PNAS COMMENTARY

Feelings and flirtations foster long-term cooperation

Carl T. Bergstrom[a,1] and Graeme D. Ruxton[b]

Birds do it (1). Bees do it (2). Yes, fleas do it (3)—and we humans do it (4). We are talking, of course, about courtship. Given the time, energy, and resources that animals invest in courtship, biologists tend focus on the ways in which these activities serve to convey information (5–8). Observing both human romantic courtship and non-romantic processes of pairwise assessment and bonding, social scientists (9–12) often reach similar conclusions. Courtship offers an opportunity to observe and assess the characteristics of a potential partner. And it also provides a chance to demonstrate your own qualities to that partner. At the same time, courtship provides a chance to assess a suitor's intentions—are they in it for the long haul, or are they planning to hop the next train out of town? This matter of intentions is important because many courtship activities lead to the formation of extended cooperative partnerships. Such partnerships raise the obvious evolutionary question: How is cooperation maintained despite opportunity and incentive for one party to exploit their partner? The range of examples of such cooperation is vast, from biparental care, territory-holding alliances, and interspecific mutualisms to cooperation among coauthors, partnerships between firms, and pacts among nations. In this issue, Sadedin et al. offer a new look at how courtship might facilitate cooperation, and in doing so offer a tantalizing clue to the puzzle of cooperation (13).

Sadedin et al. propose that courtship may interact synergistically with another mechanism involved in establishing long-term cooperation, known as emotional bookkeeping (14). The idea behind emotional bookkeeping is that when individuals interact repeatedly, it is helpful to keep track of how one has been treated by specific individuals in the past. One way to do this might be to recall the entire detailed history of all your previous interactions. But doing so requires complex mental machinery. A cognitively less demanding approach would hold a sort of an emotional temperature toward another individual and to update this temperature with each interaction. That is, one party could simply keep a running total of how positively disposed they are to the other, nudging this tally upward after positive interactions and downward after negative ones. By sidestepping the need for complex memory, emotional bookkeeping lowers the cognitive cost of conditioning present behavior on past events, and should be feasible even for simple organisms. But where to set the temperature upon first meeting a new potential partner? Set it too low and one is too distrustful to be open to potentially fruitful cooperation, too high and one is vulnerable to exploitation. Sadedin et al. suggest that a courtship period offers a solution. Begin with a low-stakes courtship period in which you can entrain the emotional bookkeeping process appropriately, and only then move on to the high-stakes business of child-rearing or whatever cooperative dilemma is in play.

To develop this hypothesis, Sadedin et al. begin with the prisoners' dilemma scenario* that is nearly ubiquitous in modeling the evolutionary stability of cooperative behaviors. Because their focus is on long-term cooperative interactions, they look at an iterated version of the game in which two paired players play repeatedly with one another, and in which each individual knows what their partner did last time and can select their strategy in light of this. In this scenario, cooperation can readily occur. A strategy called tit-for-tat—cooperating in the first interaction and then mirroring the partner's previous move thereafter—is particularly effective in this setting. Because tit-for-tat players begin by cooperating, two that meet one another should cooperate as long as they stay together. As a result, tit-for-tat is resistant to invasion by most exploitative strategies (15) and so flourishes in model populations.

However, once a repeated prisoner's dilemma model is expanded to allow for mistakes in perception or action, all bets are off. If individuals sometimes misunderstand what their partner did last time or mistakenly take one action when they meant to take the other, cooperative strategies like tit-for-tat suffer, exploitative strategies can prosper, and cooperation collapses (16). Worse still, manipulative strategies that deceive their partners without detection can thrive in the uncertainty introduced by the possibility of mistakes and/or mis-remembering. If we want to explain long-term cooperation in noisy worlds, we need to somehow expand our model. This is where, according to Sadedin et al., courtship and emotional bookkeeping come in.

