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## A misguided attack on kin selection

I don't know what's gotten into E. O. Wilson. He's certainly the world's most famous evolutionary biologist, and has gone from strength to strength over the years, winning two Pulitzer Prizes, writing great general books on not only ants but conservation and social behavior. And he's kept his hands in the ant work, producing any number of technical papers and monographs. He's even written a novel! Frankly, I don't know how he does it. I haven't always agreed with what he says—I think he overreached with the sociobiology stuff, for instance—but you have to admire the guy's knowledge, breadth, dedication to conservation, and sheer workaholicism.

But now Wilson, along with some collaborators like David Sloan Wilson and Martin Nowak, is definitely heading off on the wrong track. They're attacking kin selection, maintaining not only that it has nothing to do with the evolution of social insects, but that's it's also a bad way to look at evolution in general. And they're wrong—dead wrong.

Their latest attack on kin selection is a big paper in the new *Nature* by Wilson, Martin Nowak and Corina Tarnita, all from Harvard. They begin by arguing that the classical argument for insect eusociality (cooperatively breeding societies in which "castes" of individuals, like the workers in bees, are sterile and help the queen produce offspring)—an argument based on asymmetrical relatedness—is wrong. This failure to explain eusociality, they claim, is a severe blow to kin-selection theory.

They're right about the biology. The "textbook" explanation, based on a higher relatedness of workers to their sisters than to their own potential offspring, no longer seems feasible. It posits that queens mate only once, but in reality they often mate many times, which destroys the asymmetry of relatedness that supposedly selects for cooperative breeding. Further, other species, like aphids, termites and mole rats, are eusocial but don't show asymmetrical relatedness. Finally, lots of haplodiploid species (those in which males come from unfertilized eggs, females from fertilized ones) have asymmetrical relatedness but aren't eusocial.

But we've known all this for years! Check out the papers by Gardner & West and Strassmann & Queller cited below—they point out the same problems that Nowak et al. present as novel, but as far back as 1998. There's nothing new here.

The main problem with the Nowak et al. paper is this: they see the failure of asymmetrical relatedness to explain social insects as a *general failure of kin selection* to help us explain those groups—or anything at all. That's just wrong. There are alternative explanations for how relatedness explains the evolution of social insects (see the two papers by Strassman and Queller), including the phenomenon of sterile castes. And, although Nowak et al. claim that "the production of inclusive fitness theory must be considered meagre," there are *many* aspects of eusociality that *have* been profitably investigated, and explained, by inclusive fitness theory. Here are just a few: why worker bees commit suicide when they sting; why, when a honeybee colony divides, the remaining queen goes around stinging to death all the other future queens in their cells; why workers prefer to raise rear queens in colonies where their mothers have mated only once, but rear males in colonies where their mothers have mated multiply; and why workers in singly-mated colonies kill male larvae. And there are many others.

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Sex ratio theory, in which mothers produce different proportions of males and females, has been a particularly fruitful area for applying inclusive fitness theory. So has "altruism"—suicidal honeybees are just one example. And so are parental care and aspects thereof, especially parent-offspring conflict, a field brought to life by Bob Trivers using inclusive fitness theory. How else can you explain weaning conflict except by a conflict between the mother's genetic welfare and that of her offspring?

I'm baffled not only by Nowak et al.'s apparent and willful ignorance of the literature, but by statements that are just wrong. They flatly assert, for instance, that "inclusive fitness theory" is something different from "standard natural selection theory." But it's not: it's simply a natural extension of population genetics to the situation in which one's behavior affects related individuals. I could go on, but a little bird has told me that the big guns in the field will, soon and *en masse*, answer Nowak et al.'s arguments about both theory and data.

I can't fathom any motive, either psychological or scientific, for Wilson and Company to repeatedly denigrate the importance of inclusive-fitness theory. It's just a shame that, this late in his career, Wilson has chosen to fight the wrong battle. In the meantime, contrast his attacks on the value of kin selection with the summary paragraphs of Strassman and Queller (2007), who, after reviewing the bearing of inclusive-fitness theory on understanding social insects, conclude:

Any scientific theory purporting to account for biological complexity ought to account for this special nature of social insects. Why do their colonies show a degree of apparent purpose lacking in other aggregations, herds, and flocks? The kin selection extension of natural selection theory does explain this; cooperation results from the opportunity to give sufficiently large benefits to kin.

