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 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 Buggerall 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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- **A misguided attack on kin selection**
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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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50 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

- Richard Dawkins
Posted March 24, 2011 at 7:36 am | Permalink

Sven DiMilo asks: "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."

That is is precisely the point. There is no such thing as 'straitahead direct-fitness-benetit natural selection'. Or rather there is but it logically and necessarily INCLUDES kin selection. It is just that most people, until Hamilton, overlooked that logical necessity. Biologists in the field now understand the point, and will continue to do so notwithstanding Nowak et al's crass attempt to set the field back forty years. Nature's decision to publish their paper was, as Jerry suggests, a public disgrace.

Reply

- Sven DiMilo
Posted March 24, 2011 at 8:19 am | Permalink

That's certainly *a* point, and a good one (and of course I agree 100% with your comment, including, if that wasn't clear before, your last sentence).

But it wasn't 'precisely *the*' point that I was making. I know 'biologists in the field' and how they think about things, and they speak routinely of direct benefits and indirect benefits of social behaviors to inclusive fitness. Direct benefits are from individual reproductive success, indirect benefits are from (the *additional* fitness components of) kin selection. My point was that

« Peregrinations

Dawkins on Nowak *et al.* and kin selection

If you've read the critiques of the Nowak et al. paper on kin selection that I highlighted this morning, you may have noticed a conspicuous absence among the authors: the name of Richard Dawkins. Why, as the most famous exponent of kin selection since W. D. Hamilton, didn't he co-author one of the critiques?

It turns out that nobody asked him. I think this was simply an oversight, because all of us simply assumed that Richard would be penning his own criticism. He didn't, but he did write a brief piece on Nowak et al. for *New Scientist*, which he decided not to publish. I'm posting it here with his permission, along with a link to his excellent paper about common misunderstandings of kin selection. I'm not sure whether Richard will answer comments from readers, but you can certainly pose them below. Here's his take on Nowak et al.:

> This is no surprise. Edward Wilson was misunderstanding kin selection as far back as *Sociobiology*, where he treated it as a subset of group selection (Misunderstanding Two of my 'Twelve Misunderstandings of Kin Selection': *Zeitschrift für Tierpsychologie* 1969). Kin selection is not a subset of group selection, it is a logical consequence of gene selection. And gene selection is 'standard natural selection' theory. Inclusive fitness theory is not some kind of supernumerary excrescence, to be 'resorted to' only if 'standard natural selection theory' is found wanting (Misunderstanding One). On the contrary, inclusive fitness theory is one way of expressing what was logically inherent in the neo-Darwinian synthesis ever since the 1930s but had been largely overlooked because people didn't think hard enough about collateral kin. 'Standard natural selection theory' MINUS inclusive fitness would be like Euclidean geometry minus Pythagoras' theorem.
>
> Another way of expressing what was logically inherent in the synthesis is Hamilton's rule, rB>C: a gene for altruism will spread if the cost to the altruist, C is exceeded by the Benefit to the recipient, B, devalued by the coefficient of Relatedness, r. If you think, as Nowak et al. do, that 'Hamilton's rule almost never holds', that simply means you haven't been measuring B and C carefully enough. r is not the only term in Hamilton's inequality. B and C matter too, and your game theoretic considerations are subsumed within them.
>
> Perhaps most irritating is Nowak et al.'s concentration on haplodiploidy, which, in Hamilton's original paper was a throwaway side-issue, interesting enough to pique the interest of generations of students, but not in any sense central to his paper. Of course Hamilton was well aware that eusociality is present in diplo-diploid animals, exactly as inclusive fitness theory would predict given appropriate B/C ratios. Indeed, Hamilton himself put forward an ingenious theory of the evolution of eusociality in termites, predating by seven years the version usually attributed to Bartz (attributed by Hamilton himself, indeed, with characteristically absent-minded generosity as I described in

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The Selfish Gene, second edition p 317).

