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Going against the group

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A new theoretical model of parasite virulence published in this week's *Nature* puts a chink in the armor of group selection theory, the idea that organisms act altruistically for the betterment of groups as a whole.


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The study "contributes to this debate that evolutionary biologists really seem to enjoy, which is at what level selection seems to act," Geoff Wild, a mathematical biologist at the University of Western Ontario in London, Canada, who led the study, told *The Scientist*.

In the 1960s, group selection became a popular explanation for behaviors where individuals seemed to be acting against their own self-interest, such as nest building in social insects. However, around the same time, theoreticians showed that the same adaptations could equally be explained by considering an organism's "inclusive fitness," which includes the number of offspring sired by relatives in addition to one's own reproductive success. From a gene's-eye view, the success of one's kin can be just as good or better than selfish benefits, and so most evolutionary biologists were swayed in favor of a purely "kin selection" view of natural selection.

Over the decades, however, group selection has continued to curry favor among some researchers. One of the primary examples held up in favor of group selection is the observation that viruses living in moths and bacteria evolve to cause less damage when they are scattered among more isolated host populations. The more prudent the parasite, group selection proponents contend, the less likely the host will go extinct, and so everybody wins even if individuals act counter to their immediate best interests. But this argument overlooks the fact that when parasites are scattered across clustered hosts they also tend to be more related to their nearest neighbors. That means that parasites might be more restrained simply if it helps their kin, and by extension, their own selfish genes.

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The only way to resolve this debate, noted Wild, was to move away from verbal arguments and into the language of math. Together with the University of Edinburgh's Andy Gardner and the University of Oxford's Stuart West, Wild adapted a standard epidemiological model of hosts and parasites and investigated the effects of parasites evolving to be naughty or nice. They found that when parasites moved around less they evolved lower "birth" rates and virulence because it reduced the cost of competing with relatives of the same viral strain. "It's not really the good of the group," said Wild. "It's the good of the genealogical lineage."

The authors "take a kin selection approach and show that you can really explain the patterns in an intuitive way," Laurent Lehmann, a mathematical and evolutionary biologist at Stanford University who was not involved in the study, told *The Scientist*. "I don't think this paper will silence the debate" between group selection and kin selection advocates, he added, but "it will really help people in the community of parasite virulence realize that you can analyze the system in a relatively simple way."

Aneil Agrawal, a University of Toronto evolutionary biologist, agreed. "What they have done very nicely is provide an alternative decomposition of the factors driving the evolution of virulence in structured populations," he wrote in an email. "That is the major contribution of this paper in my opinion." But Matthijs van Veelen, a theoretical biologist at the University of Amsterdam, saw the paper's emphasis in a different light. The authors "seem to be more concerned about disproving group selectionists than about parasite virulence," he said.

The mathematics underlying both group selection and individual-level selection have long been known to be interchangeable, noted Wild, and so each theory makes equivalent predictions when they both "work." "But kin selection can work when group selection fails, so why not use the intuitive explanatory tool that is more robust?" he said. Van Veelen disagreed with this assertion. "I think there's no proof that there's equivalence," he said. In a paper published earlier this month in the *Journal of Theoretical Biology*, van Veelen reported that the two views of selection are not alike under some mathematical scenarios -- specifically, when there are complex fitness interactions.

Van Veelen's claim is "just not true," said Lehmann. The equivalence of the mathematics holds even in the face of complex selection regimes, and van Veelen has not interpreted the two evolutionary scenarios correctly, Lehmann argued.

Clearly, the debate will continue to rage on. Still, Wild hopes that his paper will quell some of the kin selection naysayers. "Really, there's no need for us to talk about groups," he said.

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