More importantly, kin selection theory has successfully predicted new findings. Although social insect colonies have clocklike design in many respects, kin selection theory predicts who is throwing sand into the clockworks, as well as which gears might be slipped and which springs sprung. Many of the predicted findings, such as sex ratio conflict and policing, were otherwise completely unexpected. The success of this approach shows that the Darwinian paradigm is capable of explaining not just the adaptations of organisms but also how new kinds of organismal entities come into being.

Finally, a big raspberry to the folks at *Nature* who decided to publish such a strange paper in the interest of stirring up controversy. If they'd gotten decent reviewers, and followed their advice, it never would have seen print.

**UPDATE:** Over at his website, Richard Dawkins has added [his own notes on the Nowak et al. paper](#). He doesn't like it either, and for many of the same reasons.

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Nowak, M. A., C. E. Tarnita and E. O. Wilson. 2010. The evolution of eusociality. *Nature* 466: 1057-1062.

Queller, D. C., and J. E. Strassmann. 1998. Kin selection and social insects. *Bioscience* 48:165-175.

Strassmann, J. E., and D. C. Queller. 2007. Insect societies as divided organisms: The complexities of purpose and cross-purpose. *Proc. Nat. Acad. Sci. USA* 104:8619-8626.

West, S. A. and A. Gardner. 2010. Altruism, spite, and greenbeards. *Science* 327:1341-1344.

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**43 Comments**

1.

**James Sweet**Posted August 30, 2010 at 11:58 am | [Permalink](#)

I don't suppose you could recommend any lay-friendly reading material about the current thinking regarding the evolution of eusociality?

I had just wrapped my head around the asymmetrical relatedness idea — and then only partially — and now you say it is wrong! Dangit...

Reply



o

**whyevolutionistrue**Posted August 30, 2010 at 12:09 pm | [Permalink](#)

I don't know of any offhand but I'll check. In the meantime, for others, I'll reprise the (probably incorrect) asymmetry argument:

In haplodiploid species, whose males come from unfertilized eggs and females from fertilized ones, a given female shares three-quarters of her genes with her sisters (if her mother mated only once). That's because all offspring get an identical half of their genome from their father (who has only one set of chromosomes and passes it on intact to his kids), and the remaining half of their genome is 50% shared with their sisters because of recombination in the mothers. In other words, the proportion of shared genes between a female and her sisters is  $50\% + 1/2(50\%) = 75\%$ , or  $3/4$  of the genome.

But a female shares only HALF of her genes with *her own offspring*. Therefore, you could argue—as early workers did—that any gene that “tells” a female to become sterile and produce more sisters (as workers do in honeybee nests) would leave more copies than a gene that “tells” her to have her own offspring. This asymmetry was the early explanation of why eusocial insects have sterile worker females.

The problem is that if females mate more than once, then their female offspring are not more highly related to their sisters than their own offspring, eliminating the evolutionary impetus for sterility. Also, although females are related by 75% to their sisters, they're related by only 25% to their brothers. Since they're related by 50% to their own sons, it would pay them, as far as *males* are concerned, to have their own offspring rather than help the queen produce more sons. Considering both male and female offspring, then, there seems to be no net genetic asymmetry that would select for sterility. But, as I said above, there are other ways that relatedness, even if symmetrical, could promote the evolution of eusociality.

For this and other reasons, the “haplodiploid” argument for the evolution of cooperative breeding is no longer very

convincing.

Reply



J.J.E.

Posted August 30, 2010 at 1:09 pm | [Permalink](#)

And if I remember correctly, empirical studies show that species/colonies with multiply mated queens tend to have more intra-nest conflicts wherein un-mated females lay unfertilized (i.e. haploid, i.e. males) than species/colonies with singly mated queens, though I could be misremembering. Is this not a verified prediction of inclusive fitness?

