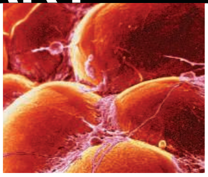

LETTERS

edited by Etta Kavanagh

Debating Sexual Selection and Mating Strategies

J. ROUGHGARDEN *ET AL*. (REVIEWS, 17 FEB., P. 965) CLAIM THAT COOPERATIVE GAME THEORY IS an ideal replacement for sexual selection theory. However, their description of cooperative and noncooperative games is misleading. Roughgarden *et al*. state that "in competitive [noncooperative] games, the players do not communicate" (text in brackets added) and that "in cooperative games, players make threats, promises, and side payments to each other; play together as teams; and form and dissolve coalitions." This contrasts with the textbook definitions: "A game is cooperative if commitments—agreements, promises, threats—are fully binding and enforcing. It is non-cooperative if commitments are not enforceable (note that pre-play communication between players does not imply that any agreements that may have been reached are enforceable)" (*1*). Thus, contrary to Roughgarden *et al*., the distinction between cooperative and noncooperative games lies in the assumption of a priori, binding "contracts" between players, and communication between individuals does not necessitate a cooperative game. In fact, signaling theory, a branch of evolutionary game theory [which is fundamentally noncooperative (*2*)], is devoted to animal communication (*3*). Furthermore, sexually interacting individuals are unlikely to be bound to any contracts they form without enforcement that is external to the interaction, which is unlikely for the vast majority of sexual (or indeed any biological) interactions; if commitments are not implicitly enforceable, then games are by definition noncooperative. Roughgarden *et al*. are correct that actions chosen while individuals interact need not be in Nash competitive equilibrium, but this does not mean we need to abandon the Nash competitive equilibrium concept, just apply it at a different level (*4*). When interactions are possible, it is the negotiation rules that are inherited and subject to selection, rather than the unconditional choice of action. There is no logical reason to apply cooperative game theory to interactions, just the old-fashioned Nash competitive equilibrium concept at the correct level (*5*).

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References and Notes

1. R. J. Aumann, S. Hart, *Handbook of Game Theory with Economic Applications* (Elsevier Science Publishers, Amsterdam, North Holland, 1992), vol. 1.
2. P. Hammerstein, in *Game Theory and Animal Behavior*, L. A. Dugatkin, H. K. Reeve, Eds. (Oxford Univ. Press, New York, 1998), pp. 3–15.
3. J. Maynard Smith, D. Harper, *Animal Signals* (Oxford Univ. Press, Oxford, 2003).
4. At evolutionary stability, negotiation rules are the best responses to each other, but this does not mean that the actions that result from using such a pair of negotiation rules are the best responses to each other. Roughgarden *et al*. are correct to emphasize that the process by which actions are chosen is important to the outcome (choice of action), but this point has been made before (*6*, *7*). Furthermore, under some modeling assumptions, the outcomes are more cooperative than with no interaction, while with other assumptions they are less cooperative (*7*–*9*).
5. For a detailed discussion of the points raised in this letter, see www.sciencemag.org/cgi/eletters/311/5763/965.
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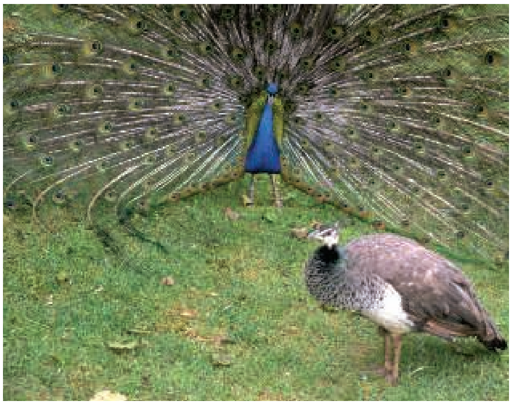

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IN THEIR REVIEW "REPRODUCTIVE SOCIAL behavior: cooperative games to replace sexual selection" (17 Feb., p. 965), J. Roughgarden *et al*. propose what superficially appears to be a radically novel explanation for reproductive social behavior. They argue (i) that sexual selection, which has been a cornerstone of the evolutionary explanation of sexual behavior since Darwin (*1*), "is always mistaken" and "needs to be replaced," and (ii) that "social selection," "expressed mathematically in a branch of game theory," is the necessary alternative. We believe that their Review is profoundly misleading. In particular, we argue that "social selection" does not represent a novel view of reproductive behavior and that, far from being an alternative to sexual selection, their models are themselves models of sexual selection.

The use of game theory models to study reproductive behavior, including the kinds of situations considered by Roughgarden *et al*., is not new in evolutionary biology. Even threats and side payments, which they specifically highlight, have been included in models for more than 10 years, and it has been recognized for still longer that a lack of alternative reproductive opportunities—which they implicitly assume—selects for cooperation between reproductive partners. They present their models as functioning "in developmental time," but the only rationale for expecting behavioral strategies to maximize payoffs within a generation is that they have been built in by selection over many generations: The correct currency to use for the payoffs in their models must therefore be fitness, as in existing game theory models.

If payoffs are in units of fitness, then the variation in payoffs in Roughgarden *et al*.'s models is by definition selection. Since sexual selection is, also by definition, due to variation in the number or phenotype of mates, the selection in the models, which arises during interactions in which mates use

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