

Why Evolution Is True

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How important is group selection?

Several people on this website have raised the question of group selection, and asked me what I thought of it. The idea that selection operates on entire groups rather than individuals, and can lead to the evolution of group-level traits (altruism is supposed to be one of these), has been revived by several people. Among them are E. O. Wilson, but especially David Sloan Wilson, who has defended his notion of group selection in a fifteen-part (!) series on HuffPo, infelicitously called "Truth and Reconciliation for Group Selection."

I've avoided discussing this topic because it's not my own area of research and it's a thicket of contentious claims and counterclaims that often seem more semantic than biological. And I don't have the mathematical expertise to appraise all the models. Nevertheless, the field seems to be converging on a solution (which is *not* without dissent!).

Fortunately, you can get an excellent summary of the state of the field in a little over an hour, thanks to the [London Evolutionary Research Network](#), a consortium of researchers who hold regular meetings and debates. Last July, they held a very nice debate, "Is natural selection at the group level an important evolutionary force?" which is now available at Vimeo.

There were four speakers, each talking for around 20 minutes, and there's a 70 minute question-and-comment session at the end. Here are the links to the separate videos.

[Herbert Gintis](#) (professor of economics, Santa Fe Institute, University of Siena, and Central European University)

[Mark Pagel](#) (professor of Biology, University of Reading)

[Samir Okasha](#) (professor of philosophy of science, University of Bristol)

[Stuart West](#) (professor of evolutionary biology, University of Oxford)

[question-and-answer and discussion session](#)

If you don't have time for all of these, by all means watch Stuart West. I don't know how he did it, but in 20 minutes he managed to sum up the whole debate, beginning with Darwin, moving through the group selection arguments of Wynne Edwards, and assessing modern D.S.-Wilsonian views of group selection. It's a masterful performance.

And, as far as I can judge these things, West's assessment is correct, and, I think, is the one that most smart people in the field are beginning to accept:

1. The old idea of selection among groups leading to the evolution of group-level traits works only under very special circumstance.
2. The "new" view of group selection (NGS) gives results that are either wrong or, when they're right, essentially equivalent to the simpler and less confusing inclusive-fitness theory (IFT), pioneered by Price and Hamilton and developed in the 1980s. I'll show Stuart's slides:

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3. Group Selection seems to spread confusion

B. Often claimed that certain group selection models are outside of KS or IF theory. But formal analysis always shows wrong and just wasting time.

Area	Authors claiming that a result requires group selection	Authors showing equivalent result with KS/IF
Sex ratios with local mate competition	Wilson & Colwell 81, Colwell 81, Sober & Wilson 98)	Frank 86, Grafen 84, Harvey 85
Sex ratios with budding dispersal	Aviles 93	Gardner 09
Eusociality	Wilson & Holldobler 05; Wilson x 2 07	Foster et al 06; Helanterä & Bargum 07; Hughes et al 07
Strong reciprocity	Gintis et al. 00-06	Lehmann et al. 07
Cooperation	Fraulsen & Nowak 07	Lehmann et al. 07b
Virulence	Sober & Wilson 98, Wilson 98	Frank 96, Wild et al. 09
Policing	Sober & Wilson 98	Ratnieks 88, Wenseleers et al. 04

It is an interesting psychological question why people are so keen to reinvent this problem?

Opposite is not true! For many things commonly modelled by IF, GS versions would be so complex that never tried (e.g. split sex ratios; Queller 2004).

3. NGS has not stimulated a productive research program. Virtually every advance in understanding the effects of group-level dynamics on the evolution of social behavior has come from IFT instead. Here West checks off which of the two theories has better helped us understand various biological phenomena (in the slide below, "GS" is group selection and "IF" is inclusive fitness theory). It's a slam dunk for IF.

2. Biological Applicability

Inclusive fitness has proved far more useful for explaining biological phenomena and making testable predictions.

The great empirical success stories of social evolution (West et al. 2008 JEB)

AREA	IF or GS?
Split sex ratios	IF
Local mate competition	IF
Kin discrimination in coop. verts.	IF
Worker policing	IF
Parent-Offspring conflict	IF
Sibling conflict	IF
Selfish genetic elements	IF
Avoidance of cannibalism	IF
Cooperation in microbes	IF
Genomic imprinting	IF

West concludes that while NGS is not usually wrong, it's not useful, and, anyway, it's not really new, since its mathematics were already worked out several decades ago. While advocates of NGS claim that they're ignored (and, at worst, persecuted), West implies that the theory is simply irrelevant. His conclusion:

Summary

Asking if selection at the group level is important is the wrong question.

The extent to which individual (direct) fitness or group fitness is being maximised depends upon model details and, for any given model, upon parameter values (and MLS does not imply group adaptations).

However, selection is always at the level of inclusive fitness. GS/MLS is not incorrect (although seems to lead to confusion) - it is just one of the many possible ways of looking at the dynamics by which IF is maximised.

But, we've known all this since the



Watch *all* the speakers if you can, for the 80-minute debate is a painless way to educate yourself on the issues. And kudos to the London Evolutionary Research Network for holding this and selecting a great panel of speakers. Let's see more of these—I'd like one on species concepts and speciation!

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