Caveat emptor. I'm a tad hazy as it has been nearly 10 years since I read this literature regularly.

Reply



Richard Dawkins

Posted August 30, 2010 at 12:50 pm | [Permalink](#)

There's nothing wrong with the theory of the haplodiploid asymmetry. You definitely haven't wasted your time wrapping your head around it. You've wrapped your head around a correct piece of theory. It's just that, in practice, many social insect queens mate more than once, thereby neutralising the asymmetry. Hamilton was well aware of this practical difficulty, which was one reason why haplodiploidy did not bulk large in his exposition of inclusive fitness theory.

Richard Dawkins

Reply



Ichthyic

Posted August 30, 2010 at 6:13 pm | [Permalink](#)

not really lay reading, but I always recommend the collected works of WD Hamilton:

Narrow Roads of Gene Land.

Moreover, for a more recent review of the evolution of social behavior in general, there was a volume published in Evolutionary Biology a few years back that IIRC is open access:

<http://onlinelibrary.wiley.com/doi/10.1111/jeb.2006.19.issue-5/issuetoc>

as a general comment, those thinking the paper under discussion here is something "new" must be new to the writings of DS Wilson.

there is nothing new in this paper, and all of it has been roundly and correctly critiqued before.

Reply

2.   
Kevin

Posted August 30, 2010 at 12:10 pm | [Permalink](#)

I predict another spate of "Darwin was wrong" news reports.

Seems like a review article (I don't have a subscription and don't want to pay \$32). Do they have any new data to support their hypotheses?

Reply



whyevolutionistrue

Posted August 30, 2010 at 12:14 pm | [Permalink](#)

No new data, nor any new arguments, either. Wilson and his colleagues have been making these same arguments for several years, and they've already been answered by other workers in the field. But, like creationists, these guys go on making the same fallacious claims.

Reply



Kevin

Posted August 30, 2010 at 3:45 pm | [Permalink](#)

Then I'll definitely wait for the counter-argument before I spend \$32 or make the less-expensive trip to the library that has the subscription.

Should I butter the popcorn?

Reply



J.J.E.

Posted August 30, 2010 at 5:19 pm | [Permalink](#)

Butter that popcorn. I suspect there will be multiple responses to this.

Reply



Ichthyic

Posted August 30, 2010 at 6:46 pm | [Permalink](#)

*I predict another spate of "Darwin was wrong" news reports.*

you mean like this?

<http://www.cosmosmagazine.com/news/3670/kin-selection-dead-eo-wilson>

Reply



Ichthyic

Posted August 30, 2010 at 6:49 pm | [Permalink](#)

...nawww, the media is still busy misinforming people about this paper:

<http://www.aolnews.com/weird-news/article/was-darwin-wrong-study-says-living-space-is-key-to-evolution/19606711>

Reply

3.

Colugo

Posted August 30, 2010 at 12:14 pm | [Permalink](#)

"Although social insect colonies have clocklike design in many respects, kin selection theory predicts who is throwing sand into the clockworks"

That could also be said of individual organisms and non-cooperators like cancer cells, or of genomes and non-cooperators like parasitic DNA. Or even symbionts that are sometimes mutual and sometimes parasitic. At any level of biological organization there are circumstances in which cooperation prevails and in which non-cooperation will occur.

So maybe group selection (using 'group' as a term for any assembly of cooperating units, whether a genome, organism, symbiont, or colony) AKA individual fitness ('group' regarded as an individual) is a special case – when cooperation prevails – of the kin selection of those constituent units.

[Reply](#)



Ian Robinson

Posted August 30, 2010 at 12:45 pm | [Permalink](#)

Bit of a tangent but if interested in a bit of scifi that touches on the subject of eusociality, then grab a copy of Frank Herbert's book "Hellstrom's Hive". It's great.

[Reply](#)



Ray Moscow

Posted August 30, 2010 at 1:47 pm | [Permalink](#)

I'm reminded of the controversy on the pages of *New Scientist* a few years ago (I think it was 3 Nov 2007) in which E.O Wilson and David Sloan Wilson seemed to champion group selection as a major driving force in evolution.

