

Fat and health

698



Dunes on Saturn's moon

702



Bring on the pain

704



LETTERS | BOOKS | POLICY FORUM | EDUCATION FORUM | PERSPECTIVES

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).

SASHA R. X. DALL,^{1*} JOHN M. MCNAMARA,² NINA WEDELL,¹ DAVID J. HOSKEN¹

¹Centre for Ecology and Conservation, University of Exeter, Cornwall Campus, Tremough, Penryn TR10 9EZ, UK. ²School of Mathematics, University of Bristol, University Walk, Clifton, Bristol B58 1TW, UK.

*To whom correspondence should be addressed. E-mail: sashadall@iname.com

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.
6. J. M. McNamara, C. E. Gasson, A. I. Houston, *Nature* **401**, 368 (1999).
7. J. M. McNamara, A. I. Houston, T. Szekely, J. N. Webb, *Animal Behav.* **64**, 147 (2002).
8. T. Killingback, M. Doebeli, *Am. Naturalist* **160**, 421 (2002).
9. T. N. Sherratt, G. Roberts, *J. Theoret. Biol.* **215**, 47 (2002).

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

different strategies, is sexual selection. We conclude that Roughgarden *et al.*'s models, rather than being alternatives to sexual selection, are in fact themselves models of sexual selection (2).

C. (KATE) M. LESSELLS,^{1*} ANDREW T. D. BENNETT,² TIM R. BIRKHEAD,³ NICK COLEGRAVE,⁴ SASHA R. X. DALL,⁵ PAUL H. HARVEY,⁶ BEN HATCHWELL,³ DAVE J. HOSKEN,⁵ JOHN HUNT,⁵ ALLEN J. MOORE,⁵ GEOFF A. PARKER,⁷ SCOTT PITNICK,⁸ TOMMASO PIZZARI,⁶ JACEK RADWAN,⁹ MIKE RITCHIE,¹⁰ BEN C. SHELDON,⁶ DAVID M. SHUKER,⁴ LEIGH W. SIMMONS,¹¹ PAULA STOCKLEY,¹² TOM TREGENZA,⁵ MARLENE ZUK¹³

¹NIOO-KNAW, Post Office Box 40, 6666 ZG Heteren, The Netherlands. ²University of Bristol, Bristol BS8 1UG, UK. ³Department of Animal and Plant Sciences, University of Sheffield, Sheffield S10 2TN, UK. ⁴IEB, School of Biological Sciences, University of Edinburgh, Edinburgh EH9 3JT, UK. ⁵Centre for Ecology and Conservation, School of Biosciences, University of Exeter, Cornwall Campus, Tremough, Penryn TR10 9EZ, UK. ⁶Department of Zoology, University of Oxford, Oxford OX1 3PS, UK. ⁷School of Biological Sciences, Biosciences Building, Crown Street, University of Liverpool, Liverpool L69 7ZB, UK. ⁸Department of Biology, University of Syracuse, 108 College Place, Syracuse, NY 13244, USA. ⁹Institute of Environmental Sciences, Jagiellonian University, ul. Gronostajowa 3, 30-387 Krakow, Poland. ¹⁰Department of Environmental and Evolutionary Biology, Dyers Brae House, University of St. Andrews, St. Andrews, Fife KY16 9TH, UK. ¹¹School of Animal Biology (M092), University of Western Australia, Crawley, WA 6009, Australia. ¹²Faculty of Veterinary Science, University of Liverpool, Chester High Road, Neston, South Wirral CH64 7TE, UK. ¹³Department of Biology, University of California, Riverside, Riverside, CA 92521, USA.

*To whom correspondence should be addressed. E-mail: k.lesSELLS@nioo.knaw.nl

References and Notes

1. C. R. Darwin, *The Descent of Man and Selection in Relation to Sex* (Murray, London, 1871).
2. For a detailed discussion of the points raised in this letter, see www.sciencemag.org/cgi/eletters/311/5763/965.

ANY TRAIT CONFERRING A COMPETITIVE ADVANTAGE for access to copulation partners or in fertilization is, by definition, under sexual selection. Since Darwin's (*I*) original proposal of sexual selection, a unitary theoretical framework has been developed that successfully explains much of the bewildering variation in sex differences, reproductive strategies, and mating systems among taxa. Sexual selection is now widely recognized as one of the most powerful agents of evolutionary change, a vital component of modern evolutionary theory and among the most intellectually dynamic areas in evolutionary biology over the past three decades.

J. Roughgarden *et al.* ("Reproductive social behavior: cooperative games to replace sexual selection," Review, 17 Feb., p. 965) propose that sexual selection theory "needs to be replaced" because it "is always mistaken" and suggest an approach based on social selection

that appears to be a drastic paradigm shift. However, their Review is based on unsupported opinion, misconceptions, failure to acknowledge contrary evidence, and attempts to claim novelty and a new perspective where none in fact exists.

