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## From the Writer

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E.O. Wilson, often dubbed “the father of sociobiology,” co-authored a controversial article entitled “The Evolution of Eusociality,” which appeared in the popular scientific journal, *Nature*, in 2010. Waves of criticism followed its publication, including a review co-signed by 103 scientists, which criticized the article for condemning inclusive fitness theory and for failing to offer a suitable alternative. While Nowak et al. expose the limitations of inclusive fitness theory, they fail to provide an alternative mathematical model to describe altruistic evolution. Such mathematical models exist, most notably described by Nowak in *SuperCooperators*, but Nowak et al.’s failure to reference such models severely undermines the merit of their proposal.

— Julie Hammond

## EUSOCIALITY: A QUESTION OF MATHEMATICS OR BAD SCIENCE?

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In 2010, an article appeared in the popular scientific journal, *Nature*, which stirred up a stew of controversy within the scientific community. The article, “The Evolution of Eusociality”, written by Martin A. Nowak, Corina E. Tarnita, and Edward O. Wilson, questioned the usefulness of the theory of inclusive fitness. Inclusive fitness had been well accepted within the scientific community since its introduction in 1963, and many evolutionary biologists were reluctant to relinquish the cherished theory. Many scientists wrote to *Nature* in response to the article’s publication defending inclusive fitness theory and condemning Nowak et al. The most notable response, co-signed by 103 scientists, revealed that this indignation was widespread within the biology community. Despite this overwhelming consensus, much of the critics’ argumentation is flawed by their failure to acknowledge the counterexamples which inclusive fitness theory fails to explain. Due to its severe limitations, Nowak et al. are correct to renounce inclusive fitness theory, although their failure to provide an alternative mathematical framework weakens their analysis of eusocial evolution.

In plain terms, inclusive fitness and its counterpart, kin selection theory, refer to the theory that organisms “have evolved to favor others who are genetically related to them” (Baumeister). That is to say, that altruistic behavior arises from an evolutionary benefit from helping someone who shares a similar gene structure. The mathematical formula of this rule is called Hamilton’s Rule, which states that altruistic genes increase when

$$rB > C$$

where  $r$  is the genetic relatedness between the recipient and the actor of the altruistic act,  $B$  is the reproductive benefit gained by the recipient, and  $C$  is the reproductive cost to the actor (Molles 185).

This theory helped to explain many unanswered questions in the animal kingdom. For example, why would a bee sting a predator and die in the process to protect the hive if its own ability to reproduce was diminished by its suicide? This question can be explained by the “haplodiploid hypothesis” (Nowak et al. 1) which states that this altruistic behavior is due to the haplodiploidy of the bees. In haplodiploid organisms, unfertilized eggs develop into male bees, which makes their genetic relatedness to their siblings greater than their genetic relatedness to their mothers. Thus, due to the high coefficient of relatedness ( $r$ ), it becomes evolutionarily advantageous for the organism to sting the predator (thereby decreasing its ability to reproduce, aka “reproductive cost  $C$ ”) because it protects the hive (which thereby increases its ability to reproduce, aka “reproductive benefit  $B$ ”) (Gadagkar 159–180). Inclusive fitness’s ability to explain this otherwise unexplainable behavior gave rise to its acceptance within evolutionary biology.

While inclusive fitness explains altruistic behavior in haploid organisms such as bees and ants, it fails to explain the altruistic behavior of diploid organisms (those who reproduce similarly to humans, where both males and females have duplicate chromosomes which are a mixture of maternal and parental genes). In diploid organisms, the reproductive cost outweighs the benefits according to Hamilton’s Rule because the coefficient of relatedness is so low, and, following Hamilton’s Rule, the organism would not evolve to be altruistic. However, altruistic behavior is still seen in many diploid organisms, such as termites. Termites explode when threatened by a predator, a behavior similar to that of the bee’s stinger mechanism (Cormier). But, because the relatedness coefficient of the termite is too small to promote the altruistic gene, Hamilton’s Rule does not accurately depict the evolutionary history of termites. Following this logic, Nowak et al. are correct in claiming that inclusive fitness is severely limited, as it does not explain altruistic behavior across all species.

