and 763 for other traits, spread over 39 species from 42 studies, covering vertebrates, invertebrates and plants. The selection gradients were then plotted for both size and other traits according to their effects on 'overall fitness' and three key 'fitness' criteria: survival, fecundity and mating success, thus covering the effects of both size and other traits on both natural selection and sexual selection.

## Size and fitness

The results are quite startling (Figure 1): size increase produces a marked increase in survival, fecundity and mating success, whereas the effects of other traits were neutral. The results overall were highly significant: 79% gave a positive effect with larger size, (with a median of 0.15), but for other traits this was 50% (with a median of 0.02), an almost neutral effect because half produced positive results and half negative. When broken down into the three components, this positive effect is seen across all three analyses, and also across all of the taxonomic groups within them, so the results are unlikely to be an artefact of methodology or taxonomic bias. Furthermore, the patterns are inconsistent with alternating selection, which has been suggested for some findings of Cope's Rule, and negative selection associated with large size was rare. Although few studies had the appropriate data, the authors

### Box 1. Effects of large size

An increase in body size is supposed to convey many selective advantages on an organism, but also presents new problems [16]. For Cope's Rule to operate, any benefits must outweigh these problems. However, benefits and costs operate at various levels: a small increase in size might confer an advantage in interspecific competition for an individual against its rivals, but to evolve gigantothermy would require many, many generations of size increase and would have little short-term benefit (for this trait). Below are some of the most common arguments both for and against large size [1,16].

#### Benefits

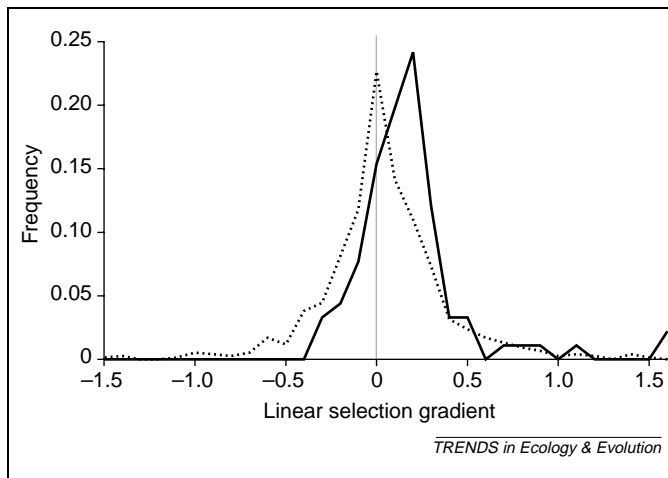
- Increased defence against predation (might be more vulnerable in some circumstances)
- Increase in predation success
- Greater range of acceptable foods
- Increased success in mating and intraspecific competition
- Increased success in interspecific competition
- Extended longevity
- Increased intelligence (with increased brain size)
- At very large size, the potential for thermal inertia (e.g. sauropod dinosaurs and tuna)
- Survival through lean times and resistance to climatic variation and extremes

#### Problems

- Increased development time (both pre- and post-natal)
- Increased requirement of food, water, and so on
- Susceptibility to extinction: a longer generation time gives a slower rate of evolution and, consequently, a reduced ability to adapt to sudden change
- Lower fecundity: switch from r-selection to a K-selection strategy produces fewer offspring with a high parental investment in each over many 'poorer' offspring

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**Figure 1.** The distribution of linear selection gradients ( $\beta$ ) for body size (solid line) and for other morphological traits (dashed line). Body size is a positive result, whereas the other traits provide only neutral selection effects. Reproduced, with permission, from [9].

tested, where possible, for stabilizing selection and showed that individual selection on size was not the primary mechanism preventing evolution towards large size.

Several biases were present and identified in the article [9]: (i) the studies were weighted towards birds, plants and insects, which might be unusual groups in terms of size change and fitness. However, Cope's Rule has also been found in several mammal groups [3,11] and the dinosaurs (D.W.E. Hone, MSc Thesis, Imperial College, London, 2001) so this potential bias might be less significant than Kingsolver and Pfennig suggest; (ii) only one component of fitness was analysed for most studies – a more comprehensive coverage might reveal counter selection; (iii) the analysis was based only on published studies, and these are unlikely to have reported marginal or non-significant results. There might be an additional bias: positive selection might be observed because small individuals are fundamentally unhealthy and die more easily (being 'the runt of the litter') rather than owing to active selection for large size. However, it is difficult to determine the extent of these possible biases, particularly in the face of such a positive set of results.

### Endless trends to gigantism

In the light of these results, why do species not continue to increase in size infinitely? The selective advantages and the measured size increases over just a few generations are several orders of magnitude higher than is required for the size increases shown in palaeontological studies of Cope's Rule. If unopposed, these trends could lead to a macroevolutionary pattern of size change.