The problems in the Review are numerous and profound. For example, all 17 points in the Supporting Online Material contain major



Eurasian oystercatcher, a sexually monomorphic wading bird.

errors of omission and interpretation. Roughgarden *et al.* fail to provide either a scholarly review of sexual selection research or a genuine alternative to sexual selection theory. In particular, unlike models of sexual selection, those proposed by Roughgarden *et al.* cannot apply to most sexually reproducing organisms and crucially are not at all novel, being instead entirely consistent with current sexual selection theory.

As with every rapidly developing field, the study of sexual selection generates debate. None of the currently unresolved issues, however, has implications that would call into question the theory of sexual selection itself. Indeed, the theoretical framework of sexual selection has proven extremely robust. It remains the best functional explanation for the evolution of the sex differences that initially puzzled Darwin and for a tremendous variety of other remarkable characters discovered as a consequence of intense research in this field during the last decades (2).

TOMMASO PIZZARI,^{1*} TIM R. BIRKHEAD,² MARK W. BLOWS,³ ROB BROOKS,⁴ KATHERINE L. BUCHANAN,⁵ TIM H. CLUTTON-BROCK,⁶ PAUL H. HARVEY,¹ DAVE J. HOSKEN,⁷ MICHAEL D. JENNIONS,⁸ HANNA KOKKO,⁹ JANNE S. KOTIAHO,¹⁰ C. (KATE) M. LESSELLS,¹¹ CONSTANTINO MACIAS-GARCÍA,¹² ALLEN J. MOORE,⁷ GEOFF A. PARKER,¹³ LINDA PARTRIDGE,¹⁴ SCOTT PITNICK,¹⁵ JACEK RADWAN,¹⁶ MIKE RITCHIE,¹⁷ BEN C. SHELDON,¹ LEIGH W. SIMMONS,¹⁸ RHONDA R. SNOOK,² PAULA STOCKLEY,¹⁹ MARLENE ZUK²⁰

¹Edward Grey Institute, Department of Zoology, University of Oxford, Oxford OX1 3PS, UK. ²Department of Animal and Plant Sciences, University of Sheffield, Sheffield S10 2TN UK. ³School of Integrative Biology, University of Queensland, St. Lucia 4072, QLD, Australia. ⁴School of

Biological, Earth and Environmental Sciences, The University of New South Wales, Kensington, Sydney 2052, NSW, Australia. ⁵Cardiff School of Biosciences, Cardiff University, Main Building, Park Place, Cardiff CF10 3TL, UK. ⁶Department of Zoology, University of Cambridge, Downing Street, Cambridge CB2 3EJ, UK. ⁷Centre for Ecology and Conservation, University of Exeter in Cornwall, Tremough Campus, Penryn, TR10 9EZ, UK. ⁸School of Botany and Zoology, The Australian National University, Canberra, ACT 0200, Australia. ⁹Laboratory of Ecological and Evolutionary Dynamics, Department of Biological and Environmental Sciences, Post Office Box 65, University of Helsinki, 00014, Helsinki Finland. ¹⁰Department of Biological and Environmental Science, University of Jyväskylä, Post Office Box 35, 40014 Jyväskylä, Finland. ¹¹NIOO-KNAW, Centre for Terrestrial Ecology, Post Office Box 40, 6666 ZG Heteren, The Netherlands. ¹²Universidad Nacional Autónoma de México, Instituto de Ecología, Departamento de Ecología Evolutiva, AP 70-275, Mexico City, DF 07510, México. ¹³School of Biological Sciences, Biosciences Building, Crown Street, University of Liverpool, Liverpool L69 7ZB, UK. ¹⁴Department of Biology, University College London, Gower Street, London WC1E 6BT. ¹⁵Department of Biology, Syracuse University, 108 College Place, Syracuse, NY 13244, USA. ¹⁶Institute of Environmental Sciences, Jagiellonian University, ul. Gronostajowa 3, 30-387 Krakow, Poland.

¹⁷Department of Environmental and Evolutionary Biology, Dyers Brae House, University of St. Andrews, St. Andrews, Fife KY16 9TH, UK. ¹⁸Zoology Building, School of Animal Biology (M092), University of Western Australia, Nedlands, WA 6009, Australia. ¹⁹Faculty of Veterinary Science, University of Liverpool, Chester High Road, Neston, South Wirral, CH64 7TE, UK. ²⁰Department of Biology, University of California, Riverside, Riverside, CA 92521 USA.

*To whom correspondence should be addressed. E-mail: tommaso.pizzari@zoo.ox.ac.uk

References and Notes

1. C. R. Darwin, *The Descent of Man and Selection in Relation to Sex* (Appleton, New York, 1871).
2. For a more detailed discussion of the points raised in this letter, see www.sciencemag.org/cgi/eletters/311/5763/965.

