

DENIM and Tweed

Ignoti, sed non occulti.

ABOUT ME



JEREMY YODER

I'm a baptized Mennonite studying evolutionary biology, an East-Coast liberal

living in Idaho, and a fan of David Foster Wallace who also appreciates "Battlestar Galactica". See also my personal site.

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DENIM AND TWEETS

- @GOPLLeader I'm an American and I support the public health insurance option. <http://is.gd/3SzSM> #sickofit about 20 hours ago
- Headed before noon tomorrow to run the @PDXmarathon. Or to travel from one end of the course to the other. We'll see about the running. 1 day ago
- Empirical pacifism? <http://ff.im/-945ep> 1 day ago [follow me on Twitter](#)



26 JUNE 2009

No room for group selection in disease evolution?



Parasites coexisting within a single host have been proposed as one of the best examples of individuals sacrificing their own reproductive fitness for the benefit of a group. A new theory paper in last week's *Nature* suggests that the apparent effect of "group selection" in this case can be explained by [individual-level selection instead](#) [5-a].

Group selection posits that organisms sometimes evolve traits that hurt their individual fitness but benefit their social group. Charles Darwin originally proposed it to explain the evolution of human moral systems: in a tribal society, helping your neighbor might cost you, but it might still help your whole tribe to compete against other tribes. So natural selection on individuals *within* a tribe may act in one way, but be opposed by *group selection* arising from competition among tribes.

This process has also been proposed to explain a common phenomenon in the evolution of disease organisms: the [trade-off between transmission and virulence](#) [PDF]. Simply put, if it's easy for a disease-causing critter to spread through a host population, it tends to do more damage to its hosts; and if it is less easy to spread, the disease [tends to do less damage](#) [5-a]. A classic case of this effect is documented in [cholera](#), which has evolved lower virulence when good sanitation practices cut off the easy route of transmission through sewage-contaminated drinking water.

Proponents of group selection say that this occurs because, under difficult transmission conditions, disease organisms must throttle back their production of offspring [lest they kill their shared host](#). But it's also possible to describe a verbal model by which reduced transmission selects for lower virulence without invoking group selection, courtesy of [kin selection](#).

Kin selection takes into account the effect of natural selection on not just the copies of an individual's genes within that individual's body, but also the copies borne by close relatives; if you're a parasite that reproduces inside your host, making more offspring also means making more *competitors* for your offspring, and thereby reducing the fitness of the genes that you share with the next generation. So, unless it's easy to disperse to new resources -- uninfected hosts -- natural selection can actually favor prudent reproduction by a parasite, which keeps the host alive longer.

The new paper in *Nature* puts some math behind this verbal model. The authors, Wild *et al.*, building on a standard disease-modeling framework, assume a world of patchily-distributed hosts infected by a single parasite species. Parasites are transmitted by host-to-host contact; it's assumed that the number of offspring a parasite produces is proportional to the chances that some of those offspring are transmitted to another host, so that more virulent parasites have a better chance of sending offspring to new, uninfected hosts.

Under this model, the authors show that the fitness of a mutant, more virulent parasite, differs from that of its less-virulent competitors in several important ways: A more virulent mutant has

- an increased chance of killing its host;
- an increased chance of sending offspring to another patch of hosts;
- increased competition from the offspring it produces that do not disperse to another patch;
- increased competition experienced by those offspring; and
- a greater chance that, by killing its host, it will make way for an uninfected replacement host for its offspring.

When the parasites can disperse to new patches with maximum efficiency, they simply evolve to maximize their own fitness at the expense of the host -- but as dispersal becomes more restricted, the costs of competition exert selection on *individual parasites* to evolve reduced virulence.

Wild *et al.* conclude that, because their model replicates the transmission-virulence trade-off without invoking group selection, they can reject the group

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DENIM & TEES



There must be *dozens* of people interested in a t-shirt illustrating the [Wright-Fisher model](#), right?

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selection hypothesis. In fact, they strongly suggest that group selection may not matter much in natural systems:

The multilevel (group) selection and kin selection (inclusive fitness) approaches to social evolution have long been known to be mathematically equivalent and, if the analyses are performed correctly, do not lead to conflicting predictions. Thus, *irrespective of the relative strengths of within-group versus between-group selection, individuals are predicted to maximize their inclusive fitness.* [In-text citations removed; emphasis added.]

Clearly this result shows that group selection isn't necessary to create the transmission-virulence trade-off. On the other hand, it doesn't provide a good comparison of group-level and individual-level selection, because (so far as I can see) it doesn't explicitly *contain* an effect of group selection. It's one thing to show that group selection isn't necessary, but it's another to show that its effects would be overwhelmed by individual-level selection.

References

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POSTED BY JEREMY AT 00:05

LABELS: DISEASE VIRULENCE, EVOLUTION, RESEARCH BLOGGING, SCIENCE

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Regis said...

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JUNE 29, 2009 7:56:00 PM PDT

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