Despite this glaring fault of inclusive fitness theory, a number of scientists spoke up in its defense in response to Nowak et al.’s paper. The most notable response was co-signed by 103 scientists . . . a remarkably

large number of critics (Abbot et al.). They argued that Nowak et al. were wrong to suggest a sharp distinction between inclusive fitness theory and natural selection. “Natural selection explains the appearance of design in the living world, and inclusive fitness theory explains what this design is for” (Abbot et al.). This definition—for which the authors failed to supply a source—is extremely weak because it is vague: many theories exist to explain the appearance of design in the living world, intelligent design for example. Usually, “standard natural selection” refers to the theory proposed by Charles Darwin in his book, *On the Origin of Species*. Darwin, anticipating the use of altruistic behavior as a counterargument to his theory, included a section in his book addressing this issue and offered that an entire group of organisms may be thought of as the evolving specimen (157–159). This sounds exactly like what Nowak et al. propose, where a population of organisms may be viewed as a whole in terms of their evolution. So, if we are to assume “standard natural selection” to be that which was proposed by Charles Darwin, then his theories in fact support Nowak et al. and weaken the argument of Abbott et al.

Despite this fault, some of their arguments are valid. They write, “[Nowak et al. are] incorrect to say that inclusive fitness requires a number of ‘stringent assumptions’ such as pairwise interactions, weak selection, linearity, additivity, and special population structures” (Abbot et al.). They cite several sources which correspond with recent scientific studies that have endeavored to make a more general form of Hamilton’s rule. While they are right to correct Nowak et al., this “general form” is still not general enough to explain the behavior of the termites. This is because while the “general form” no longer requires pairwise interactions or weak selection, it still cannot account for when genetic relatedness is low. Thus, it still cannot explain altruistic behavior in termites and other diploid organisms. They are so focused on clinging to inclusive fitness that they fail to acknowledge its limitations of predicting the proliferation of altruistic genes in *all* organisms.

Another of their arguments is flawed in its philosophy. They claim that “inclusive fitness has facilitated, not hindered, empirical testing of evolutionary theory” (Abbot et al.). On the surface, this seems perfectly fine, because “testing” sounds very scientific . . . But, by definition, a theory cannot be tested. If it can be tested, it is a law (Helmenstine). Both inclu-

sive fitness and natural selection are only theories. Abbot et al.'s claim that inclusive fitness has facilitated empirical testing of evolutionary theory is therefore invalid. By "testing of evolutionary theory," one may hypothesize their meaning to have been that experiments have shown results which fit with the predictions of inclusive fitness theory. While this coincidence may lend support, *it does not prove the theory*. This concept can be difficult to grasp, so a parallel situation may be considered for the reader's benefit. Just as advocates of inclusive fitness argue that events such as bacteria becoming resistant to antibiotics are evidence of evolution, advocates of theism claim that events such as a person suddenly being healed are evidence of God. While this occurrence may lend support, this does not *prove* the existence of God. Similarly, experiments can lend support for, but cannot *prove* evolutionary theory, nor can they prove inclusive fitness theory.

While a theory cannot be proved, it can be *disproved*. If observations in the physical world do not match that which is predicted, then the theory is no longer credible (Helmenstine). Again, any diploid organism that displays altruistic behavior (such as the termite) provides a strong counterexample to inclusive fitness theory, thereby disproving it. While genetic relatedness may be a factor in the proliferation of altruistic behavior, inclusive fitness theory as it exists today is disproved. Following this logic, Nowak et al. are correct in denouncing inclusive fitness theory.

Another article critiquing "The Evolution of Eusociality" claims that Nowak et al. are committing a fallacy by claiming that "family structure can be replaced by any form of population structure . . . given the lack of empirical evidence." The source given here is E.O. Wilson's book *The Insect Societies*. It is unclear to what empirical evidence they are referring, but since Wilson wrote the book listed as their source, it would be reasonable to assume that Wilson has the authority on this topic. Wilson is one of the authors of "The Evolution of Eusociality," so it would follow that he would be aware of any lack of empirical evidence supporting family structure being replaced by population structure when he wrote the controversial article. The question becomes: is there a lack of empirical evidence on this topic, and does a lack of evidence disprove a theory? Usually, a lack of evidence is not enough to disprove a theory; a counterexample is needed. So, this argument becomes irrelevant because the "lack of empirical evi-

dence” is too vague to adequately convey its significance, and, even if there were no evidence, the theory would still be considered valid.

