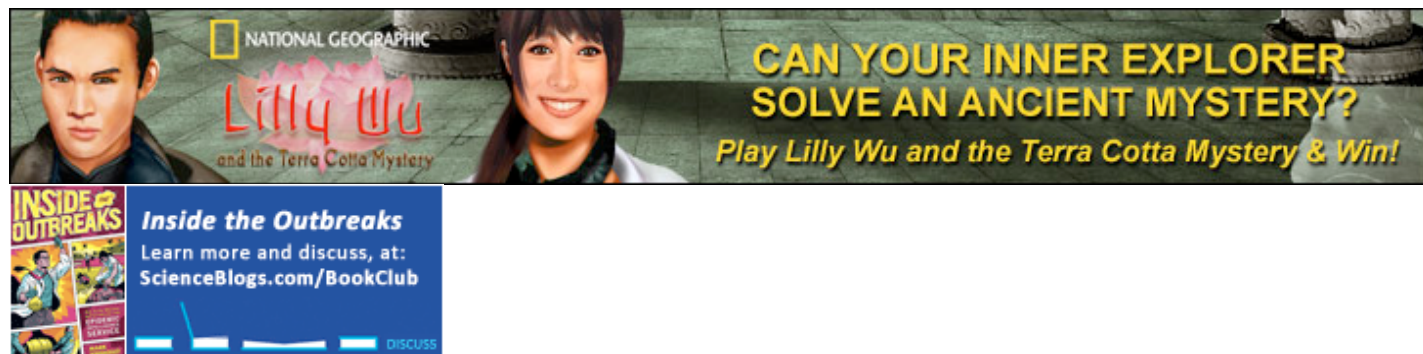
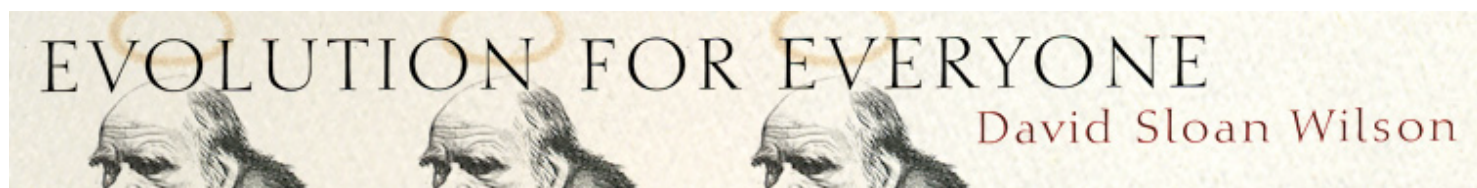


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Profile



I am an evolutionist who studies all aspects of humanity in addition to the biological world, as I relate in my book *Evolution for Everyone: How Darwin's Theory Can Change the Way We Think About Our Lives*. In addition to my academic research, I manage a number of programs and websites for expanding evolution beyond the biological sciences in higher education ([EvoS](#)), public policy formulation ([The Evolution Institute](#)), community based research ([Binghamton Neighborhood Project](#)) and the study of religion ([Evolutionary Religious Studies](#)).

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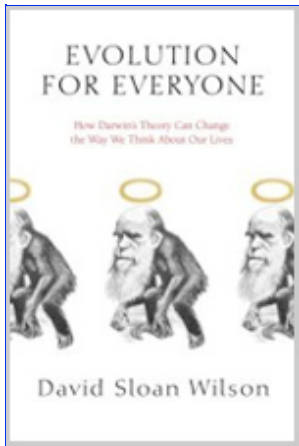
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[139 Co-authors Can't Be Wrong--And That's The Problem](#)

Category: [Truth and Reconciliation in Group Selection](#)

Posted on: March 25, 2011 2:22 PM, by [David Sloan Wilson](#)

The March 24 issue of *Nature* includes [5 responses](#) to the critique of inclusive fitness theory by Martin Nowak, Corina Tarnita, and Edward Wilson published earlier in *Nature*. One of the responses has 139 co-authors, illustrating the degree to which the evolution community has become aroused. I am reminded of the old record album titled "50,000,000 Elvis Fans Can't Be Wrong." In science, when you can't be wrong, that's a problem.

Before proceeding, I want to stress that I do not agree with the Nowak et al. article in all respects, as I have already explained in two previous posts ([1,2](#)).