IN THEIR REVIEW "REPRODUCTIVE SOCIAL behavior: cooperative games to replace sexual selection" (17 Feb., p. 965), J. Roughgarden *et al.* mischaracterize theory and research on human mating strategies. Although they provide one decontextualized quote from Buss (*I*), the characterization that men pursue a singular strategy of promiscuous mating while women pursue low-quantity monogamous mating is factually incorrect.

Evolutionary psychologists have long theorized and empirically verified that humans possess a menu of mating strategies: Both women and men pursue long-term committed mating, short-term mating, serial mating, polygynous mating, polyandrous mating, and mixed mating strategies (including extra-pair copulations) (*I*, 2). A particular individual's mating strategy is predictably contingent on sex ratio, mate value, influence from kin, and cultural norms (*I*–3).

Contrary to Roughgarden's statement that it is "axiomatic" in evolutionary psychology that only males pursue promiscuity, much

theoretical and empirical research documents the adaptive benefits to females of short-term mating (1). These include access to resources, advantageous mate switching, and possibly beneficial genes. Men typically benefit from long-term committed mating (e.g., increased offspring survival) and incur costs when pursuing promiscuous mating (e.g., violence from other men and decrement in mate value) (2).

These findings do not negate the importance of the differential parental investment in driving the intrasexual and intersexual components of sexual selection (4). Nor do they contravene well-documented sex differences in these components, which follow logically from parental investment theory (2, 3). It is precisely because both sexes invest so heavily parentally when pursuing long-term mating that evolutionary psychologists stress that both sexes fully engage in mutual mate choice and intrasexual competition for desirable mates. Reducing the well-documented diversity of human mating strategies to outmoded clichés about male promiscuity and female monogamy does a gross disservice to the current scientific understanding of human mating.

DAVID M. BUSS

Department of Psychology, University of Texas, Austin, TX 78712, USA.

References

1. D. M. Buss, *The Evolution of Desire* (Basic, New York, 1994/2003).
2. D. M. Buss, *Evolutionary Psychology* (Allyn & Bacon, Boston, 2004).
3. S. W. Gangestad *et al.*, *Proc. R. Soc. London B* **272**, 2023 (2005).
4. R. Trivers, in *Sexual Selection and the Descent of Man: 1871–1971* (Aldine, Chicago, 1972), pp. 136–179.

IN THEIR REVIEW (17 FEB., P. 965), J. ROUGHGARDEN *et al.* assert that the theory of sexual selection is a wholesale failure and advocate an approach based on cooperative game theory. They introduce a standard “tragedy of the commons” type game between two players and suggest that communication between players might promote the evolution of larger payoffs through cooperation. This negotiation was introduced into evolutionary game theory long ago (1), and similar types of behavioral flexibility have been incorporated into models of sexual conflict between parents (2). It is clear from these more rigorous analyses that neither communication through repeated interactions, nor selection for behavior that sometimes favors the common good, undermines the basic premises of sexual selection theory. On the contrary, the model developed by Roughgarden *et al.* for the dynamics of individual versus team play is a case in point. This is nothing more than a restatement of the

well-known idea that an individual’s evolutionary interests can sometimes conflict and sometimes coincide with those of its partner. (3). It is precisely this idea that underlies the widespread understanding that the form of a species’ mating system greatly influences the extent to which sexual conflict versus sexual cooperation predominates (4).

TROY DAY,¹

DAVID HOULE,² LOCKE ROWE³

¹Departments of Mathematics and Biology, Jeffery Hall, Queen’s University, Kingston, ON K7L 3N6, Canada.

²Department of Biological Science, Florida State University, Tallahassee, FL 32306–1100, USA. ³Department of Zoology, University of Toronto, Toronto, ON M5S 3G5, Canada.

References

1. R. Axelrod, W. D. Hamilton, *Science* **211**, 1390 (1981).
2. J. M. McNamara *et al.*, *Nature* **401**, 368 (1999).
3. L. Keller, *Levels of Selection in Evolution* (Princeton Univ. Press, Princeton, NJ, 1999).
4. G. A. Parker, in *Sexual Selection and Reproductive Competition in Insects*, M. S. Blum, N. A. Blum, Eds. (Academic Press, New York, 1979), pp. 123–166.

IN THEIR REVIEW “REPRODUCTIVE SOCIAL behavior: cooperative games to replace sexual selection” (17 Feb., p. 965), J. Roughgarden *et al.* make claims that have already been rebutted and debated (1–4). Darwin’s views have been misrepresented again. A quotation

asserts that Darwin attributed secondary sexual characters to “females choosing mates who are ‘vigorous and well-armed ... just as man can improve the breed of his game-cocks by the selection of those birds which are victorious in the cock-pit.’” The words before the ellipsis are taken from page 229 of the second edition of *The Descent of Man*, whereas those to the right are from page 226. The ones on the left are part of a discussion on a difficulty in the theory of female choice. Those on the right are concerned with male combat and do not refer to female choice.

