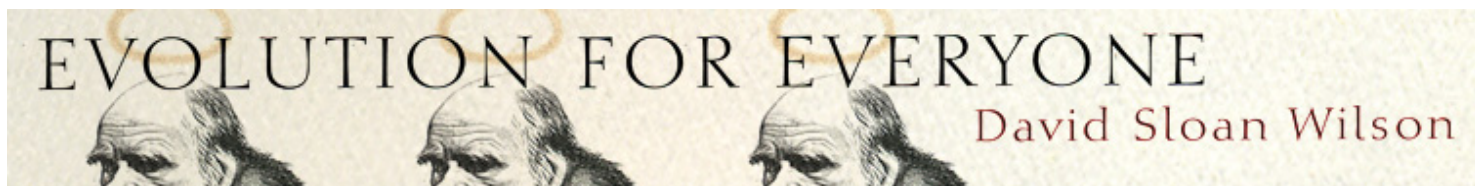


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Profile



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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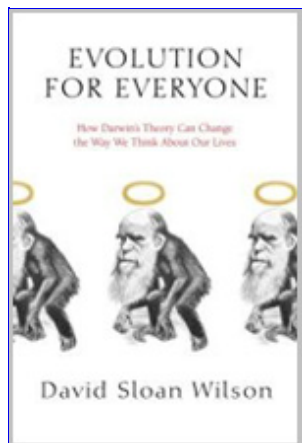
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[Open Letter to Richard Dawkins: Why Are You Still In Denial About Group Selection?](#)

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

Posted on: September 4, 2010 9:13 AM, by [David Sloan Wilson](#)

Dear Richard,

I do not agree with the cynical adage "science progresses--funeral by funeral", but I fear that it might be true in your case for the subject of group selection.

In your response to the [recent article in *Nature* by Martin Nowak, Corina Tarnita, and E.O. Wilson](#), which critiques inclusive fitness theory, you say this about group selection:

Edward Wilson was misunderstanding kin selection as far back as Sociobiology, where he treated it as a subset of group selection ... Kin selection is not a subset of group selection, it is a logical consequence of gene selection. And gene selection is (everything that Nowak et al ought to mean by) 'standard natural selection' theory: has been ever since the neo-Darwinian synthesis of the 1930s.

I do not agree with the Nowak et al. article in every respect and will articulate some of my disagreements in subsequent posts. For the moment, I want to stress how alone you are in your statement about group selection. Your view is essentially pre-1975, a date that is notable not only for the publication of *Sociobiology* but also [a paper by W.D. Hamilton](#), one of your heroes, who correctly saw the relationship between kin selection and group selection thanks to the work of George Price. Ever since, knowledgeable theoretical biologists have known that inclusive fitness theory includes the logic of multilevel selection, which means that altruism is selectively disadvantageous within kin groups and evolves only by virtue of groups with more altruists contributing more to the gene pool than groups with fewer altruists. The significance of relatedness is that it clusters the genes coding for altruistic and selfish behaviors into

different groups.

Even the contemporary theoretical biologists most critical of multilevel selection, such as Stuart West and Andy Gardner, acknowledge what you still deny. In an [earlier feature on group selection published in Nature](#), Andy Gardner is quoted as saying "Everyone agrees that group selection occurs"--everyone except you, that is.

You demonstrate more ignorance about group selection when you contrast it with gene selection. You correctly say that gene selection is standard natural selection theory. Essentially, it is a popularization of the concept of average effects in population genetics theory, which averages the fitness of alternative genes across all contexts to calculate what evolves in the total population. For that reason, it is an elementary mistake to regard gene selection as an alternative to group selection. Whenever a gene evolves in the total population on the strength of group selection, despite being selectively disadvantageous within groups, it has the highest average effect compared to the genes that it replaced. Please consult the installment of my "Truth and Reconciliation for Group Selection" series titled "[Naïve Gene Selectionism](#)" for a refresher course. While you're at it, check out the installment titled "[Dawkins Protests--Too Much](#)".

The Nowak et al. article includes several critiques of inclusive fitness theory that need to be distinguished from each other. One issue is whether inclusive fitness theory is truly equivalent to explicit models of evolution in multi-group populations, or whether it makes so many simplifying assumptions that it restricts itself to a small region of the parameter space. A second issue is whether benefiting collateral kin is required for the evolution of eusociality and other forms of prosociality. A third issue is whether inclusive fitness theory, as understood by the average evolutionary biologist and the general public, bears any resemblance to inclusive fitness theory as understood by the cognoscenti.