Finally, Nowak et al. do Darwin an injustice, in discussing his theory of the evolution of worker sterility in social insects. They paraphrase Darwin's 'well-flavoured vegetable' analogy. Let me quote it exactly: "Thus, a well-flavoured vegetable is cooked, and the individual is destroyed; but the horticulturalist sows seeds of the same stock, and confidently expects to get nearly the same variety . . . I do not doubt that a breed of cattle, always yielding oxen with extraordinarily long horns, could be slowly formed by carefully watching which individual bulls and cows, when matched, produced oxen with the longest horns; and yet no one ox could ever have propagated its kind. Thus I believe it has been with social insects . . ." It is true that Darwin goes on to phrase his idea in terms of benefit to the colony, but his analogy of the long-horned (castrated) oxen could not be clearer. No colony is involved. This is early inclusive fitness theory. It is entirely clear that, if Darwin had been alive to read Hamilton on social insects, he would have embraced inclusive fitness, not as an add-on to natural selection theory but as the logical way to express it in the age of the gene.

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- **A misguided attack on kin selection**

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35 Comments

1. 
   Kevin
   Posted March 24, 2011 at 7:47 am | Permalink

   Ouch. Prof Wilson just got a spanking.

   Reply

   - 
     NewEnglandBob
     Posted March 24, 2011 at 8:29 am | Permalink

     Not for the first time, but this time clearly warranted.

     Reply

   - 
     Frank
     Posted March 24, 2011 at 11:21 am | Permalink

     Wilson has not been the only bright scientist to misunderstand kin selection and fail to see it as a logical and inevitable consequence of genic level selection (not group selection). After reading Stephen Jay Gould's magnum opus, The Structure of Evolutionary Theory, I got a general sense that

New book shows that humans are genetically nice, ergo Jesus

A while back I mentioned the disagreement that I (and many others) had with a recent *Nature* paper by Martin Nowak, Corina Tarnita, and E. O. Wilson. I characterized their paper as a "misguided attack on kin selection," for it claimed not only that kin selection was something different from natural selection (it's not—it's a *subset* of natural selection), but also that kin selection was both unproductive and incoherent. I argued that kin selection was certainly coherent, and, more important, had made many contributions to our understanding of nature. A published exchange on this issue, in which I am participating, will appear in *Nature* on March 24.

In the meantime, there's a report at the *Daily Telegraph* about not only that paper, but a new book by Nowak (coauthored by *New Scientist* editor Roger Highfield), *SuperCooperators*. (A review by Manfred Milinski has just appeared in *Nature*.) The *Telegraph* report is dicey on the scientific issues. For example, it says this about the concept of inclusive fitness (the idea that the "fitness" attached to a gene involves not only its direct reproductive effects on its carrier, but its ancillary effects on other individuals carrying the gene):

> This concept is considered central to biology, since it provides the best explanation for why existence is not simply a dog-eat-dog, Darwinian struggle. But Prof Nowak is doubtful. "Inclusive fitness is somewhat like an epicycle," he says, referring to the Ptolemaic model of the solar system with the Earth at its centre, which required the planets to move in complicated flower patterns to explain their movement in the sky. "Somehow you have the impression that there is some reality attached to it, but the actual mathematical description of any evolutionary process shows that evolutionary fitness is an unnecessary concept."

To equate a well-established evolutionary concept like inclusive fitness with a bogus model of planetary motion is simply invidious. And to say that inclusive fitness has no "reality" is just ignorant. Even though Nowak denies that inclusive fitness is a useful biological concept (and here he's dead wrong, as the published responses will show), he can't say it's not real, for it's simply a combination of fitnesses of a gene's carrier with those of like-gened individuals with which it interacts. Finally, to say that "evolutionary fitness is an unnecessary concept" is bizarre, for even if Nowak rejects the whole idea of *inclusive* fitness, there is still the valid and very important idea of *individual fitness:* the relative reproductive contribution of carriers of a gene. Every evolutionist knows how valuable that concept has been in making evolutionary models of nature and, more important, in *understanding* nature. Rejecting that idea is like claiming that the whole gene-centered approach to evolution is wrong.

Indeed, in the next paragraph Nowak brings up the importance of a gene-centered approach:

> Instead, Nowak stresses that co-operation and altruism are just as important. "The two pillars of evolution are mutation and natural selection: mutation generates diversity, and natural selection chooses the winner. What I want to argue in this book is that, in order to get complexity, there is a third principle, co-operation. It's not just a small

> phenomenon, it is something that is really needed to explain the world as we see it." Without it, he says, we would have a world without multi-cellular creatures – or even without cells, just monomolecular replicators in an organic soup.