It is generally accepted practice in all branches of learning that quotations will accurately reflect what the author has asserted. Readers of a scientific journal also expect authors to follow the rules of logic and common sense. Irrespective of whether the innovations proposed by Roughgarden *et al.* are meritorious or not, the conclusion that Darwin’s theory is wrong does not follow from the premises. That a theory may need to be supplemented does not mean that it has to be replaced. That there are cases to which a theory does not apply does not mean that it is false.

MICHAEL T. GHISELIN

Center for the History and Philosophy of Science, California Academy of Sciences, 875 Howard Street, San Francisco, CA 94103, USA. E-mail: mghiselin@calacademy.org

References

1. J. Roughgarden, *Calif. Wild* **58** (no. 3), 18 (2005).
2. M. T. Ghiselin, *Calif. Wild* **59** (no. 1), 13 (2006).
3. J. Roughgarden, *Calif. Wild* **59** (no. 2), in press.
4. M. T. Ghiselin, *Calif. Wild* **59** (no. 2), in press.

THE NASH BARGAINING GAME (1), FIRST APPLIED to intramarital negotiations more than 25 years ago, is the standard model for resource allocation within marriages (2, 3). It also forms the core of the model proposed by J. Roughgarden *et al.* (“Reproductive social behavior: cooperative games to replace sexual selection,” *Reviews*, 17 Feb., p. 965) as an alternative to sexual selection models.

Unlike virtually all of the game theoretical models used in biology (which are noncooperative games), the Nash bargaining game is a cooperative game-theory model. Cooperative and noncooperative games form two distinct branches of game theory, with fundamentally different assumptions. Roughgarden *et al.* assume players choose strategically which one to apply, but it is impossible to choose environmental constraints. If the circumstances meet the assumptions of cooperative game theory, then cooperative game theory is the only correct model; if the situation meets the assumptions of noncooperative game theory, then noncooperative game theory’s predictions will follow.

One critical assumption that differs between the two branches of game theory is that cooperative game theory requires that threats

always be enforced, even though “in general, to execute the threat will not be something [the player] would want to do, just of itself” (1). If we agree with Roughgarden *et al.* that “a sense of friendship resides in animal bonding, a joy or synergy in the spirit of cooperation that allows animals to sense and experience the product, not merely the sum, of their individual well-beings,” then we may also allow that the pair-bond relationship includes the vengeful hatred and spite required to fulfill the assumptions. Evolution does not provide an explanation for why such behavior should be expected, nor do Roughgarden *et al.* A sensible alternative to spite would be for players to revert to playing the evolutionarily stable strategy (ESS), which returns us completely to the realm of noncooperative game theory.

PETER L. HURD

Department of Psychology, University of Alberta, Edmonton, AB T6G 2E9, Canada.

References

1. J. F. Nash, *Econometrica* **21**, 128 (1953).
2. S. Lundberg, R. A. Pollak, *J. Econ. Perspect.* **10**, 139 (1996).
3. T. C. Bergstrom, *J. Econ. Lit.* **34**, 903 (1996).

IN THEIR REVIEW ARTICLE “REPRODUCTIVE SOCIAL BEHAVIOR: cooperative games to replace sexual selection” (17 Feb., p. 965), J. Roughgarden *et al.* propose replacing Darwinian sexual selection theory with a vague new model of cooperative “team-play dynamics.” Game theorists have developed dozens of “equilibrium refinement” theories and “replicator dynamic” models (1) that can solve the same problems as team-play dynamics without relying on Roughgarden’s mystical “joy or synergy in the spirit of cooperation.”

Roughgarden’s cooperation theory also cannot explain the dozens of recent papers documenting ovulatory cycle shifts in female human mate preferences (2). Resource benefits from sexual relationships are stable across the ovulatory cycle, but potential good-genes benefits from mating are only relevant in the high-fertility period a few days before ovulation. Thus, women have evolved to focus more during this high-fertility period on male good-genes indicators such as facial masculinity (3, 4), pheromones (5), behavioral dominance (6), and artistic creativity (7). These cycle shifts are stronger among women in long-term relationships with men who lack these characteristics (8). The Roughgarden *et al.* model cannot explain these good-genes preferences, because it focuses on the direct ecological benefits of efficient coordination in mating games.

