Deep Thoughts and Silliness by Bob O'Hara
Just what it says on the tin
view profile

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SATURDAY, 19 SEP 2009 - 15:53 UTC

Kin are a Group

A few days ago Eric Michael Johnson (formerly of this parish) put up a post about **laboratory evidence for the breakdown of the selfish gene**, which he started like this:

> My previous post on a potential problem for the selfish gene theory in explaining cooperative behavior resulted in a fair amount of heated discussion. However, there are quite a few misconceptions regarding the controversy surrounding the selfish gene, group selection, multilevel selection, generalized reciprocity, etc. that need to be clarified.

He then went on to perpetrate some of these same misconceptions.

Eric claims that selfish gene theory needs expanding to include multi-level selection. He illustrates this with an experiment Bill Muir carried out many years ago. Bill is a chicken breeder[1], and was worried about the welfare of battery hens. These hens are kept together in small groups, without having bountiful acres to run around in. Instead, they would squabble and fight, which would decrease egg production as well as making them unhappy chickens. Bill had the idea of selecting chickens that would be more sociable, and he did this by breeding from chickens which were in the most successful group. He did this and raised an über-race of sociable chickens who would produce lots of eggs whilst doing little more than sipping tea and nattering about how Edith in bay 73 has never been the same since she tried to remove her comb and escape to Antarctica.
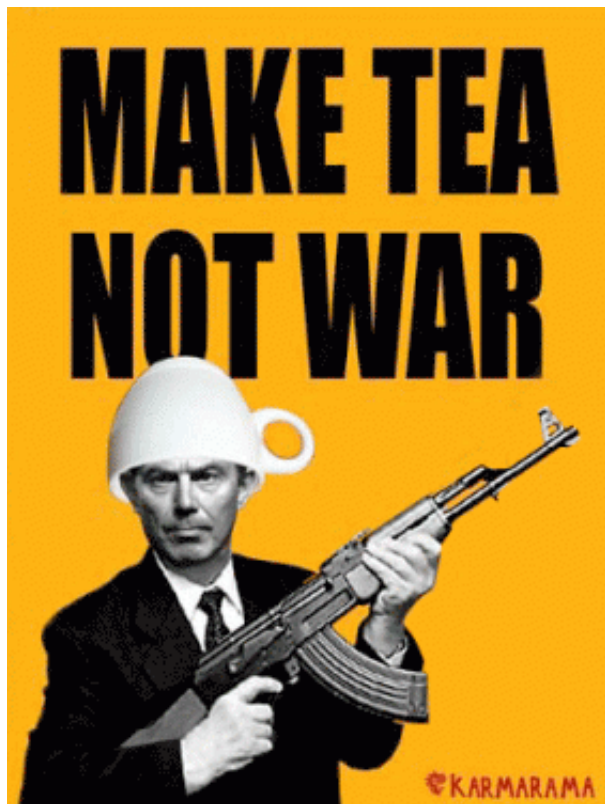
How do we explain this? If we put some nice chickens in with nasty, selfish, chickens, the nice ones get bullied. So, individually they are not as fit. But, the group as a whole is fitter so it makes sense to think about what happened at the group level. Hence we can talk about group level selection.

This is a subject with a long and rancourous past, so a potted (and not entirely inaccurate) history is useful.

in the bad old days there was old groups selection, where the chickens' behaviour would be explained as acting "for the good of the group". This was swept away in the late 60s when it was realised that this argument didn't work: if that's what was going on, a bully hen would be able to dominate. Another explanation, kin selection (i.e. helping relatives) was also developed. But in the 1970s group selection made a comeback, partly due to the work of David Sloan Wilson who formalised the idea and explored the conditions when it works. This caused a lot of controversy, debates etc. much, no doubt, to the bemusement of Bill Muir. There are several reasons for the rancour: it was caught up in the sociobiology debates, for example. These debates have largely died down, but oddly the mention of group selection is still perceived as an anathema. People will happily work on the evolution of social behaviour, studying systems where it is obvious that there is selection at the group level, but are utterly unable to let that phrase pass their lips. I find this rather comic.

What makes this really odd is that the scientific issues have been settled. We know group level selection can work, and through George Price we have a powerful tool to analyse it. Ironically this development is an application of selfish gene theory. The idea behind selfish gene theory is to think about evolution in terms of genes, rather than individuals. So, for basic kin selection we know that individuals who are more related are more likely to share genes, and hence an altruistic trait that increases their fitness by enough will spread. But you've all read *The Selfish Gene*, haven't you?

Anyway, this same argument can be used for groups. If I help the members of my group, at a personal cost to myself, and if they are more likely to share my helping gene than a random member of the population, then that gene will become more frequent than if I was helping random individuals. We see precisely this in the chickens: a gene for not beating up your neighbours means that you are less likely to get food. But if several of you in a group have that gene, the group as a whole benefits because there is less fighting. As long as the increase in the average fitness of the group is larger than my loss of fitness from being nice, being nice wins out. There is obviously a balance between the individual and group levels, and Price worked out the tools to make sense of this**[2]**.

Eric's suggestion that selfish gene theory breaks down is wrong: we can use precisely this tool to understand the experiment. It is not the only way to analyse the situation, though. David Sloan Wilson developed a "new" group selection, which is more formal than the old one. This is equivalent to a kin selection approach, so if there is a debate, it is over which approach is better. i.e. which one gets results.