If there's a way for cooperation and altruism to evolve without conferring genetic benefits on their carriers, or on groups of related individuals, I'd like to know how! "Cooperation" is not a third principle on top of mutation and natural selection, it is a behavior that evolves by either natural selection (as it must have done in the many species that do cooperate without culture, like social insects) or is *socially* mandated by complex creatures like humans. It's clear in the article, though, that Nowak is talking about *evolved* cooperation, and that takes genes and therefore differential fitness of cooperators versus noncooperators.

I've tried to fob off Nowak's strange statements as the misunderstandings of a lay reporter, but since they're verbatim quotes that's hard to do. This seems more to me like a publicity grab, especially because Nowak does a lot of name-dropping to tout his expertise:

> His speciality is using mathematical equations to model and predict biological behaviour. "I talked to Bill Hamilton a lot, when I was at Oxford. And I talked an awful lot with Richard Dawkins as well. But I've never written a paper with them," he says. "I have written a paper with John Maynard Smith, and one with Ed Wilson," he adds, casually dropping two giants into conversation. And who are the ones who have most influenced you, I ask. "Robert May [the former chief scientific adviser to the government], influenced me very, very much."

Well, so be it. The final judgment of science does not depend on big names, but on truth, and the field will ultimately judge whether Nowak, Tarnita and Wilson's attempt to overturn a dominant paradigm of evolution will bear any fruit. I predict that it won't. And I'll reserve judgment on Nowak and Highfield's book until I read it.

But I must deplore Nowak's use of biology to sell Jesus, and to push accommodationism. Here he is on science versus faith:

> Nowak, however, sees no conflict. "I think that science and religion are components of what people need and what people want in terms of the search for truth. I don't see science as constructing or providing an argument against well-formulated and thoughtful religious philosophy." He is a Catholic, but in his book he quotes with approval Einstein's line about God as a sort of abstraction, seen in the beauty of nature's laws. I ask him to expand, but he shies away. "I am very open-minded, very curious, very keen to learn from other different traditions, different approaches." He does, however, believe in the divinity of Christ.
>
> The great irony of his work, which heartens and amuses his religious side, is that he is, in essence, making a scientific argument that the virtues preached by Jesus – compassion, concern, love for your neighbour – are encoded into the laws of biology. "The mathematical analysis shows that winning strategies in the game of co-operation have to be hopeful, generous and forgiving."

As Church Lady would say, "Well, isn't that *special!*" What Nowak fails to consider is that yes, maybe altruism and compassion are in our genes, but so perhaps are aggression, spite, xenophobia, and hatred. There is precisely as much evidence for genetically evolved compassion and love among nonrelatives as there is for genetically evolved traits that we consider "bad"—that is, very little. What we know is that altruism and compassion are near-universal among human societies, but so are aggression, spite, *Schadenfreude*, and the like. We *think* that we may have evolved morality, altruism, and the like, for, as Frans de Waal points out repeatedly, building blocks of those traits are seen in other primates. But so too do we see aggression, hostility, and even murder in our

primate relatives. I agree with Steve Pinker that our genome probably contains information prompting for both "good" and "bad" behaviors. For there are reproductive benefits to be gained by being, at times, either an angel or a devil.

Why does Nowak concentrate on just the wonderful behaviors we've evolved? Could it be . . . . *Templeton*?

The *Telegraph* article says this about Nowak:

> What riles some scientists is that he is not just the holder of prestigious prizes, but also a committed Christian. In particular, he is on the board of advisers of the Templeton Foundation. . .

I can't confirm that he's currently on the main advisory board of Templeton (the "N" page doesn't list him), but he used to be. My data show him serving in that capacity from at least 2005 to 2009, and I can't get earlier records. But he *is* currently on another Templeton board: the 12-member board of the Templeton Advanced Research Program of the Metanexus Institute. The purpose of this board, according to Templeton, is twofold:

> The primary goal of this new research program is to foster innovation in research design as well as the scientific scope and impact of religion and spirituality.
> A second goal is to encourage the development of creative insights into the forces that shape and expand world religions and the human conceptualization of God.

