

# WHY EVOLUTION IS TRUE

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## Big dust-up about kin selection

Last August I wrote about a new paper in *Nature* by three Harvard biologists, Martin Nowak, Corina Tarnita, and Edward O. Wilson. Their paper was, as I called it, a “misguided attack on kin selection,” referring to the form of selection in which the reproductive success of a gene (usually a gene that affects behavior) is influenced not only by its effects on its carrier, but also by its effects on related individuals (kin) carrying the same gene. This idea, introduced to evolutionary biology by George Price and W. D. Hamilton, has been enormously productive, explaining all sorts of things from parental care and parent-offspring conflict to sex ratios in animals and, perhaps most important, the evolution of “altruism.” Nowak et al.’s paper attacked the idea that this form of selection—based on a gene’s “inclusive fitness”—was important in explaining anything; indeed, they didn’t even see kin selection as a form of natural selection. My original post details most of my objections to their paper.

Now, seven months later, *Nature* has published a spate of objections to the Nowak et al paper: there are five critiques and a response to them by Nowak et al. Here are the papers and links:

“[Inclusive fitness theory and eusociality](#)” by Patrick Abbot et al. I am an author on this paper, along with *one hundred and thirty six other authors*. The list of authors and their institutions, which occupies two pages of the three-page letter, reads like a Who’s Who of social evolution. It’s telling that nearly every major figure in the field lined up against Nowak et al.

“[Only full-sibling families evolved eusociality](#)” by Jacobus J. Boomsma et al.

“[Kin selection and eusociality](#)” by Joan E. Strassmann, Robert E. Page, Jr., Gene E. Robinson and Thomas D. Seeley, four big names in social insect evolution

“[Inclusive fitness in evolution](#)” by Regis Ferriere and Richard E. Michod

“[In defence of inclusive fitness theory](#)” by Edward Allen Herre and William T. Wcislo

and the reply, called simply

“[Nowak et al. reply](#)”

I won’t go through the critiques, but their main points are these:

- Nowak et al.’s insistence that there’s a difference between inclusive fitness theory and “standard natural selection” theory is simply wrong. The former is just a special case of the latter taking into account the effects of a gene in one body on the effects of other bodies also carrying that gene. As Ferriere and Michod note:

“In fact, there is only one paradigm: natural selection driven by interactions, interactions of all kinds and at all levels. Inclusive fitness has been a powerful force in the development of this paradigm and is likely to have a continued role in the evolutionary theory of behaviour interactions.”

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- Nowak et al.'s insistence that kin selection theory requires a number of restrictive assumptions that makes it largely invalid is also wrong.
- Nowak et al.'s insistence that the idea of kin selection has been of no value in understanding nature is wrong. Our own paper gives many examples in which kin selection theory has clarified or advanced our understanding of phenomena like eusociality in insects (the phenomenon of an insect colony that contains a cast of nonreproductive individuals), sex ratio, altruism spite, alarm-calling, and so on. Further, the idea of kin selection has led to testable predictions—predictions that have been verified.
- Nowak et al.'s own "new" theory for explaining eusociality becomes a disguised form of kin selection when it tries to explain eusociality.

Curiously, in their very short reply, Nowak et al. don't really address the criticisms, but merely reiterate what they said in their original article. They resort instead to legalisms, explaining away the success of kin selection theory by saying this:

Abbot et al. claim that inclusive fitness theory has been tested in a large number of biological contexts, but in our opinion this is not the case. We do not know of a single study where an exact inclusive fitness calculation was performed for an animal population and where the results of this calculation were empirically evaluated.

This is a misunderstanding of how kin selection theory—indeed, all of evolutionary theory—is used. You don't have to perform an "exact inclusive fitness calculation" to make predictions. (It's nearly impossible anyway to "exactly" measure fitness in nature under *any* form of selection!) In sex ratio theory, for example, one can predict that if a female wasp is the only individual parasitizing a fly pupa, and all offspring wasps mate within the pupa, then you need produce only enough males to fertilize all your daughters, producing a female-biased sex ratio. But if more than one unrelated wasp parasitizes that pupa, you must invest in more sons to compete with the other wasps' sons in fertilizing females, and so your relative production of males should increase. That prediction has been amply verified without "exact" fitness calculations. (Indeed, insofar as quantitative predictions can be made, they've fit the data remarkably well.)

In his piece on the kerfuffle, [Carl Zimmer also noticed the non-responsive nature of Nowak et al.](#) :

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.