GEOFFREY MILLER

Psychology Department, University of New Mexico, Albuquerque, NM 87131, USA. E-mail: gfmiller@unm.edu

References

1. K. Binmore, L. Samuelson, *Rev. Econ. Stud.* **66**, 363

- (1999).
2. S. W. Gangestad *et al.*, *Curr. Dir. Psych. Sci.* **14**, 312 (2005).
3. I. S. Penton-Voak *et al.*, *Nature* **399**, 741 (1999).
4. C. N. Macrae *et al.*, *Psych. Sci.* **13**, 532 (2002).
5. S. W. Gangestad *et al.*, *Proc. R. Soc. London Ser. B* **265**, 927 (1998).
6. S. W. Gangestad *et al.*, *Psych. Sci.* **15**, 203 (2004).
7. M. G. Haselton, G. F. Miller, *Hum. Nature* **17**, 50 (2006).
8. E. G. Pillsworth *et al.*, *J. Sex Res.*, **41**, 55 (2004).

IN 1977, *SCIENCE* PUBLISHED A LANDMARK paper bringing together ecology and sexual selection to explain the diversity of mating systems (1). This framework has survived largely intact, with only changes in emphasis arising through insights into the importance of conflicts of interest between mating partners, and the near ubiquity of multiple mating by females (2). In their Review “Reproductive social behavior: cooperative games to replace sexual selection” (17 Feb., p. 965), J. Roughgarden *et al.* dismiss this framework in its entirety by stating that sexual selection is fatally flawed.

Sexual selection arises from the differential reproductive success of individuals, regardless of gender, that results from competition for mates (3). The caricature of the sexes (aggressive or showy males, coy or choosy females) that Roughgarden *et al.* deride is merely that—a caricature. It is not a basis for dismissing sexual selection any more than a rubber sheet and a football are a basis for a detailed discussion of the action of gravity. The crucial point is that sexual reproduction requires two individuals to pool their resources to produce offspring. Any heritable variation that leads to some individuals being more successful at finding mates than others will drive evolution by sexual selection, as will the existence of genes that allow individuals to invest less than their partner in a given mating and to use these resources for future reproduction. Roughgarden *et al.* need to show that such variation rarely occurs if they are to refute sexual selection. The empirical data are against them, however (2–4).

The competition and conflict fundamental to sexual reproduction cannot be dismissed, even if it may pay individuals to cooperate in some circumstances. The existence of benefits to cooperation does not remove conflict, as is apparent from animal and human societies (5). Sexual selection happens, however fervently some people may wish that it did not.

DAVID M. SHUKER^{1*} AND TOM TREGENZA²

¹Institute of Evolutionary Biology, School of Biological Sciences, University of Edinburgh, West Mains Road, Edinburgh, EH9 3JT, UK. ²Centre for Ecology and Conservation, School of Biosciences, University of Exeter, Cornwall Campus, Penryn TR10 9EZ, UK.

*To whom correspondence should be addressed. E-mail: david.shuker@ed.ac.uk

References

1. S. T. Emlen, L. W. Oring, *Science* **197**, 215 (1977).
2. G. Arnqvist, L. Rowe, *Sexual Conflict* (Princeton Univ.

- Press, Princeton, NJ, 2005).
3. M. Andersson, *Sexual Selection* (Princeton Univ. Press, Princeton, NJ, 1994).
 4. S. M. Shuster, M. J. Wade, *Mating Systems and Strategies* (Princeton Univ. Press, Princeton, NJ, 2003).
 5. F. L. W. Ratnieks, K. R. Foster, T. Wenseleers, *Annu. Rev. Entomol.* **51**, 581 (2006).

IN THEIR REVIEW, "REPRODUCTIVE SOCIAL behavior: cooperative games to replace sexual selection" (17 Feb., p. 965), J. Roughgarden *et al.* propose the use of game theory to describe reproductive behavior. The logic is well-argued, but the theory depends on individuals making choices through the use of reasoning, and there is little evidence that animals use reasoning to make choices. In the scenarios that the authors describe, the benefits are to the species, not to the individual animal. In many cases, as they point out, breeding leads to a decreased fitness and survivability of the individual.

An alternate to the assumption that individuals make choices on the basis of reasoned judgments about what constitutes a benefit to the species is that they make choices as a result of pushes from internal chemical signals. For instance, a male leopard roaming his territory picks up a scent of a female in heat; this stimulates a number of biochemical pathways that result in an urge for him to find the female and

eventually mate with her. No reasoned thought at all is required.

Choices could also be made by females in this manner: for example, a chemical push evolved in female lions that causes them to prefer male lions with darker manes. Whether this push results in better genetics for lions is irrelevant. Once females mate and have a litter, another set of chemical signals takes over that pushes her to take care of her offspring rather than abandon them. In other species, there is no chemical push, so females abandon their offspring to survive on their own.

