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The Loom

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Last summer I [wrote](#) in the *New York Times* about a controversy over one of the most influential concepts in the recent history of evolutionary biology. Known as inclusive fitness, it basically says that helping relatives can be a good way to pass on your genes, because they've got your genes too.

In August, *Nature* published a lengthy [paper](#) by Martin Nowak, E.O. Wilson, and Corina E. Tarnita in which they argued that inclusive fitness was mathematically flawed and basically superfluous. I had no trouble finding other scientists who were ready to say all sorts of scathing things about Nowak et al. I'm no fan of ginning up fake debates, but when somebody says, "This paper, far from showing shortcomings in inclusive fitness theory, shows the shortcomings of the authors," the story writes itself.

Seven months later, *Nature* has finally published some "Brief Communication Arising" letters from some of these critics. The first letter alone has **137** co-signers.

Their ranks include plenty of major players in the field of evolution (including John Alcock, Tim Clutton-Brock, Stephen Emlen, Paul Sherman, Mary-Jane West Eberhard, and Richard Wrangham). The tenor of the letters is more dignified than the comments I got for my story, but the message is unchanged:

We believe that their arguments are based upon a misunderstanding of evolutionary theory and a misrepresentation of the empirical literature.

The authors of the first letter argue that Nowak et al don't get inclusive fitness. They claim it needs lots of stringent assumptions, when, in fact, it's a general theory. They also challenge the idea that inclusive fitness doesn't provide any more insights into biology. They offer a list of such insights, such as why animals cooperate with each other, why they can act spitefully, and why mothers produce different ratios of males and females. Inclusive fitness has proven particularly useful for addressing last question—what's known as sex allocation. It explains how the ratio of males to females changes with the density of females, the mortality rate, and many other factors—and it does so for species as varied as mammals, birds, spiders, and plants.

Nowak et al respond to all the criticism and don't budge in their own stand. They claim that their critics have misinterpreted their own argument. And they claim that sex allocation does not require inclusive fitness. Oddly, though, they never explain why it doesn't, despite the thousands of papers that have been published on inclusive fitness and sex allocation. They don't even cite a paper that explains why. They conclude by writing,

Inclusive fitness theory is neither useful nor necessary to explain the evolution of eusociality or other phenomena. It is time for the field of social evolution to move beyond the limitations of

inclusive fitness theory.

[Image from [Alex Wild](#)]

March 23rd, 2011 3:31 PM by [Carl Zimmer](#) in [Evolution](#), [The Tangled Bank](#), [Writing Elsewhere](#) | 6 comments | [RSS feed](#) | [Trackback >](#)

6 Responses to “Inclusive Fitness: Return to the Wrestling Ring”

1. 1. [Chris Lindsay](#) Says:
[March 23rd, 2011 at 3:58 pm](#)

I got my popcorn in hand and just sitting back, enjoying the show. Although it is a feisty debate, it doesn't seem like both sides have the evidence (unlike, say the homo floresiensis controversy or the North American Pleistocene extinction controversy).

2. 2. [RossM](#) Says:
[March 23rd, 2011 at 5:37 pm](#)

Science isn't about democracy – it needs evidence. This debate, one hopes, will result in better thinking about the existing evidence and someone conceiving an experiment to demonstrate that one view is more likely. The last thing we need is two groups saying “is” “isn't” “is” “isn't”. I do think that Nowak et al need to address all the arguments raised.

3. 3. [The inclusive fitness warriors dig in – MYRMECOS - Insect Photography - Insect Pictures](#)
Says:
[March 23rd, 2011 at 6:04 pm](#)

[...] Carl Zimmer [...]

4. 4. [Benjamin Hardisty](#) Says:
[March 23rd, 2011 at 6:15 pm](#)

I felt that this whole flap is over emphasis on different factors in the Price equation. I also get the impression that both sides are just trying to trump up their publications lists in Nature. The fact is, relatedness has to count for something in promoting the evolution of altruism, but just how much it accounts for in various scenarios is debatable. This whole acrimonious debate is pointless I think. To say that kin selection is never an explanation is quite silly, but to say that it's the only explanation for the evolution of altruism, reciprocal altruism, parceling etc, is also quite silly. Regardless, I think the kin selection and sex allocation literature is vast, and rather convincing.

