COPE'S RULE

Pp. 209-210 in Pagel, M. (ed.) *Encyclopedia of evolution*. Oxford University Press, New York.

Cope's Rule is the observation that animal groups tend to evolve through time towards larger body size. Edward Drinker Cope (1840-1897) never formally stated this rule, but it is implicit in many of his writings. Cope is famous for his work on dinosaurs and fossil mammals; indeed, his long-standing rivalry with Othniel Charles Marsh (1831-1899) is well known. Cope was an evolutionist, and he wrote textbooks that promoted Darwinism. In these, he reconstructed phylogenies of reptiles and mammals, and in doing so, he noted how mean body size increased through time; classic examples include the evolution of the horses from terrier-sized *Hyracotherium* from the Eocene to the modern, which is twenty times the size.

There has been debate about whether Cope's rule should be termed a law, but that is not possible because of exceptions to his observation, and also because, if it were termed Cope's law, there would be an implication of an innate force that drove animals to become bigger. Exceptions to Cope's observation include many cases of evolution to small size, for example on islands (dwarf dinosaurs in the Romanian Cretaceous, dwarf Pleistocene elephants on Mediterranean islands), or in association with adaptations to cave life or burrowing. A rule is, according to *Webster*, 'a generally prevailing condition,' which is the true status of Cope's observation.

Why should body size generally increase within animal lineages? Most discussions have focussed on the advantages of being big:

- improved ability to capture prey (lions) or to escape predation (sauropod dinosaurs, elephants);
- greater reproductive success (sexual selection);
- increased intelligence (brain size relates to body size);
- expanded size range of acceptable food (giraffes, elephants);
- decreased annual mortality (as a result of the above);
- extended individual longevity (life span relates broadly to body size);
- increased heat retention per unit volume (Bergmann's rule: body size of endotherms increases polewards).

But the story is not so simple: there are disadvantages with large size, particularly the fact that large animals require a great deal of food, and hence can have problems when food is sparse. Elephants have to migrate huge distances merely to find enough fodder. In addition, large animals are rare, so, during crises, size is clearly exposed as a specialization, like an unusual dietary requirement, and a lineage of large animals is, on the whole, more exposed to extinction, than a related lineage of smaller animals.

To a large extent, Cope 's rule is a statistical artifact of the splitting nature of evolution. After it originates, a clade inevitably splits and expands. So, through time, the diversity of body forms increases. Add to that the observation that the founders of clades are always small, then there is only one way that evolution can go, as Steven Stanley has observed. Through time, it is inevitable that the range of body sizes exhibited by a clade will increase, and the size of the largest species will increase. However, the size of the smallest species often remains rather constant, or even reduces. With increasing variance in

body size through time, the mean body size often does not increase.

So Cope 's rule is true, and there are indeed genuine advantages to large body size. But there is no driving principle here. We tend to notice large animals, and forget that all we are seeing is an increase in variance through time, while mean body size of most clades remains constant.

BIBLIOGRAPHY

Cope, E. D. 1896. *The primary factors of organic evolution*. Chicago: Open Court Publishing Company. One of several publications in which Cope gave examples of the increase of body size in evolutionary lineages of mammals.

Damuth, J. and MacFadden, R. J., eds 1990. *Body size in mammalian paleobiology*. Cambridge: Cambridge University Press. Case studies of body size patterns among mammals.

Jablonski, D. 1996. Body-size evolution in Cretaceous molluscs and the status of Cope 's rule. *Nature* 385: 250-252. Demonstration that Cope 's rule does not apply as an overriding principle among molluscs.

Peters, R. H. 1993. *The ecological implications of body size*. Cambridge: Cambridge University Press. The role of body size in microevolution and ecology.

Stanley, S. M. 1973. An explanation for Cope 's rule. *Evolution* 27: 1-26. An investigation of many examples of Cope 's rule, and demonstration that it is more a matter of evolving from small ancestors than specifically evolving to be big.