In summary, the game theory idea might be better argued with chemical pushes as "rewards" and lack of pushes as "penalties" in the authors' line of reasoning. Nevertheless, the use of game theory and the associated mathematics of reproductive behavior research could prove extremely useful in this field.

JEFFREY STEWART

Aeri Park Institute of Molecular Biology and its Applications,
3000 Kent Avenue, West Lafayette, IN 47906, USA.

Response

WE THANK THE MANY PEOPLE WHO HAVE RESPONDED to our Review. We offer specific replies before raising general themes.

We agree with Dall *et al.* that social behavior should be viewed in two tiers: one tier in

evolutionary time for which the "old-fashioned" evolutionary stable strategy (ESS) is appropriate, and the other in behavioral/developmental time. The strategies developed in behavioral time may represent an ESS too, provided the players play as individuals, or may represent a Nash bargaining solution (NBS) if players play as a team. We introduce the terminology of competitive game versus cooperative game following Axelrod (1), who refers to the "fundamental form" of the prisoner's dilemma as a game in which "the players can communicate with each other only through the sequence of their own behavior" (p. 12), and who discusses the tit-for-tat strategy as a way to obtain "cooperation without friendship or foresight" (chapter heading, p. 71). In contrast, the games we envision employ friendship as the mechanism for attaining coordinated team play and for discerning team welfare (2).

We agree with Lessells *et al.* that "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." We understand the evolutionary tier as producing the capabilities for developing social behavior through bargaining, threats, communication, and team play, and not directly producing the social behaviors themselves. The selection coefficients induced on

genetic variation for such developmental capabilities are computed from the generation-long integral of the fitness accumulation rates realized by the strategies that these capabilities produce. We do not “implicitly assume” that a “lack of alternative reproductive opportunities ... selects for cooperation between reproductive partners.” We hypothesize that cooperation is beneficial on its own merits to increase the number of offspring successfully reared, regardless of the availability of alternative mates. Our theory is not about selection resulting from “variation in the number or phenotype of mates” but is about variation in the number of offspring successfully reared and is not an extension of sexual selection theory (2).

In response to Pizzari *et al.*, we acknowledge that sexual selection theory has become “a unitary theoretical framework” and a “vital component of modern evolutionary theory.” We appreciate that workers in this subject feel that “none of the currently unresolved issues ... has implications that would call into question the theory of sexual selection itself.” We beg to differ (2).

Emphasizing human mating as a “menu” of strategies not limited to the male-promiscuity-female-monogamy template, as Buss does in his Letter, is helpful. Still, the Letter confirms the axiomatic status of sexual selection in evolutionary psychology because various items in

the mating-strategy menu are explained as circumstantial deviations from normal templates said to “follow logically from parental investment theory.”

We agree with Day *et al.* that “neither communication through repeated interactions, nor selection for behavior that sometimes favors the common good, undermines the basic premises of sexual selection theory.” Sexual selection theory is being challenged in its assumption that the male-female relationship begins with sexual conflict from which cooperation may be derived, whereas we hypothesize that the male-female relationship begins with shared investment that may devolve into conflict. Cooperative game theory implements this alternative to sexual selection theory—it does not by itself contradict sexual selection theory.

Ghiselin’s fastidious pagination obscures the clear Darwinian vision that female choice breeds males to be both well armed and ornamented, like a fighting cock (3). We quote the phrase, “vigorous and well-armed,” from p. 222 of the second edition of *The Descent of Man*, and the phrase referring to breeding game-cocks from p. 218. If one prefers a less succinct but equivalent quotation drawn completely from a single paragraph residing on a single page, consider instead: “the more vigorous females, which