Prof. Dawkins wrote a letter to NS criticising this idea, I think correctly, but it was rebuffed by E.O. Wilson himself.

As a layperson, the article seemed to me an attempt to resurrect "group selection" as a viable theory after it has its ass kicked in *The Selfish Gene* three decades earlier. As far as I know, no-one has managed to demonstrate any mechanism by which group selection could work without it being undercut by "selfish" agents (genes) acting at a more basic level.

[Reply](#)



Ken Pidcock

Posted August 30, 2010 at 2:34 pm | [Permalink](#)

I'd recommend that young biologists follow this closely. It's going to provide you with something to teach your students about the sociology of the scientific community. I will confess that it is not yet clear to me what that something will be.

In present company, I will assume that I am insufficiently informed to recognize the flaws in Nowak et al. that are so apparent to others.

Reply



J. G. Cox

Posted August 30, 2010 at 4:01 pm | [Permalink](#)

You're mostly correct, but, as always, it's a bit more complex than that. The current consensus is that group selection (indeed, selection at all levels) does occur. In fact, it's a unavoidable statistical fate. However, selection at the individual (or genetic) level is usually stronger and usually opposed to selection at other levels.

It's been a while since I've looked at that stuff, but I think that Leticia Aviles at UBC did some work with colonial spiders that operated that exhibited those special conditions.

Reply



J. G. Cox

Posted August 30, 2010 at 4:02 pm | [Permalink](#)

Oops, that comment was supposed to be a reply to Ray Moscow.

Reply



S.K.Graham

Posted August 30, 2010 at 6:25 pm | [Permalink](#)

Well yes and no. Group selection is "valid" in the same sense that individual selection is "valid" — both are only valid insofar as what is really happening is differential success of genes reproducing.

Reply



MadScientist

Posted August 30, 2010 at 4:01 pm | [Permalink](#)

Did E.O. write it himself or is his name just on there? Is it senescence creeping in? I'm always surprised to see he's still about and doing things. It needn't have anything to do with age though; I just remembered that a lot of very good scientists from the past have all had their share of just plain wrong ideas. Even Einstein, after decades of thinking about it, gave up on his Grand Unified Theory (or was it the "Theory of Everything") and had even told people it's not going to work (of course many of those people didn't believe him and just went on).

Reply



SteveF

Posted August 30, 2010 at 5:53 pm | [Permalink](#)

Nowak (who's a brilliant evolutionary biologist BTW) wrote it.

Reply



Marella

Posted August 30, 2010 at 9:51 pm | [Permalink](#)

Not quite as brilliant as we thought it would seem.

Reply



SteveF

Posted August 31, 2010 at 4:46 am | [Permalink](#)

No, he's undoubtedly brilliant. Also, he has a very helpful webpage with large numbers of his papers available to read:

<http://www.ped.fas.harvard.edu/people/faculty/>

Well worth checking out

On a general note, it's positive how many evolutionary biologists put their papers online for anyone to read. Michael Lynch and Gunter Wagner are other good examples.

Reply

9.



Alex SL

Posted August 30, 2010 at 4:10 pm | [Permalink](#)

Well, to be honest, I have never felt that the kin selection explanation of eusociality is very convincing. When I first read of it as a student, my immediate reaction was: "but what about termites"?

This is not saying that inclusive fitness does not tell us anything relevant about parent-offspring conflicts, but it fails as an explanation of eusociality the second you realize that there are eusocial organisms that have diploid males, and that is shrewdly ignored in many books or articles discussing eusocial hymenoptera. In that sense, I welcome more awareness-raising discussion, even if it should get started by a questionable argument.

Reply



Jeremy

Posted August 30, 2010 at 5:19 pm | [Permalink](#)

The fact that termites are eusocial simply demonstrates that relatedness asymmetries (like you get with haplodiploidy) are not necessary for the evolution of eusociality. However, termite eusociality in no way undermines kin selection as an explanation for eusociality. After all, termite colonies are composed of family groups (i.e. kin selection is a viable explanation) as is the case for all other eusocial species. There is a tendency to confuse the "haplodiploidy hypothesis" with kin selection in general. Also, it should be noted that a fairly recent paper using ancestral reconstruction showed that monogamy is most likely ancestral in eusocial lineages, which detracts somewhat from the argument that multiple mating by queens argues against the haplodiploidy hypothesis. Plus, eusocial thrips are haplodiploid, suggesting that there *might* still be something to the haplodiploidy hypothesis. Of course ecological factors, which determine the costs and benefits, are also very important in all cases. Relatedness only alters how large the B/C ratio has to be.