The first indication that the gang of 139 has adopted a position that can't be wrong comes on the first page of their response, where they state:

Nowak et al. appear to have confused the completely general theory of inclusive fitness with models of specific cases.

What does it mean for an evolutionary theory of social behavior to be completely general? It means that

any conceivable example of social evolution can fit within its framework.

Being a completely general theory is a virtue. Consider the standard definition of genetic evolution as any kind of genetic change, whether by mutation, selection, drift, linkage disequilibrium, and so on. It is important to account for all kinds of genetic change, but it is vacuous to point to any particular example and declare "that's genetic evolution!" Progress requires explaining specific cases within the framework--that the beaks of Darwin's finches are largely a product of selection; that the floppy ears of domesticated foxes are a byproduct of selection for docile behavior; that some debilitating diseases can be explained by selection-mutation balance; that many mitochondrial genes evolve by drift and can be used as molecular clocks, and so on.

Inclusive fitness theory did not start out as a completely general theory, able to accommodate any conceivable example of social evolution. The gang of 139 should be able to agree on that point and the passage by W.D. Hamilton quoted by Nowak et al. in their reply provides a reminder if needed. The original theory was confined to genealogical relatedness and made a host of assumptions about additive fitness effects, population structure, and so on. Some of these assumptions were explicit and others were implicit, requiring decades to reveal their inadequacies.

Modern inclusive fitness theory *does* aspire to be a completely general theory, which can be regarded as a *virtue*, as I have already stressed. After it has achieved that exalted status, however, it is vacuous to point to any given example of social evolution and declare it as proof of inclusive fitness theory--just as it would be vacuous to point to any given example of genetic evolution and declare it as proof of genetic evolution theory. Yet that is precisely what the gang of 139 is doing with its catalog of inclusive fitness theory success stories.

Let's take a look at some examples to see what I mean. One of the most striking predictions of Hamilton's original theory was that the extra-high cooperativeness of eusocial insect colonies can be explained by the extra-high relatedness of sisters in haplo-diploid species. It was a great idea that turned out to be wrong, as every expert acknowledges today. Incidentally, [Richard Dawkins is once again distorting history when he calls this a "throwaway side-issue"](#). It was regarded as a big damn deal, as any serious scholar of the period can attest.

In any case, the failure of the $3/4$ relatedness hypothesis did not threaten inclusive fitness theory as a whole, even in its original formulation. Hamilton's rule has three terms and a low value of r can be compensated by a suitably large b/c ratio. Today we know that eusocial species span a wide range of r values, including very low values, caused by colonies founded by multiple queens and/or queens that mate with multiple males. When we focus on the *origin* of eusociality, it appears restricted to monogamous lineages to the best of our current knowledge. The gang of 139 treats this as a big damn deal and a confirmation of inclusive fitness theory, but what if it had turned out otherwise or if future research leads to a different conclusion? What if examples are found for the origin of eusociality in which $r=1/4$ or $1/8$ rather than $1/2$? That would no more threaten inclusive fitness theory than the rejection of the $r=3/4$ hypothesis.

Even zero relatedness, as most people understand the term, would not pose a threat to inclusive fitness theory. Imagine that groups form totally at random but that the social behavior benefits the whole group, including the individual actor. Inclusive fitness theory can be formulated so that this results in a positive value of r , admittedly a small value, but good enough if the b/c ratio is suitably large. Once inclusive fitness theory has become "completely general" it can accommodate any outcome of social evolution and pointing to any particular outcome as a success story for the general theory is vacuous.

How can we go beyond the meaningless listing of examples to address the substantive issues at stake? Here are some suggestions.

1) Explain the specific cases. Recall my example of what saves the theory of genetic evolution from being vacuous--by explaining specific cases within the framework. We need to understand the importance of specific factors such as: a) relatedness compared to the ecological factors that determine

the b/c ratio; b) genealogical relatedness compared to other factors that contribute to r, such as assortative interactions or multigenerational population dynamics; c) the importance of complex genotype-phenotype relationships as opposed to additive genetic effects; d) the impact of specific population structures, and so on.