Last year there was a to and fro about this. That well known beat combo West, Griffin and Gardner had written a **review of models of social evolution**, and (D.S.) Wilson responded **with a call for pluralism**: for his approach to be allowed space. The **response to this** was academic pwnage. This was particularly devastating:

> Wilson's first example of the insights provided by group selection is the effect of population viscosity (limited dispersal) on the evolution of cooperation or altruism (**Wilson et al., 1992**). This problem of population viscosity and cooperation was considered by Hamilton from an inclusive fitness perspective. Hamilton (1964, 1972) suggested that population viscosity (limited dispersal) could favour cooperation because it would tend to keep relatives together – in this case, altruism directed indiscriminately at all neighbours could be favoured, because those neighbours tend to be relatives. However, Hamilton (1971, 1975) later realized that things might not be that simple, as population viscosity would also keep relatives together to compete, which would select against cooperation. The question is, what the relative importance of these opposing forces is?
>
> **Wilson et al.'s** key contribution was to show that, in a simple-case scenario, these two opposing forces seem to cancel out, and so population viscosity has negligible influence on the evolution of cooperation. However, group selection methodology could not provide an analytical account of this phenomenon (see also **Wright, 1945**). Consequently, Wilson et al. were forced to use a simulation approach, that had to rely on specific parameter values and was less useful for general interpretation. This problem was solved by Taylor with the use of kin selection methodology – in just a few lines of algebra, he was able to analytically show how and why the effect of increased competition between relatives exactly cancelled the effect of increased relatedness (**Taylor, 1992**). This provides a clear demonstration of how the kin selection approach is easier to use (it allowed an analytical solution), while also providing a more general

solution (that did not assume specific parameter values), and could be easily applied to a range of biological examples (see **West et al., 2002a**).

In other words, we can do things your way, but it's slow and nowhere near as good. Put simply, a selfish gene approach is well developed, and is more powerful: we can get nice analytic results that explain what's going on.

I think it must be frustrating for people who actually work on this subject to see these arguments come out. Indeed, this is what Kern Reeve and Laurent Keller wrote ten years ago in their **introduction to a book on levels of selection**:

> First, however, we wish to make yet one more attempt to bury the issue that usually usurps discussions of the levels of selection at the expense of the truly interesting issues raised by these two problems; that is, the question of what unit is the "true" fundamental unit of selection. … In our opinion, these questions have been satisfactorily answered repeatedly, only to reappear subsequently with naive ferocity in new biological subdisciplines (e.g., the group-selection controversy is currently generating copious amounts of smoke within the human sciences; see, e.g., Wilson and Sober 1994 and responses; Sober and Wilson 1998). The particularly frustrating aspect of these constantly renewed debates is that, even though they seemed to be sparked by rival theories about how evolution works, in fact, they often involve only rival metaphors for the very same evolutionary logic and are thus empirically empty.

> Thus, we first pause to heap one more shovelful of dirt on the units-of-selection debates (a) and (b) above by very briefly reviewing what we believe to be their well-established, correct (if not universally known) resolutions.

If they decide to write a second edition, this may only need slight editing.

[1] Well, animal geneticist. But chicken breeder sounds funnier.

[2] Actually, he was re-deriving Bill Hamilton's kin selection results, but saw that the ideas extended to groups.

11 comments   permalink

Last updated: Saturday, 19 Sep 2009 - 15:53 UTC

all tags   kin selection group selection selfish gene even more selfish jean evolution

Comments

Saturday, 19 Sep 2009 - 16:37 UTC
Richard Grant **said:**

I'll take your word for it, ~~Eric Henry Grrl~~ Bob.

Saturday, 19 Sep 2009 - 16:45 UTC
Bob O'Hara **said:**

Actually, I'm Bill.

Saturday, 19 Sep 2009 - 16:58 UTC
Richard Grant **said:**

Nope. This is Bill.

Saturday, 19 Sep 2009 - 17:06 UTC
Bob O'Hara **said:**

I'm another Bill. One that isn't as attractive to women in Helsinki nightclubs.

Saturday, 19 Sep 2009 - 18:38 UTC
Eric Michael Johnson **said:**

Nice review Bob. I linked to it on my post. However, I disagree that with you that "the scientific issues have been settled". I think Wilson and Wilson's paper in Quarterly Review of Biology has reopened this question for a number of biologists.

Saturday, 19 Sep 2009 - 21:18 UTC
Bob O'Hara **said:**

I don't see that review as saying anything new, though. It's the same old arguments that Reeve and Keller were complaining about. If it hadn't been written by a couple of Wilsons, it would have sunk into obscurity.

Sunday, 20 Sep 2009 - 03:30 UTC
Bora Zivkovic **said:**

You say "If I help the members of my group, and if they are more likely to share my helping gene, then that gene will become more frequent than if I was helping random individuals." Sloan and Wilson model shows that the clause "more likely to share my helping gene" is not necessary. Thus, inclusive fitness is only a subset of group selection.

Sunday, 20 Sep 2009 - 08:54 UTC
Bob O'Hara **said:**

Sorry, Bora, I was unclear there: more likely than over the whole population (i.e. summed over all groups), and I also assumed a fitness cost of helping. I've revised the post, now. I assume the "Sloan and Wilson" model you're referring to is from Sloan Wilson's 1975 paper (yay, also open access!), and he shows that these are (now) the conditions.

"[I]nclusive fitness is only a subset of group selection" doesn't make any sense. Group selection is the process, inclusive fitness is a tool used to analyse that process.

Monday, 21 Sep 2009 - 01:20 UTC
Alejandro Correa **said:**

And the beast: _ ¿which is thinking?_

Monday, 21 Sep 2009 - 06:47 UTC
Bob O'Hara **said:**

Oh, he's one of those that mistakes "The Selfish Gene" for "The Selfish Individual". Embarrassingly for me, it works too.

Tuesday, 22 Sep 2009 - 15:23 UTC
Heather Etchevers **said:**

This is Bill

He gets pecked by chickens all the time.

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