A duel between mathematical models supports the reigning theory of the genetics of altruism

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Even Darwin was vexed by the cooperative behavior of insects such as these leaf cutter ants, which didn't seem to fit with his theory of natural selection. Why would ants help other ants when it didn't benefit them directly? Inclusive fitness, the theory that creates room for altruism, has recently been attacked. Evolutionary biologist David Queller comes to its defense. Credit: Bandwagonman at en.wipideiaThis file is licensed under the Creative Commons Attribution-Share Alike 3.0 Unported, 2.5 Generic, 2.0 Generic and 1.0 Generic

It isn't that often that a scientific controversy is featured in the New Yorker, but in 2012 an article titled "Kin and Kind" describing a tempest over a biological theory appeared in its pages.

The tempest was provoked by an article in the Aug. 26, 2010 issue of *Nature*. Written by Harvard mathematicians Martin A. Nowak and Corina E. Tarnita and Harvard biologist Edward O. Wilson, it questioned the validity of the theory of inclusive fitness.

Inclusive fitness theory, proposed by British biologist W. D. Hamilton in 1964, expanded Darwin's definition of "fitness"—an organism's success in passing on its genes—to include the genes of its relatives. This expansion made altruism in the service of kin a competitive strategy.

The *Nature* article, title "The Evolution of Eusociality." asserted that inclusive fitness theory, which has been a cornerstone of evolutionary biology for the past 50 years, had produced only "meagre" results and that mathematical models based on standard natural selection theory provide a "simpler and superior approach."

This provoked a prolonged argument among evolutionary biologists that is still not resolved. But in the March 31 issue of *PLOS Biology* David C. Queller, PhD, a well-known evolutionary biologist at Washington University in St. Louis, suggests a way out of the impasse.

Queller, the Spencer T. Olin Professor in the Department of Biology, and his co-authors Stephen Rong, who graduated from Washington University with a bachelor's degree in math and is now a graduate student at Brown University, and Xiaoyun Liao, a former research assistant at Rice University with expertise in mathematical modeling, adopted the model the Harvard writers had proposed as an alternative to inclusive fitness and tested it to see whether it supported the claims the authors made in the *Nature* paper.

It didn't. "They had a modeling strategy that should work and should be fine, but they weren't careful enough when they made claims about their models' novel results," Queller said. But he also argued that the two mathematical models are essentially equivalent in that they ultimately predict the same results.

Inclusive fitness and social insects

Inclusive fitness was originally developed to explain eusociality, a extreme form of altruism found in social insects, where non-reproducing colony members give up their right to reproduce and devote their lives to caring for the offspring of a single reproducing member.

Hamilton's inclusive fitness theory was invented to solve this paradox, which vexed even Darwin. Hamilton calculated that sterile castes could evolve if altruistic sterility sufficiently benefited relatives also carrying the altruistic gene.

Kin selection and inclusive fitness quickly became the dominant mode of thinking about the evolution of eusocial insects and their success in this area led to their application to many other problems in social evolution.

But the Harvard authors asserted that while "empirical research on eusocial organisms has flourished, revealing rich details of caste, communication, colony life cycles, and other phenomena . . . almost none of this progress has been stimulated or advanced by inclusive fitness theory, which has evolved into an abstract enterprise largely on its own."

Queller saw nothing wrong with the mathematical models the Harvard authors proposed in *Nature* but was puzzled by some of the assertions they made. "I went through their paper trying to pull out conclusions that appeared to be different from the conclusions you get from inclusiveness theory," he said. "He settled on three claims, which he then tried to prove by running 'experiments' with the Harvard-style models."

Do shared genes drive the evolution of social behavior?

In inclusive fitness theory, relatedness is essential to the evolution of eusociality. But the Harvard authors claimed it is a consequence of eusociality rather than a cause. "Once eusociality has evolved, colonies consist of related individuals because daughters stay with their mothers to raise further offspring," they wrote.

"Although they said relatedness was not important, in their mathematical models they didn't actually vary relatedness," Queller said. "To test their claim we allowed some mixing between the offspring of different mothers before the offspring decided to stay with the colony to help her or to abandon her and leave," he said.

"When you 'lower' relatedness," he said, "it makes eusociality hard to evolve, and if you make it zero, you never get eusociality. So varying relatedness in their model takes us back to what we thought we already knew from inclusive fitness theory."

Are the queen and the workers in conflict?

"It follows from inclusive fitness theory is that unless all members of a colony are genetically identical, there will be a region of the benefit/cost space where the queen and workers are in conflict," Queller said. What's good for the inclusive fitness of one may not be good for the inclusive fitness of the other."

But the Harvard authors wrote that "the queen and her workers are not engaged in a standard cooperative dilemma." The workers, they said, are "robots," built by the queen as part of her reproductive strategy rather than independent agents.

But, Queller said, they tested only "offspring control models" (models where the decision to stay with the colony or to leave was controlled by genes expressed by workers). To check for conflict Queller compared models with offspring agency to ones with maternal agency (where the decision to stay to help is controlled by genes expressed by the queen).

As predicted by inclusive fitness theory, he said, the two cases evolve quite differently, and mothers benefit from stay-at-home offspring under conditions where offspring would be better off leaving.

"So as inclusive fitness theory predicts, you get regions of conflict where the queen would like her workers to stay but the workers want to leave. The mathematics says they're not robots," Queller said.

How hard is it to evolve eusociality?

Finally, the Harvard authors wrote, their model showed that it was very difficult for a solitary species to evolve to become eusocial despite the intuitive advantages of cooperation among members of a group.

This claim is less fundamental than the two others, Queller said, and it is true that eusociality has evolved only 10 or 20 times in the course of evolution.

"But we also showed that this result hinged on heavily biased assumptions," Quellers said. "We showed that modifying either the fitness function in their model or the worker decision rule made it easier to achieve eusociality. "

"So the essence of my paper," Queller said, "is that there really isn't much disagreement. The things we thought were important from inclusive fitness theory show up as important in their models as well."

Fully aware of the irony of a fight over selflessness, he hopes that his assertion that the dueling models are essentially equivalent will help resolve the debate.

Provided by Washington University in St. Louis

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