E. O. Wilson, often dubbed as “the father of sociobiology,” has written extensively on a variety of topics, ranging from entomology to environmentalism (“E.O. Wilson Biography”). In *Letters to a Young Scientist*, Wilson laments that excessive mathematics deter many young adults from pursuing scientific careers, and calls for more qualitative descriptions in scientific journals. Convinced that less mathematics would reach a wider audience, it is possible that Wilson persuaded Nowak et al. to forego a mathematical description in favor of a qualitative description. Another possible explanation concerning Nowak et al.’s lack of mathematics is that such a mathematical description would necessitate a paper much longer than that of a standard scientific article. Regardless of the reason, the absence of a mathematical model weakens Nowak et al.’s argument, as their criticism of Hamilton’s Rule is incomplete without offering a quantitative alternative. It is unfortunate that Nowak et al. fail to include this quantitative analysis, as Martin Nowak has clearly derived these concepts in *SuperCooperators: Altruism, Evolution, and Why We Need Each Other to Succeed*, where he describes the evolution of altruism using game theory. While calculus and statistics are standards in the biology curriculum, advanced mathematical topics like game theory are often overlooked (Dionne). As a result, it is possible many of Nowak et al.’s critics had insufficient background knowledge to properly evaluate the article. It is unfortunate that Nowak et al. do not reference *SuperCooperators* in their article, as much controversy could have been avoided had such a reference been provided.

Indeed, a lack of sufficient background knowledge seems to be at the root of the controversy. In the article co-signed by 103 scientists, the last paragraph may be a reflection of the critics’ inability to translate Nowak et al.’s qualitative proposal to a quantitative model: “Ultimately, any body of biological theory must be judged on its ability to make novel predictions and explain biological phenomena; we believe that Nowak et al. do neither” (Abbot et al.). This is unnecessarily pessimistic, as cost and benefit calculations associated with game theory have been extremely successful in explaining many situations, and are often employed by actuaries as well as anyone attempting risk analysis. Indeed, these cost and

benefit calculations are not so different from the assumptions of the critics' beloved inclusive fitness theory, where  $C$  is the cost and  $B$  is the benefit in Hamilton's Rule. The difference between inclusive fitness theory and game theory is that, in game theory, the entire population is taken as a system, whereas inclusive fitness theory studies only an individual organism. But, when evolution involves many organisms interacting and mating with one another, why should the population not be taken as a system? It is true that there are often too many organisms within a population to perform such a calculation by hand. So, had the use of game theory been proposed in the 1960's when Hamilton proposed inclusive fitness theory, game theory may have been less useful because there would have been too many variables to perform such a calculation. But, this is no longer the case, as computers today are capable of such calculations. Consequently, the argument that Nowak et al.'s proposition is unable to make novel predictions regarding biological phenomena is invalid.

Matt Zimmerman, an evolutionary biologist at U.C. Davis, argues that the controversy stems not only from a mathematical misunderstanding, but also from differing definitions of Hamilton's Rule. Nowak et al. focus on the limitations and counterexamples of Hamilton's Rule, generalizing Hamilton's Rule to be the mathematical description of inclusive fitness theory (Zimmerman). The critics, on the other hand, generalize inclusive fitness theory to be more than Hamilton's Rule, and take inclusive fitness theory to be the concept that altruistic genes are more likely to be evolved if the coefficient of genetic relatedness is high. Zimmerman proposes that the critics fail to recognize that Nowak et al. are *not* proposing that relatedness never has anything to do with altruism, but rather that this theory only works in a limited number of cases, and a more general theory should exist to explain more forms of behavior. Zimmerman offers that this sharp divide in opinion is not a reflection of either party's scientific prowess, but rather is due to a difference in definitions.

In summary, Nowak et al. are correct in their claims regarding the limitations of Hamilton's Rule and inclusive fitness theory, but are so vague in their promotion of game theory that it is unsurprising that their article met such a negative response. With further mathematical explanations of their proposal, namely Nowak's *SuperCooperators*, their proposal of the use of game theory with regard to evolutionary biology should

stimulate further research into evolutionary processes, especially with the use of computer simulations. Criticism of “The Evolution of Eusociality” is largely philosophical in nature, and much of the critics’ argumentation is flawed. Today, few articles are being published today which continue to renounce their ideas. Just as *On the Origin of Species* was initially extremely controversial but became the cornerstone of modern evolutionary biology, so too will “The Evolution of Eusociality” eventually come to be accepted by the scientific community.

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