If the Nowak et al. paper is so bad, why was it published? That's obvious, and is an object lesson in the sociology of science. If Joe Schmo et al. from Biggerall State University had submitted such a misguided paper to *Nature*, it would have been rejected within an hour (yes, *Nature* sometimes does that with online submissions!). The only reason this paper was published is because it has two big-name authors, Nowak and Wilson, hailing from Mother Harvard. That, and the fact that such a contrarian paper, flying in the face of accepted evolutionary theory, was bound to cause controversy. Well, *Nature* got its controversy but lost its intellectual integrity, becoming something of a scientific *National Enquirer*. Oh, and boo to the Templeton Foundation, [who funded the whole Nowak et al. mess and highlighted the paper on their website.](#)

The lesson: if you're a famous biologist you can get away with publishing *dreck*. So much for our objective search for truth—a search that's not supposed to depend on authors' fame and authority. I feel sorry for co-author [Corina Tarita](#), a young scientist with splendid qualifications, for this

paper will always cast a shadow over her career.

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This entry was written by [whyevolutionistrue](#) and posted on March 24, 2011 at 5:21 am and filed under [evolution](#). Bookmark the [permalink](#). Follow any comments here with the [RSS feed for this post](#). Post a comment or leave a [trackback](#): [Trackback URL](#).

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## 14 Comments



1.

Sven DiMilo

Posted March 24, 2011 at 5:34 am | [Permalink](#)

Thanks very much for the linx & summary; I'm looking forward to digging in later.

Quick question: Why would kin selection be invoked to explain parental care? That seems to me like an obvious product of straightahead direct-fitness-benefit natural selection.

[Reply](#)



2.

NewEnglandBob

Posted March 24, 2011 at 5:35 am | [Permalink](#)

I am making a huge amount of popcorn and making sure the big monitor is working well and taking a front row seat to be able to enjoy the show that is happening.

Nowak, Tarnita, and Wilson being refuted by 150+ of the heavies of evolutionary biology is like watching a car accident while driving past it. One can not help but stare.

I can guess which side DS Wilson is on, but that car wreck is getting old.

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3.

Sven DiMilo

Posted March 24, 2011 at 5:43 am | [Permalink](#)

I feel sorry for co-author Corina Tarita, a young scientist with splendid qualifications

?

She seems to be a mathematician who has never [published](#) on biology without Nowak.

Now a paper with EO Wilson (a biologist even mathematicians have heard of) in *Nature* (a scientific journal even mathematicians have heard of)?

It probably won't hurt her career a bit. Hey, the reply even goes on her CV as another *Nature* pub for the bean-counters.

[Reply](#)



4.

Ben

Posted March 24, 2011 at 5:48 am | [Permalink](#)

There's several misconceptions here.

Nowak et al. are not disputing that relatedness and interactions between relatives are important for the evolutionary success of a gene. Their argument is against the mathematical formulation of inclusive fitness theory. Making IF calculations requires certain mathematical manipulations which are not possible in general. They only work if a number of assumptions hold, as detailed in the mathematical appendix to their original paper.

Inclusive fitness can be a useful rule of thumb for making qualitative predictions. But mathematically, it's not a good tool. Population genetics and evolutionary game theory are much better for deriving quantitative results.

Reply



whyevolutionistrue

Posted March 24, 2011 at 5:57 am | [Permalink](#)

Their argument is against inclusive fitness as a tool for understanding nature, not just its mathematical formulation. And, as the critiques show—and will become evident when two longer critiques are published soon—you're just flat wrong in saying that those mathematical manipulations are "not possible in general" or work only if "a number of assumptions hold". Did you read the third paragraph of Abbott et al.? I get the impression you didn't read the critiques.

And inclusive fitness IS population genetics! It's not something different.

Reply

5.



James Sweet

Posted March 24, 2011 at 5:50 am | [Permalink](#)

You don't have to perform an "exact inclusive fitness calculation" to make predictions. (It's nearly impossible anyway to "exactly" measure fitness in nature under any form of selection!)

I will go one stop further and assert that it *is* impossible to exactly measure inclusive fitness. I came up with the below thought experiment while chatting with Bjørn Østman. Don't be too distracted by the use of the peacock; it arose during a conversation relating partially to sexual selection, so that was the convenient example.