During or after this time—that is, *after* Nowak had taken a position on Templeton's advisory boards—he got this kind of dosh:

- A grant from Templeton to Nowak on "The Evolution and Theology of Cooperation: The Emergence of Altruistic Behavior, Forgiveness and Unselfish Love in the Context of Biological, Ethical and Theological Implications." Amount: $2 million (work conducted at Harvard University).
- A grant from Templeton on "Foundational questions in Evolutionary Biology", which runs from 2009-2013. Nowak is the leader of this project at Harvard, and the amount is $10,500,000 (!)
- A series of four Templeton-sponsored research lectures at Johns Hopkins University in March, 2010. I have no information about how much Nowak got paid to talk, but it's surely not trifling.

Since I'm not sure when Nowak started on the Templeton board, I can't confirm that he got the following monies when he was already advising them:

- A grant from Templeton to the Royal Society of London in affiliation with Nowak, George F. R. Ellis, John Polkinghorne, and Ziauddin Sardar for two lecture series: "The Nature of Human Knowledge and Understanding." Total amount: $281,885; dates 2004-2007.

I suspect, but don't know, that one also gets money for being on the two advisory boards that I mentioned above. Nowak also contributed to the Templeton essay collection "Does evolution explain human nature?", which was published in *the New York Times* and for which contributors received a fee.

Has Templeton been happy with Nowak's work? I suppose so, since they keep giving him money, and the *Nature* paper he wrote with Tarnita and Wilson, attacking the idea of kin selection, is prominently highlighted at the Templeton website. And it can't hurt that he's a Catholic who believes that Jesus was divine. His message, that evolution produces results exactly consistent with the teachings of Jesus, certainly buttresses Templeton's mission of uniting (or conflating) science and faith. Look for Nowak to nab a Templeton Prize in the coming years.

Let me close by saying two things. First, I consider it ethically marginal for Templeton to put people on their advisory boards and then fill those people's pockets with stupendous amounts of cash. That's tantamount to the organization existing to enrich itself. And it gives people the idea

that if you want to get a lot of money for yourself or your research, then simply agree to help the Templeton Foundation. As Sunny Bains pointed out in her recent report on the organization, it's not that Templeton always takes its high-performing grantees and makes them members of its advisory board; rather, it often gives grants to members of the board *after* they're already on it. That is not a good practice.

Second, this attack on kin selection, and Nowak's book, seem to me to involve more than just finding out the truth about nature and imparting that truth to the public. They appear to involve the darker side of human nature—the side that Nowak seems to ignore in his warm-and-fuzzy book. It's the side that involves greed, money, ambition, dubious ethics, and an overriding concern for one's legacy and place in the pantheon of science.

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56 Comments

1. 

   Richard Dawkins
   Posted March 16, 2011 at 12:01 pm | Permalink

   I have read the book by Nowak and Highfield. Parts of it are quite good, but the quality abruptly, and embarrassingly, plummets in the chapter on kin selection, possibly under the influence of E O Wilson (who has been consistently misunderstanding kin selection ever since Sociobiology, mistakenly regarding it as a subset of group selection). Nowak misses the whole point of kin selection theory, which is that it is not something additional, not something over-and-above 'classical individual selection' theory. Kin selection is not something EXTRA, not something to be resorted to only if 'classical individual selection' theory fails. Rather, it is an inevitable consequence of neo-Darwinism, which follows from it deductively. To talk about Darwinian selection MINUS kin selection is like talking about Euclidean geometry minus Pythagoras' theorem. It is just that this logical consequence of neo-Darwinism was historically overlooked, which gave people a false impression that it was something additional and extra. Nowak's otherwise good book is tragically marred by this elementary blunder. As a mathematician he really should have known better. It seems doubtful that he has ever read Hamilton's classic papers on inclusive fitness, or he couldn't have misunderstood the idea so comprehensively. The chapter on kin selection will discredit the book and stop it being taken seriously by those qualified to judge it, which is a pity.

   Richard

   Reply

   - 

     KP