5. 5. [John S. Wilkins](#) Says:
[March 23rd, 2011 at 9:16 pm](#)

This is what I call a “methodology war”. These are common in science and usually mask political differences (i.e., scientific politics). They occur in a science usually when progress has stalled on crucial research questions.

Wilson has previously argued in favour of group selection by claiming that kin selection is a form of group selection, so the group selectionists won (his 2007 paper with David Sloan Wilson in *QRB*). The obvious response is that kin selection is an outcome of (purely individual level selection) inclusive fitness, and people did respond that way. So denying that inclusive fitness even exists blocks that objection.

What facts tell for or against this? Basically if the math works, then one can claim inclusive fitness

is explanatory, but there can be no experimentum crucis that will show that the working math is true. So wiggle room persists and hence: methodology war.

6. 6. *Christopher Kandrak* Says:

[March 23rd, 2011 at 10:17 pm](#)

That was a great debate. But some things are questionable

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• About The Loom

Carl Zimmer writes about science regularly for the New York Times and magazines such as Discover, where he is a contributing editor and columnist.

He is the author of seven books, the most recent of which is [The Tangled Bank: An Introduction To Evolution](#). His website is carlzimmer.com and his address is blog at carlzimmer dot com .



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I once wondered aloud if scientists had tattoos of their science. [The answer was yes](#), and [this ever-growing collection](#) is the evidence. I'll be publishing a book about them called *Science Ink* in fall 2011. [Here are instructions](#) if you want to submit one of your own to the blog.



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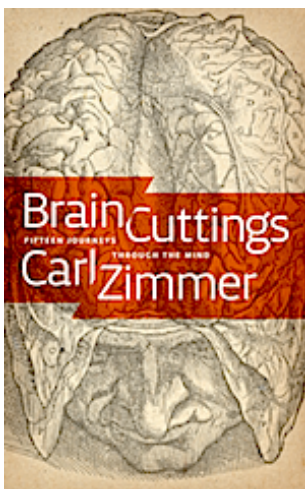
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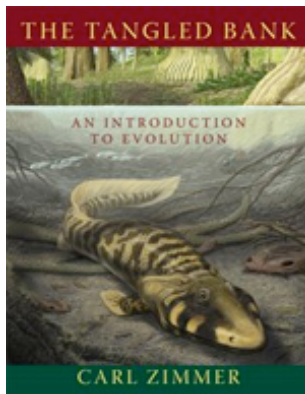
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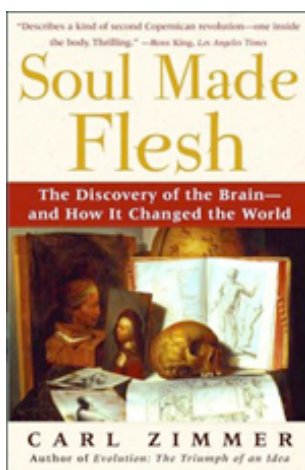
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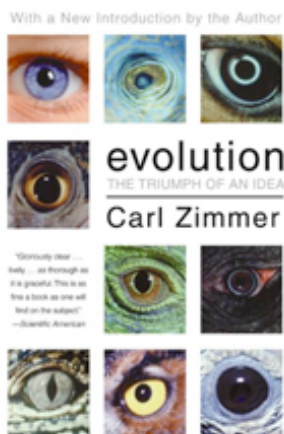
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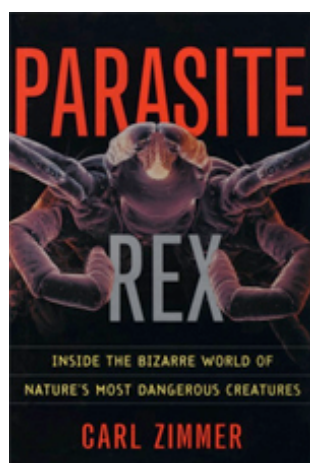
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--Moby Dick



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