

curves reconstructed for dinosaurs are realistic, because other types of curve might fit better, and few data at their lower ends are currently available.

A third crucial question is how birds and their immediate dinosaurian relatives became small. Erickson [1], we think, misstates our results [10,11] when he says: 'It was posited that selection favored reduced body size because it enabled decreases in wing loading and improved power-to-weight ratios.' Our general analysis of growth patterns in dinosaurs showed that adult size and absolute growth rate are usually correlated [12]. As bird ancestors became miniaturized, they retained similar adult body proportions as their larger ancestors. Once bird ancestors became small, regardless of selection pressures, a geometrically similar wing size at this smaller body size would have automatically lowered wing loading, and thus increased aerodynamic lift. Given the scaling of power requirements, we implied that this consideration might be useful in analyzing early flight evolution.

We agree on the potential value and use of bone histology in fossil (and living) vertebrates to understanding the growth strategies of extinct animals. However, the opening chapters of this book are just being written.

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## What's wrong with inclusive fitness?

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In a recent issue of *TREE*, Foster *et al.* [1] defend inclusive fitness theory [2] from recent challenges [3,4]. The main author of these challenges, E.O. Wilson, argues that inclusive fitness (also called kin selection [5]) might not be the main explanation for the evolution of altruism and eusociality. By contrast, Foster *et al.* claim not only that inclusive fitness is the most prominent explanation for altruism, but also that genetic 'relatedness is always required for altruism to evolve' [1]. Here, we take issue with their claim about genetic relatedness and place the debate in a larger historical context.

The key finding of inclusive fitness theory is Hamilton's rule [2], which predicts that an altruistic trait will increase in frequency when the inequality  $rb > c$  is satisfied. Here,  $b$

is the average fitness benefit provided by the altruistic behaviour and  $c$  is its average cost. The claim by Foster *et al.* that genetic similarity between altruists and their recipients is always required stems from the  $r$  term, which is traditionally seen as a measure of relatedness, and which obviously must be  $>0$  to satisfy Hamilton's rule. Ironically, in the form of Hamilton's rule [6] that is required to address conditional traits such as eusocial sterility, the 'relatedness coefficient',  $r$ , no longer depends on kinship or genetic similarity, and the indirect fitness concept of inclusive fitness theory is not used.

As Wilson and Hölldobler point out [4], traits for eusocial sterility must be phenotypically plastic. For such conditional behaviours, Queller [6] showed that  $r$  needs to be calculated using the assortment between the genotype of each individual and the phenotype (i.e. behaviours) of those with whom they interact. Queller's more general version of

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Hamilton's rule does not measure genetic similarity and it is thus not fundamental to Hamilton's rule [7]. Genetic similarity is just one way to create the necessary degree of genotype–phenotype assortment. Queller's version also calculates the average direct fitness benefits to carriers. This highlights the phenotypic effect that colony-level adaptations (e.g. sterile workers) [3,4,8] have on selection among reproductive individuals (e.g. queens), rather than on the indirect fitness of sterile workers themselves.

In the traditional view of inclusive fitness,  $rb$  measures the indirect fitness of an average altruist via its enhancement of direct fitness to its relatives. Alternatively, and more simply, Hamilton's rule can be interpreted in terms of the direct fitness of carriers of the altruistic genotype of interest, where  $rb$  measures how much the personal reproduction of an average carrier is enhanced by help from others, related or not. Although these alternative fitness accounting methods can yield the same result, the direct fitness approach used by Queller is more general; for example, it enables one to analyse interspecific mutualisms [7]. A preference for the indirect fitness accounting method (which requires genetic similarity) does not imply that genetic similarity is actually required either by Hamilton's rule or as a causal mechanism in the evolution of altruism and eusociality in general [9].

The debate between Foster *et al.* and Wilson and Hölldobler must also be viewed in its historical context [8,10]. Foster *et al.* list several 'fallacies' in their Table 1 as though these are simple mistakes that anyone should be able to avoid, when, in fact, they were discovered only after decades of research. There was a time when kin selection was regarded as an alternative to group selection, when 3/4 relatedness was thought to be the primary explanation of eusociality, when  $r$  meant genealogical relatedness, when the focus on  $r$  obscured the importance of ecological factors (encompassed by  $b$  and  $c$ ), and so on. One by one, the predictions that appeared to issue from kin selection theory failed, leading to an expanded form in which 'relatedness' ( $r$ ) can now be positive even in randomly formed groups.

Although we are not necessarily endorsing all their arguments, Wilson and Hölldobler's most important claim is that colony-level selection is necessary and sufficient to explain

the evolution of eusociality. This was the explanation that historically preceded kin selection theory, which Hamilton's focus on genetic relatedness appeared to replace. Colony-level selection for eusociality is made possible by colony-level adaptations that produce sufficient assortment between the genotype of reproductives and the phenotypic help from non-reproductives. The efficiency of these adaptations in delivering fitness benefits to reproductives matters, whereas the degree of relatedness to non-reproductives does not. This assortment produces heritable phenotypic variation at the colony level, which depends on genetic variation among colonies, but the amount of genetic variation need not be exceptional and can even be random, just as random genetic variation among individuals can be sufficient for individual-level selection. The expanded version of 'kin selection' described by Foster *et al.* is correct only insofar as it converges upon the theory that it appeared to replace.

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## Free journals for developing countries

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The science publishers, Blackwell, Elsevier, Harcourt Worldwide STM group, Wolters Kluwer International Health and Science, Springer-Verlag and John Wiley, were approached by the WHO and the *British Medical Journal* in 2001. Initially, more than 1500 journals were made available for free or at significantly reduced prices to universities, medical schools, and research and public institutions in developing countries. In 2002, 22 additional publishers joined, and more than 2000 journals are now available. Currently more than 70 publishers are participating in the program.

Gro Harlem Brundtland, the former director-general of the WHO, said that this initiative was "perhaps the biggest step ever taken towards reducing the health information gap between rich and poor countries".

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