2) Understand the difference between the original theory of inclusive fitness and the completely general theory. A large fraction of the evolution community and the bulk of the general public still associates inclusive fitness theory with Hamilton's original formulation, as represented by the simple rule $br-c>0$. This rule is based on a host of simplifying assumptions, as the gang of 139 will readily agree. Modifying the assumptions results in a modification of the rule, requiring additional terms or a re-interpretation of the original terms. In some modern versions of inclusive fitness theory, for example, the term r represents an equation with multiple terms that interact in a non-linear fashion. Representing the equation as a single term gives an illusion of simplicity and similarity with the original formulation that simply doesn't exist. In short, going beyond the original theory requires going beyond Hamilton's rule, yet Hamilton's rule is still preserved as a kind of sacred object, even by the gang of 139 and the other responses to the Nowak et al. article.

3) Realize that there is more than one completely general theory. A completely general theory of social evolution provides categories that can accommodate any conceivable example. There is more than one way to sort examples into categories; hence there is more than one completely general theory of social evolution. In fact there are many, even many that sail under the name of inclusive fitness theory. Insofar as they all provide general accounting systems, they are all inter-translatable, but failure to translate appropriately leads to endless confusion, even among the cognoscenti. The idea that inclusive fitness theory does not invoke group selection is an outstanding early example of this confusion, which nearly everyone [except Richard Dawkins](#) now acknowledges. I would like to publicly request the assistance of the gang of 139 to help Dawkins understand what they already know.

4) Recognize the strengths and weaknesses of any particular completely general theory. There is potentially an infinite number of ways to sort examples into categories, hence an infinite number of completely general theories of social evolution. The merits of any particular system of categories and the justification for more than one turns out to be a complicated philosophical issue discussed under the term "pluralism" (see the conclusion of [Unto Others](#) for a detailed discussion). I am happy to acknowledge that inclusive fitness theory has led to useful insights, in contrast to Nowak et al. and in agreement with the gang of 139. However...

5) Just because a completely general theory has resulted in insights doesn't make it the best one. Suppose that I got everyone to bend over, look between their legs, and maintain that posture for the rest of their lives. No doubt they would manage after a fashion, although not as well as by standing up and looking straight ahead. Inclusive fitness theory has been the dominant paradigm for the evolution of social behavior for the last 50 years. Merely pointing to the fact that it has achieved insights says nothing whatsoever about its merits compared to other completely general theories.

6) Learn to distinguish axioms from results that can be otherwise. It is the stated goal of inclusive fitness theory to render all forms of natural selection as maximizing at the individual level of the biological hierarchy, which dictates how the theory is constructed. Compare this with multilevel selection theory, in which a given trait might, or might not, evolve by individual-level selection. If all traits are individual-level adaptations according to mls theory, this is a meaningful result because it could have been otherwise. If all traits are individual-level adaptations according to inclusive fitness theory, this is merely an axiom of the theory. For more, see my previous posts titled "Homage to George Williams and the last gasp of individualism ([1,2,3,4,5](#))".

7) Know your history. If scientists don't keep careful track of what was said and meant during the history of a subject, there is no hope for the rest of the world. The level of historical accountability for the subject of inclusive fitness theory is rock bottom and Richard Dawkins is among the very worst offenders. The historical account that Elliott Sober and I provide in [Unto Others](#) has largely withstood the test of time and is now being elaborated by historians of science such as Oren Harman in [The Price](#)

[of Altruism](#) and Mark Borello in [Evolutionary Restraints](#). When this period of evolutionary thought is studied with the same thoroughness as the early period, the degree of revisionism among scientists engaged in the controversy will become painfully apparent.

8) Is inclusive fitness theory a completely general theory? Finally, there is the question of whether inclusive fitness theory, even in its current form, can accommodate all outcomes of social evolution. One assumption of inclusive fitness theory is that all the evolutionary processes taking place in a multi-group population, including selection favoring some traits within groups, other traits between groups, and so on, can be averaged to calculate their net effects on evolutionary change in the total population. This assumption is biologically warranted when there is a global dispersal stage of the life cycle, but it is not necessarily warranted when groups are permanently isolated or dispersal is always local within a continuously distributed population. In these cases, it can be very difficult or even impossible to combine everything that is going on in the many patches into a fitness value that can be applied to individual organisms, as if they are trying to maximize something. Perhaps there is an exceptionally clever member of the gang of 139 who can do it, but at some point one has to ask "what is the point?"

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