In an e-mail discussion among theorists on both sides of the debate that I organized several years ago, I conducted a citation analysis comparing Hamilton's original 1964 papers on group selection with his 1975 reformulation in the light of the Price equation. These papers are cited in a ratio of approximately 15:1 with no tendency for citations of the 1975 paper to increase in frequency over the decades. In other words, most evolutionary biologists still have a pre-1975 conception of inclusive fitness theory, no matter how much it has been elaborated by the cognoscenti. This degree of illiteracy about foundational issues is an embarrassment for the field of evolutionary biology. The Nowak article is a wake-up call for the average evolutionary biologist and the general public to reconsider the conventional wisdom about inclusive fitness theory, in addition to the debates that will take place among the cognoscenti.

Richard, if you wish to join the debates among the cognoscenti, you will need to abandon the priestly way that you make pronouncements, expecting what you say to be taken on faith, and rejoin the ranks of scientists who hold each other accountable for what they say.

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1

My take on the fierce reactions, not just by Dawkins, but basically by most of the people on the kin

selection camp (notable exception Alan Grafen), is that they fail to criticize the actual assumptions of the model in the paper. They should **take on the challenge and do the maths to counter the arguments** presented by Nowak, Tarnita and Wilson. That would be more insightful than just embarking on verbal theorizing that is in the end bound to be shallow and susceptible to end up diluted in semantic unsubstantial issues.

If the model is wrong, **they should come up with reasons why, for instance, the assumptions do not hold in the real world.** If they claim that the worker-centered approach is a better one, or an equivalent one, they should do so by coming up with a model with similar assumptions in which the traditional approach yields equivalent, or even better (simpler?) predictions. None of the critiques has even dare to delineate such an approach.

The debate seems to be completely ignoring the paper, and rather bringing an old discussion without a common ground. For instance, part A in the supplemental information has been completely dismissed in the reactions. That is a key issue, because it shows (formally!) the shortcomings of inclusive fitness, which, granted, is not equivalent to kin selection, but is definitely the tool of choice to do the accounting when thinking of kinship as the leading force of selection.

All in all, **I'd like to see a healthy formalization of the debate. The key issue here is a mathematical model**, and that should be what the debate is about. All this reactions dismissing the actual model are sad, and do not help science.

Posted by: [Julian Garcia](#) | [September 4, 2010 11:05 AM](#)

2

My take is that theoretically the gene selection theory is correct, but that the math is too horrendous to do, and probably involves some knowledge we don't have with sufficient precision. (E.g., how to you model epigenetic modifications?)

I feel that the group selection approach is theoretically more manageable, and also gives answers in good (though not perfect) agreement with what a gene oriented theory would provide. For an analogy, consider Newtonian and Einsteinian physics. Newtonian is much easier to use, and is good enough for most purposes. Einsteinian provides slightly more accurate results, and occasionally the difference is significant. The difference is that we don't really have a full mathematical workup of genetic evolution, and probably can't at the current stage of our knowledge. But it's still the "right" theory. Just not a practical one.

Posted by: Charles Hixson | [September 4, 2010 3:02 PM](#)

3

Julian (or others in the know), what is Alan saying about the matter? I've not seen comments from him yet.

Posted by: JP | [September 5, 2010 12:45 AM](#)

4

I am not aware of any group selectionist who has successfully dismantled the three main arguments against group selection:

- "For the good of the group" behavior is often not an ESS and will not be selected for.
- Groups are not sufficiently isolated.
- Differential reproduction and extinction of group occurs too slow for group selection to be a significant mechanism.

These criticisms are made routinely in textbooks on behavioral ecology (eg. Krebs & Davies) for decades. Or is the biological establishment putting "lies in the textbooks" as Hovind so frequently claimed?

Also, Dr. Wilson is making the appeal to novelty fallacy.

Posted by: Emil Karlsson | [September 5, 2010 6:18 AM](#)

5

This was one of the big surprises after taking a Evo course having read Dawkins. There are experiments that show group selection works, it's accepted, blah blah blah. It doesnt seem fair for him to promote "Evolution" while actually only promoting his view of it and not the consensus.

Posted by: Doazic | [September 5, 2010 6:36 AM](#)

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