Within the study [9], development time was shown to correlate positively with size increase; that is, increased size leads to an increase in development time (although few studies were appropriate for this and these were mainly for plants). Therefore, an increase in developmental time is an obvious limitation on rapid size increase, but cannot account for the observed lack of stabilizing selection. Whereas a recent study of tyrannosaurid dinosaurs [12] showed that development need not be a limiting factor on large size, this appears to be the

exception rather than the rule. Even with the accelerated development seen in *Tyrannosaurus rex*, it still developed more slowly in absolute terms than did its close relatives among the tyrannosaurs.

Kingsolver and Pfennig [9] also suggest that mass extinctions account for the cap on size increase, as large organisms are more vulnerable to environmental crises [13]. These opposing trends and the variation demonstrated might explain why Cope's Rule is found in some groups and not in others.

However, there are probably additional caps at the species or generational level that could prevent the large short-term size increases predicted by these results (Box 1). First, there is the issue of morphological constraints on current size: for example, the giraffe *Giraffa camelopardis* might not be able to grow larger than it is as it could not achieve the necessary arterial pressure for the blood to reach a head on a longer neck; also, the pied kingfisher *Ceryle rudis* would no longer be capable of hovering if it became heavier, preventing it from feeding. Second, there are the probable effects of niche overlap. Most organisms are restricted ecologically to an 'n-dimensional morphospace', enclosed on all sides by the morphospaces of other species. If an organism becomes too large, it will encroach on the morphospaces of other species, leading to increased competition. The species increasing in size will be less adapted to competition in this niche than is the incumbent species and will be outcompeted and forced to return to its existing niche. There is also the issue of the 'evolutionary clock', which limits the ability of large organisms to adapt to severe changes because of their long generation times. Small organisms can adapt or even speciate to survive times of mass extinction [7], terminating larger species. Finally, an extreme case of size increase might ultimately lead to divergence and speciation (as shown in the Galapagos finches *Geospiza* spp. [14]), although this would be impossible to determine over such a short time period.

### Prospects

Cope's Rule appears to be alive and well, but where do we go from here? To test Cope's Rule fully, we need to cover the intermediate ground of multiple generations in extant lineages, and across shorter palaeontological timescales. Alroy's recommendation of using lower taxonomic levels for tests of Cope's Rule [3] has yet to be followed on a larger scale, with only a few studies being carried out since [15]. There is still scepticism among many palaeobiologists about the reality of Cope's Rule. It would be ironic if Cope's Rule turned out to be a statistical artefact [5,7,8], and was not supported by Cope's [2] original macroevolutionary observation, and yet the traditional explanation for this supposed trend (the fitness advantage of large size) turned out to be a valid evolutionary driving force [9].

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## Letters

## Taxonomic inflation: species concept or historical geopolitical bias?

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In a recent article in *TREE* [1], Isaac et al. examine taxonomic inflation, which they describe as 'where known subspecies are raised to species as a result in a change of species concept'. Their argument is that more species are erected under the phylogenetic species concept than under the biological species concept. However, we argue that this inflation is due to a historical geopolitical bias affecting current predictions of expected genetic diversity within species.

Genetic data, typically mitochondrial DNA (mtDNA) sequences, are being used increasingly in the identification of new species [2]. Estimates of expected levels of genetic divergence within, as opposed to between, species have been made [3], and a high degree of genetic divergence between populations is used to infer species status [4]. For many species, this is more practical than applying a biological species concept [5]. But what is 'high' genetic divergence? Johns and Avise produced a yardstick with which to answer this by estimating sequence divergence between, and within, taxa for a variety of vertebrates [6]. Later studies often compare their results with this to confirm whether the genetic divergence in their study is high.

However, early phylogeographical works were heavily geographically biased as systematists tended to work on organisms found on their doorsteps; for example, the first mtDNA population-level studies were performed on pocket gophers because of their 'local availability' [7]. DNA sequencing was also expensive and, owing to this constraint, as well as to the logistical difficulties involved

in sampling in tropical countries, most early molecular ecology studies were carried out in North American and northern European countries, and on organisms from these areas. For example, of the studies using sequence data published in the journal *Evolution* between 1991 and 1994, 60% were of North American organisms, whereas none were of African species. Similarly, in a combined analysis of previously published phylogeographical analyses [8], of 23 studies concerning terrestrial amphibians and reptiles, 14 were from the USA, and four from Europe. The only African representative was the model amphibian, *Xenopus*.

Although economically rich, North America and northern Europe are generally genetically depauperate, as a result of only recent recolonization by most vertebrates following the last glacial period [9]. Therefore, estimates of 'typical' levels of genetic divergence within species were biased downwards. As DNA sequencing became cheaper, and as research began to focus on organisms in the tropics, higher levels of divergence within species were reported. Thus, when comparative data from reptiles were reassessed to include more recent data [10], out of 35 genera the four with the highest divergence between sister taxa were all from Africa. These genera had approximately twice the average divergence of all the other genera included in the study, and over three times the divergence between sister-species compared with that first reported [8]. This threefold increase has often been explained as resulting from the occurrence of cryptic species, leading to the observed taxonomic inflation.

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