Reply



Alex SL

Posted August 30, 2010 at 5:21 pm | [Permalink](#)

Sorry, should have said the haplodiploid argument for eusociality.

[Reply](#)



J.J.E.

Posted August 30, 2010 at 5:23 pm | [Permalink](#)

What books have you been reading that have made the claim that eusociality requires haplodiploidy? That may be your first problem. Eusociality is predicted under conditions that do not require haplodiploidy, though as others point out, under certain areas of parameter space, you can get eusociality under haplodiploidy much easier than for diploidy. It just so happens that the parameters that promote such conditions may not be common (i.e. queens are often multiply mated) and so the hymenoptera-centric explanation may not be very useful. But that doesn't say very much about inclusive fitness in general or its influence on the evolution of eusociality in particular.

[Reply](#)



S.K.Graham

Posted August 30, 2010 at 6:21 pm | [Permalink](#)

Normal diploid offspring are as related to each other (siblings) as to their parents. So devoting resources to creating more siblings is just as viable a strategy as producing offspring.

[Reply](#)



Alex SL

Posted August 30, 2010 at 11:26 pm | [Permalink](#)

I have no problem with kin selection and messed up my first comment.

The thing is just I have read several popular science explanations giving the haplodiploid explanation, and I never understand why we need convoluted ideas like entirely instinct-driven workers "deciding" to raise their siblings instead of children when a very simple one is available: those queens that can produce infertile slaves to help them are able to out-compete those that cannot. If you are a honeybee worker that "decides" to raise her own family, you're toast and your mother is toast. End of story.

[Reply](#)



S.K.Graham

Posted August 31, 2010 at 2:56 am | [Permalink](#)

If the workers were clones of the queen your queen-making-slaves idea would work — for the same reason the all the cells in your body could be seen as "slaves" working ultimately for the benefit of your the germ-line cells in your gonads, which are the only cells that get a

chance to pass on copies their genes via sperm or egg to the next generation (mutations in your germline can be passed to offspring, for example, but mutations in your heart, skin, or brain cell a passed only to their daughter cells and ultimately will die with you).

The workers get half their genes that come from the father, and it is not necessarily in the interest of those genes (from the father) to help the queen to produce daughter-queens unless the father's genes are also in those daughter-queens (which may not be the case sincwe queen mates with multiple males). It could potentially be in best interest of genes-from-father for the worker to reproduce directly. And since the workers do not get all the Queen's genes, the Queen's daughter-queens may not share all the worker's genes-from-mother either. So it is a question of kin-selection cost benefit whether the genes-in-worker a best served by the worker staying sterile or reproducing on its own.

The idea of queen \*forcing\* workers to be slaves somehow is debunked because the weaknesses that allow the workers to be thus force would not be selected, unless the same gene (and hence same weakness) was in the queen. After all, before there were queens, how was it decided who reproduced? There must have been transition stages of colonies with multiple queens, dominance competitions, and so forth. In fact you will find types of wasps (and I think ants) that exhibit a spectrum from "all (or nearly all) reproducers" to "one and only one queen-mother".

Reply



Alex SL

Posted August 31, 2010 at 6:20 am | [Permalink](#)

I understand the idea, but my point is: what if the decision is between having genes for a worker caste and not being competitive enough to survive? The latter situation would not help the genes in an egg-laying daughter very much, no matter what their interest.

Also, I simply don't buy the weakness also in the mother argument. That is what specialization is; the "weakness" of my somatic cells not to be able to reproduce is also not shared by my parent's gametes. And note that that also goes for chimeras.

Reply

10.



