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Nowak-style models refute Nowak's conclusions about eusociality

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In 2010, Nowak, Tarnita, and Wilson challenged the utility of the inclusive fitness approach, using the evolution of eusociality as a test case. The paper has drawn many responses defending inclusive fitness, but little response on the alternative method for modeling the evolution of eusociality, which the authors claimed to be superior. They used their model to support three claims that differ from standard inclusive fitness results. First, they argued that relatedness was unimportant in the evolution of eusociality. Second, they argued that eusociality is much more difficult to evolve than inclusive fitness theory seems to predict. Third, though inclusive fitness theory predicts conflict between queen and workers, they argued that the queen and her colony were selected as a whole and the distinction between queen and worker genes was not important. Here we investigate these three claims, using exactly the kinds of models advocated by Nowak et al. but guided by inclusive fitness thinking. All three of their claims turn out to be flawed. First, we show that relatedness is essential by showing that eusociality does not evolve in a model with zero relatedness. Second, we show that eusociality is much easier to evolve if we employ more reasonable fitness functions and decision rules. Finally, models with eusociality genes expressed in queens give different results than models with eusociality genes expressed in workers, generating worker-queen conflict, as previously shown by inclusive fitness models. In each case, Nowak et al. overgeneralized from specific assumptions or parameter values. More thorough use of their own preferred modeling strategy does not support these generalizations but instead supports the conventional inclusive fitness results. While their methods can be good for modeling complexity, they can also make it easy to miss the important generalities that inclusive fitness makes so clear.