50,000 years ago, two peacock brothers were walking through some bushes near a mountain. One brother's tail was slightly larger than the others. This caused him to get momentarily caught in the bushes, while his brother continued on unimpeded. At that moment, a landslide occurred which crushed the smaller-tailed brother, but spared the longer-tailed brother as the momentary delay prevented him from being in the path of the avalanche. He frees himself from the bushes and goes on to leave many offspring.

So now do we have a  $10^{-10}$ % contribution to the inclusive fitness of "long tail" owing to "prevents peacock from walking into avalanche"? If not, why not, without invoking teleological reasoning?

The best answer I can come up with is that there is an implicit assumption that, on average, for every peacock who is spared from walking into an avalanche by a momentary delay, there is another

peacock who would have been spared if he *hadn't* been delayed. But we can't prove that assumption, and in any case even if we had, we would not expect the numbers to be precisely equal, just approximately equal — so if we wanted to do an "exact" calculation of fitness, we are still potential left with some negligible mathematical contribution to the fitness of a longer tail due to random events like walking into a landslide.

This is an intentionally absurd example, but that's exactly the point I am making: Even if it were practical to calculate inclusive fitness "exactly", such a metric would be *useless*, because it merely tells you what has already happened. Any useful concept of fitness is *by necessity* an approximation, because it needs to exclude factors that we believe would cancel themselves out over a long enough period of time (like a long tail saving a peacock from an avalanche).

It's kind of like how I get uncomfortable when car insurance companies try to over-refine their risk estimations. If you overdo it, it defeats the point. The perfect risk assessment is this: If you don't get in an accident, you get insurance for free; if you do get in an accident, your premium is exactly what the insurance company paid out for your accident. In other words, no insurance. Risk assessment in insurance is *by necessity* an approximation, because otherwise it's useless. Same with fitness, in my opinion.

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6.

Diego

Posted March 24, 2011 at 5:56 am | [Permalink](#)

I have often felt in the past that the only reason a particular paper was published by Nature is that it went against the prevailing paradigm, even if the article would have been better as ripped up paper to line an eagle's nest. Nature choosing controversy over integrity happens time and again and I am no longer surprised by it.

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Sven DiMilo

Posted March 24, 2011 at 6:00 am | [Permalink](#)

\*shrug\*

They're selling adspace, after all.

[Reply](#)



James Sweet

Posted March 24, 2011 at 6:10 am | [Permalink](#)

Nature choosing controversy over integrity happens time and again and I am no longer surprised by it.

Does this suggest that controversy is "Naturally" selected for?

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Dan

Posted March 24, 2011 at 6:47 am | [Permalink](#)

I'm no longer surprised by it but I am still routinely disgusted by it. I think Coyne is right that this paper would not have been published with different authors, which to my mind makes a strong argument for double blind peer review.

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Dr. I. Needtob Athe

Posted March 24, 2011 at 6:31 am | [Permalink](#)

"I am an author on this paper, along with [i]one hundred and thirty six other authors[/i]. The list of authors and their institutions, which occupies two pages of the three-page letter, reads like a Who's Who of social evolution. It's telling that nearly every major figure in the field lined up against Nowak et al."

I'm confident that you're on the right side of this dispute, but still, that argument is uncomfortably reminiscent of an infamous book titled "Hundert Autoren gegen Einstein" (Hundred authors against Einstein)

[http://en.wikipedia.org/wiki/100\\_Authors\\_Against\\_Einstein#Hundred\\_authors\\_against\\_Einstein](http://en.wikipedia.org/wiki/100_Authors_Against_Einstein#Hundred_authors_against_Einstein)

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whyevolutionistrue

Posted March 24, 2011 at 6:34 am | [Permalink](#)

Just because we're numerous—and there are many authors working directly in the field of inclusive fitness—doesn't mean that we're *wrong!*



[Reply](#)



James Sweet

Posted March 24, 2011 at 6:47 am | [Permalink](#)

Argument ad unpopulum.

[Reply](#)



Helen Wise

Posted March 24, 2011 at 6:43 am | [Permalink](#)

I've gone back to your original postings, popped over to Prof. Dawkins' house and read his posting about this, and visited other ancillary sites as they appealed and occurred, and have just generally spent an enjoyable hour or two with this reading—all to diffuse my frustration that the Nature articles are behind pay walls. (Even if they weren't, I am probably short one or two of the mental bed springs necessary to completely comprehend the underlying science and/or math, anyway.)

That said, and revisiting an earlier topic, I think I'm going with Nowak for the Templeton prize win.

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