Jeff

Posted August 30, 2010 at 5:20 pm | [Permalink](#)

It's not too surprising that David Sloan Wilson is also among those challenging kin selection. I mean, what else do you expect from a guy who denied his son his birthright machete?

Anyway, I wonder how long will it be before the creationists start spinning this as "proof" of a crisis in evolutionary theory. I give it less than a week...

Reply



11.

S.K.Graham

Posted August 30, 2010 at 6:17 pm | [Permalink](#)

What do you mean “the big guns”? Don’t be so modest. You are one of the big guns... aren’t you?

I’ve been waiting for some big guns to come out against this foolishness... your blog is the first I’ve seen.

I never much bought the haploid nature of bees & ants and \*necessary\* for eusociality (and obviously it isn’t given termites, etc.). After all, ordinary diploid offspring are as closely related to their siblings as to their parents, so it is just as advantageous to help an diploid parent reproduce as to reproduce oneself. Or is there something I’m missing in that line of reasoning?

I think Nature can be forgiven, considering E.O.Wilson’s stature in the field. If I were an editor, my thinking would be to let the larger community of evolutionary biologists as a whole hash it out. Reviewers are just a first line of defense. The critique after the publication, which is happening now, is where the real battles are fought.

Wilson is very fond of his ants and clearly \*wants\* very much to see more than the selfish gene at work in the evolution of social behaviors.

Reply



o

Rerun

Posted August 30, 2010 at 6:19 pm | [Permalink](#)

He means the big guns in the field of kin selection

Reply



12.

Thanny

Posted August 30, 2010 at 7:10 pm | [Permalink](#)

The more biology I read, the more pervasive I find a particularly bad notion – that an explanation must be singular, must apply always, and must have equal applicability between the present and the past.

In the minds of some, it seems, complex webs of causation are just too much to think about. If a contributing factor cannot be said to act alone, or have its effects isolated by experiment or model, then it cannot be a factor at all. It’s really abysmal reasoning, and it’s shocking to see it practiced by people who should know better.

Of \*course\* the fact that females are more related to sisters than their own offspring has influenced both the origin and development of eusociality in haplodiploid insects. That doesn’t mean it’s either necessary or sufficient – termites and solitary haplodiploids show that well enough.

An analogy of what sloppy thinking I see here on the part of Wilson and his new compadres. Say you have a certain type of car which crashes more frequently than others of its type. Someone notices that the wheels seem to have a design flaw which causes the tires to blow out very often, and calls this a contributing factor in the increased accidents. Perfectly reasonable. Now someone comes along and plays up the accidents where the tires were intact, and says, “See!? These accidents cannot possibly be caused by a faulty wheel design.”

More directly to the case of multiple matings with haplodiploids, I

have to say I disagree with Jerry's characterization of its affect on sister-sister relatedness. Sisters with a common father have 3/4 relatedness, while those with different fathers 1/2, just as their own offspring would have. But it's not about individual relatedness. It's about the odds of a gene impacting a copy of itself in another body. No matter how many times the queen mates, a gene in a haplodiploid female will always have a >50% chance of finding itself in a sister, averaged over the hive (ignoring queen replacement effects in this case). It will always be exactly 50% for offspring. Even if you assume it's a contest between 51% and 50%, consider what I've read many times now about mice and elephants – assuming a mere 1% increase in size, it'd take only about 1000 generations to turn a mouse into an elephant. Even such tiny differences, over millions of years in a rapidly reproducing insect, will have an immense impact.

Reply



whyevolutionistrue

Posted August 30, 2010 at 7:26 pm | [Permalink](#)

You forgot about the males.

Reply



Thanny

Posted August 30, 2010 at 10:07 pm | [Permalink](#)

I didn't forget about the males, but didn't address them because I was well on my way to a novella already.

Haplodiploid males are a wash in this scenario, as it doesn't matter how many times the queen mates – workers will be equally related to each male they rear (again, adjusted for queen replacements), there being no paternity.

Reply



Sven DiMilo

Posted August 30, 2010 at 8:49 pm | [Permalink](#)

you have to admire the guy's knowledge, breadth, dedication to conservation, and sheer workaholism.

And also his writing—some of it's really beautiful.

