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Letter

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]) may not be the main explanation for the evolution of altruism and eusociality. In contrast, Foster *et al.* claim that inclusive fitness is not only the most prominent explanation for altruism, but that genetic “relatedness is always required for altruism to evolve” [1, p. 59]. 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 in 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 [4] point out, 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* (behaviours) of those with which they interact. Queller’s more general version of 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 facilitates a focus on 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 an average carrier's personal reproduction is enhanced by help from others—related or not. While these alternative fitness accounting methods can yield the same result, the direct fitness approach used by Queller is more general; for example, it allows one to analyze 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 seen in its historical context [8,10]. Foster *et al.* list a number of “fallacies” in their Table 1 as if 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), etc. One by one, the predictions that seemed 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.

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 seemed 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; 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 seemed to replace.

- 1 Foster, K.R. *et al.* (2006) Kin selection is the key to altruism. *Trends Ecol. Evol.* 21 (2), 57-60
- 2 Hamilton, W.D. (1964) The Genetical Evolution of Social Behavior I and II. *J. Theor. Biol.* 7, 1-52
- 3 Wilson, E.O. (2005) Kin Selection as the Key to Altruism: Its Rise and Fall. *Social Research* 72, 159-168
- 4 Wilson, E.O. and Hölldobler, B. (2005) Eusociality: Origin and consequences. *Proc. Natl. Acad. Sci.* 102, 13367-13371
- 5 Maynard Smith, J. (1964) Groups Selection and Kin Selection. *Nature* 201, 1145-1147

- 6 Queller, D.C. (1985) Kinship, Reciprocity and Synergism in the Evolution of Social Behaviour. *Nature* 318, 366-367
- 7 Fletcher, J.A. and Zwick, M. (2006) Unifying the Theories of Inclusive Fitness and Reciprocal Altruism. *Am. Nat.* 168 (3), (in press)
- 8 Boomsma, J.J. and Franks, N.R. (2006) Social insects: from selfish genes to self organisation and beyond. *Trends Ecol. Evol.* 21 (6), 303-308
- 9 Fletcher, J.A. and Doebeli, M. (2006) How altruism evolves: assortment and synergy. *Journal of Evolutionary Biology* (in press)
- 10 Sober, E. and Wilson, D.S. (1998) *Unto Others, The Evolution and Psychology of Unselfish Behavior*, Harvard University Press