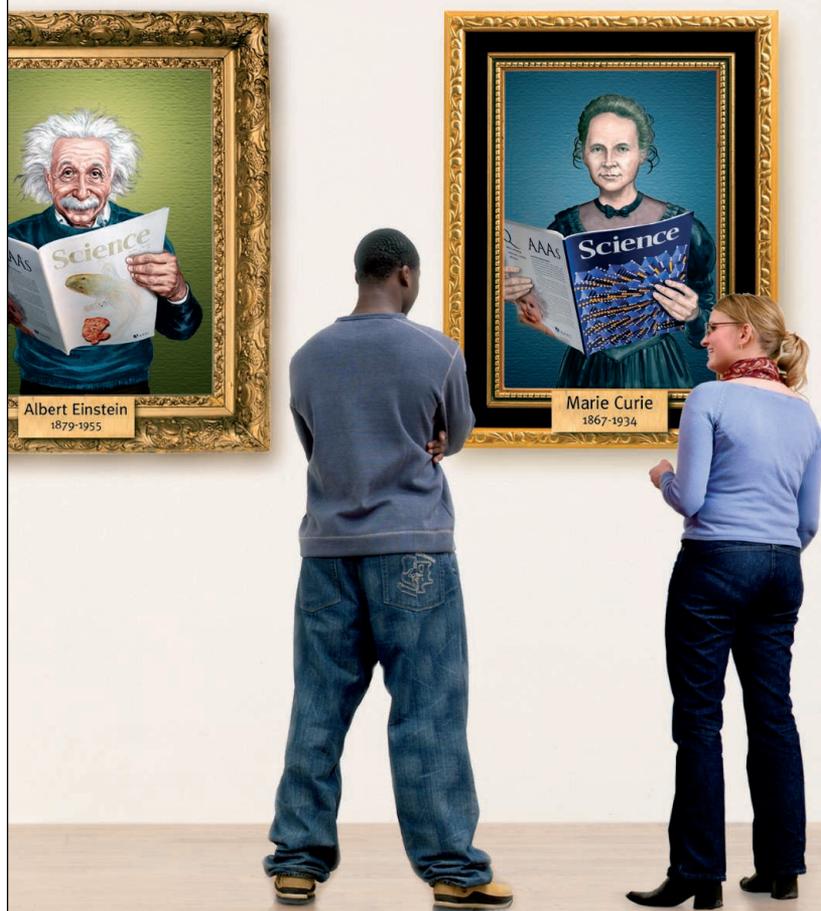
are the first to breed, will have the choice of many males ... this apparently has sufficed during a long course of generations to add not only to the strength and fighting powers of the males, but likewise to their various ornaments or other attractions.” (p. 222). Ghiselin’s rebuttal was itself rebutted (4).

We agree with Hurd “that the pair-bond relationship includes ... vengeful hatred and spite,” which offer one way for threats to be enforceable. To this list we would add the grief that attends the breakdown of a relationship. These capabilities, as well as those for communicating and for forming friendships, result from dynamics in the evolutionary tier. We agree too that reverting to competitive play leads to an ESS within the behavioral tier that might itself constitute a sufficient threat to motivate seeking the NBS without the need to further postulate hatred, spite, or grief.

In reference to Miller’s Letter, the joy of friendship is not “mystical” and can be confirmed with assays of pleasure-producing hormones or neurons if need be. Preference for the “male good-genes indicators” that women are said to have may instead indicate preference for direct benefits that men may provide. These preferences may be especially pronounced at times during the ovulatory cycle when the need for direct benefits is high because of the immi-

Career advice, insight and tools.

Turn to the experts for the big picture.
Visit www.ScienceCareers.org



Your career is too important to leave to chance. So to find the right job or get career advice, turn to the experts. At ScienceCareers.org we know science. And we are committed to helping take your career forward. Our knowledge is firmly founded on the expertise of *Science*, the premier scientific journal, and the long experience of AAAS in advancing science around the world. Put yourself in the picture with the experts in science. Visit www.ScienceCareers.org.

ALBERT EINSTEIN and related rights TM/_© of The Hebrew University of Jerusalem, used under license. Represented by The Roger Richman Agency, Inc., www.albert-einstein.net.

ScienceCareers.org

We know science



ment possibility of conceiving children. Good-gene explanations from evolutionary psychology remain unconvincing because (i) a stable polymorphism among good and bad genes cannot be maintained in the face of sustained directional selection from female choice against bad genes every generation, and (ii) large direct ecological benefits mask minuscule indirect genetic benefits.

Shuker and Tregenza write that “sexual selection... results from competition for mates.” Instead, our theory focuses on selection resulting from how to maximize number of young successfully reared, not from mate competition. We hypothesize that the social dynamics within reproductive groups normally revolve around this objective, not mate competition. Sexual selection theory states that “the existence of genes that allow individuals to invest less than their partner in a given mating” will evolve. Instead, we propose that mating partners are not playing to make the other do most of the work, but to do whatever is necessary to raise the largest number of young together. We disagree that sexual conflict is “fundamental to sexual reproduction.” Instead, we envision that mating begins with shared investment, and that conflict may appear secondarily if the partners cannot agree on a distribution of work and control. By our theory, cooperation is logically and causally prior to conflict, and by sexual selection theory, conflict is logically and causally prior to cooperation. Asserting that “sexual selection happens, however fervently some people may wish that it did not” assumes the conclusion before the alternative has been investigated.

We do not assume “the benefits are to the species, not to the individual animal,” as Stewart states. In our theory, the animals that work as a team accrue individual benefits. We agree that mechanisms of cooperation that yield cooperative outcomes without requiring the players to “use reasoning to make choices” need further research.

The spectacular acceptance of natural selection theory contrasts with sexual selection theory. When evolutionary change is attributed to natural selection, alternative hypotheses of genetic drift and/or recurrent mutation are tested as well, and for some molecular traits, these alternatives are preferred. In contrast, sexual selection theory has lacked alternatives. We suggest that if sexual selection theory is correct, its credibility will be enhanced once it is successfully tested against alternative hypotheses.