Reply



Diego

Posted August 30, 2010 at 9:17 pm | [Permalink](#)

These were precisely the same kinds of objections that were raised in my mind by this paper.

It certainly didn't help that when I heard advance word about the paper on the journal's podcast that the journalists discussing the paper couldn't come up with a clear synopsis.

Reply



Marella

Posted August 30, 2010 at 9:58 pm | [Permalink](#)

It's always sad when great people screw up their legacy with bullshit as they get older. Like Napoleon invading Russia and Einstein with quantum theory.

[Reply](#)

16.



Walter S. Andriuzzi

Posted August 31, 2010 at 3:32 am | [Permalink](#)

Quoting from Carl Zimmer's article on nytimes online, "Dr. Ratnieks argues that the Harvard researchers cannot rule out kinship as a driving force in social evolution because their model is flawed. It does not include how closely related animals are". That seems to me a serious flaw.

As my first comment in this blog I would like to congratulate Jerry for his homonymous book. It is just great 😊

[Reply](#)

17.



Richard Dawkins

Posted August 31, 2010 at 3:51 am | [Permalink](#)

To expand on the point about haplodiploidy being incidental to Hamilton's classic double paper of 1964, out of 49 pages (in the \*Narrow Roads of Gene Land\* reprint), the haplodiploidy hypothesis occupied a mere three and a half pages. This was followed by another three pages discussing the fact that Hymenopteran queens often have multiple mates — precisely the point advanced by Nowak et al as a 'new' criticism! Hamilton then went on to discuss the case of the termites (which are not haplodiploid) thereby anticipating another of the 'new' criticisms. The termites, as Hamilton also pointed out, have a completely different tell-tale predisposition to eusociality under his theory, namely recurrent inbreeding, which raises the coefficient of relatedness in a way parallel to the 'haplodiploidy effect'.

Given that Nowak et al seem to think haplodiploidy is central to Hamilton's theory, I am astounded that they totally fail to mention the work of Robert Trivers and Hope Hare on sex ratio biases in Hymenoptera (see \*The Selfish Gene\* for a full discussion of this work, which is alluded to by Jerry above). Trivers and Hare calculated optimal sex ratios from the point of view of a queen, and from the point of view of a worker ant, given haplodiploidy. If the queen exerts power over the ratio of males to females, the stable ratio of colony investment in males versus reproductive females would be 1:1. If the workers have control over the sex ratio, there would be three times as much investment in females as in males. They went on to measure the actual ratios in 20 species of ants and found a female bias as per the haplodiploidy prediction. There was even an 'exception that proves the rule' in the form of slave-making species whose workers have no power because the work is all done by slaves. The Trivers/Hare study has been criticised on various grounds, but it is astonishing that Nowak et al ignore it completely.

In any case, the most important point is that Hamilton's theory does not — and never did — stand or fall by the enigmatic special case of haplodiploidy. On the contrary, by far the bulk of work using the theory has been done on ordinary diploid organisms, and the bulk of Hamilton's own thinking on the subject concerned diploid organisms. Hamilton's theory of Inclusive Fitness is not something set apart from 'Standard Natural Selection Theory'. It *is* Standard

Natural Selection theory, made complete by filling in a logical implication that had previously been overlooked.

Reply



NewEnglandBob

Posted August 31, 2010 at 4:57 am | [Permalink](#)

Who could ask for anything better than the clear explanations of Jerry Coyne and Richard Dawkins! May I suggest a collaborative book?

Reply

18.



GM

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From what I have seen, Boomsma's Monogamy hypothesis explaining eusociality has gained some steam. It was mentioned by name in the West et al. (2010) paper cited above and those authors seem quite content with Boomsma's explanation. Specifically, Boomsma took the standard " $rB > C$ " argument, modified C so that it was " $0.5B > 0.5C$ " (because offspring on average are related to the parent by 0.5), and then cancelled to get " $B > C$ " so that any factor tipping the balance towards helping siblings will start to push a system towards cooperative breeding and possibly eusocial castes. I wonder if Nowak et al (I haven't read the paper or the 41 pages of supplementary material yet) addressed this idea.

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