The alternative of social selection that we propose views heterosexual mating as similar to funding a joint investment. A new narrative to explain reproductive social behavior then unfolds focused on the control of this investment. For example, we do not take the promiscuous-male-monogamous-female template as a norm, but as a derived case (5). Male

promiscuity is likely when the initial control and feeding of young resides solely with the female, as in mammals. In this situation, to have a part in controlling or feeding the young, the male must also control and feed the female, or alternatively, he may cede control of his reproductive destiny in hopes of finding enough other mates to yield sufficient offspring who are successfully reared without his help. In birds, however, the monogamy percentage is reversed relative to mammals because male birds have a part in controlling, feeding, and protecting eggs in the shared nest from the moment the eggs are laid. Male promiscuity is thus a strategy of last resort—a response to exclusion from parental involvement, not a norm.

JOAN ROUGHGARDEN,¹
EROL AKÇAY,¹ MEEKO OISHI²

¹Department of Biological Sciences, Stanford University, Stanford, CA 94305–5020, USA. ²Sandia National Laboratory, Post Office Box 5800, Albuquerque, NM 87185–1137, USA.

References and Notes

1. R. Axelrod, *The Evolution of Cooperation* (Basic Books, New York, 1984).
2. Our reply to the expanded versions of the Letters by Dall *et al.*, Lessells *et al.*, and Pizzari *et al.* can be found at www.sciencemag.org/cgi/eletters/311/5763/965.
3. C. Darwin, *The Descent of Man* (Prometheus Books, New

York, ed. 2, 1874).

4. J. Roughgarden, *Calif. Wild* **59** (no. 2), 5 (2006).
5. J. Roughgarden, *Evolution's Rainbow* (University of California Press, Berkeley, CA, 2004), p. 57.

CORRECTIONS AND CLARIFICATIONS

News Focus: “Life in silico: a different kind of intelligent design” by K. Krieger (14 Apr., p. 189). The article should have noted that Anil Mallavarapu of the Virtual Cell Program at Harvard Medical School is the inventor and author of the “Little b” program and is leading the project.

Reports: “Toward automatic reconstruction of a highly resolved tree of life” by F. D. Ciccarelli *et al.* (3 Mar., p. 1283). The authors wish to acknowledge the valuable sources for some unpublished data that were accidentally omitted. Five of the 191 genomes used were preliminary. Sequence data of 52 genes from *Fibrobacter succinogenes* (U.S. Department of Agriculture-CSREES grant 2000-52100-9618), *Gemmata obscuriglobus* (Department of Energy grant DEFC0295ER61962), and *Acidobacterium capsulatum* (NSF grant MCB0237365) were obtained from The Institute of Genomic Research (TIGR) through its Web site, www.tigr.org. The sequencing was undertaken at TIGR with support from the respective sequencing consortia. *Giardia lamblia* data were taken from the Web site www.mbl.edu/Giardia [A. G. McArthur, *FEMS Microbiol. Lett.* **189**, 271 (2000)], and for *Solibacter usitatus*, open reading frames were extracted by homology searches against the NCBI GenBank database (this genome was sequenced by the Joint Genomics Institute and funded by the Department of Energy).

Reports: “The spatial extent of 20th-century warmth in the context of the past 1200 years” by T. J. Osborn and K. R.

Briffa (10 Feb., p. 841). Data used in the analysis are available at www.ncdc.noaa.gov/paleo/pubs/osborn2006/osborn2006.html. The URL for these data was not included in the paper because it was assigned only on the day of publication of the manuscript.

News Focus: “Development out of sync” by E. Pennisi (18 Nov. 2005, p. 1109). Christopher Rose’s affiliation was incorrect. He is at James Madison University.

Reports: “Gigantic photoresponse in 1/4-filled-band organic salt (EDO-TTF)₂PF₆” by M. Chollet *et al.* (7 Jan., 2005, p.86). There was an error in temperature reported in the inset of Fig. 3A. The correct temperature is 30 K. The corrected caption should be “(Inset) Raman spectrum in the low-energy region for the I phase observed at 30 K.” The sentence on p. 88, third column, second full paragraph, line 3 should read “The 84 cm⁻¹ band observed at 30 K (red) softened as the sample temperature was increased (Fig. 3B, inset, red circles).”

Letters to the Editor

Letters (~300 words) discuss material published in *Science* in the previous 6 months or issues of general interest. They can be submitted through the Web (www.submit2science.org) or by regular mail (1200 New York Ave., NW, Washington, DC 20005, USA). Letters are not acknowledged upon receipt, nor are authors generally consulted before publication. Whether published in full or in part, letters are subject to editing for clarity and space.