Courtship can take numerous forms and serve various purposes, but in this model, courtship provides an opportunity for two individuals to interact with negligible stakes when they first meet, before beginning a series of high-stakes prisoner's dilemma games. There may be some opportunity cost to entering into courtship interactions,

Author affiliations: [a]Department of Biology, University of Washington, Seattle, WA 98195; and [b]School of Biology, University of St. Andrews, St. Andrews KY16 9AJ, United Kingdom

Author contributions: C.T.B. and G.D.R. wrote the paper.

The authors declare no competing interest.

See companion article, "Emotions and courtship help bonded pairs cooperate, but emotional agents are vulnerable to deceit," 10.1073/pnas.2308911120.

[1]To whom correspondence may be addressed. Email: cbergst@uw.edu.

Published January 22, 2024.

*Recall the story. Two suspects are being sweated by the police in separate interrogation rooms. Each is offered the following deal: If you and your partner both say nothing, you will both go to jail for 1 y. But if you squeal on him and he keeps quiet, you can go free and he will serve 3 y. If you both squeal then you will both go to jail for 2 y. In this scenario, a prisoner serves a shorter sentence if he squeals, irrespective of what his partner does. So rationally both prisoners squeal and go to jail for 2 y. But if they had been able to coordinate and avoid the temptation for each to act in pure self-interest, both could have walked free in half the time.

but the outcome is of little direct payoff consequence. Courtship also offers an opportunity for partners to feel one another out without having to go through a costly separation process if matters do not work out. In Sadedin's model, players can break off interactions during courtship for free, but once paired, "divorce" is costly. Importantly, the outcomes of courtship interactions do influence emotional temperature. Each side can decide unilaterally to divorce, but movement from courtship to the main interactions needs the agreement of both parties.

In PNAS, Sadedin et al. offer a new look at how courtship might facilitate cooperation, and in doing so offer a tantalizing clue to the puzzle of cooperation.

What the authors found was that on their own, emotions can be a liability because they are vulnerable to exploitation by deceivers. When one can manipulate a partner's emotions and fool them into thinking that they are benefiting from cooperation when they are not, that partner is at a decided disadvantage. However, the combination of costly courtship and divorce makes such exploitation harder. Likely cheats will be unwilling to invest in costly courtship, because the potential for divorce limits the ability to exploit a partner through the main phase of the relationship. Should a selfish actor reveal their true colors, their partner would divorce them soon after. This advantage of courtship is strengthened by emotions, Sadedin et al. argue, because emotional bookkeeping allows individuals to more effectively screen out unreliable partners during the courtship process.

A challenge of doing theoretical work on combinations of complex behaviors such as courtship and emotional bookkeeping is that these systems can be refractory to analytical modeling. This leaves little alternative but to use simulation methods—an approach that can make it challenging to pinpoint the important interactions, let alone to assess the robustness or fragility of results. The authors have dealt with these challenges as best as possible. The model seems defensible in all its assumptions to us, and their crossed design gives a thorough picture of the model's robustness to parameter choices. But parameter choices are only one small part of a model's formulation. This is a complex model with elaborate encoding of phenotypes, and there are many components of the model for which equally defensible alternative formulations exist. We look forward to work that explores how robust this model's predictions are to such variations. For example, what happens when agents can explicitly condition their behavior on the phase of the interaction? Would it pay off to pose as a knight during courtship and reveal oneself as a knave when the stakes get higher? We also note that the model outcomes are often highly variable between replicates. This is not uncommon for stochastic agent-based models, but more painstaking explorations of the nature of this variation might uncover interesting predictions about the existence of alternate states and trajectories, for example.

Both the emotional bookkeeping and courtship aspects of this model should trigger further interesting investigation. To us, the existence of a generalized emotional scoring for the suitability of potential partners seems entirely plausible, and ripe for both empirical and theoretical exploration. In particular, in this model, positive emotions were driven only by direct experience of a specific partner in a single context—but we can imagine how it could also be triggered by observation of the individual interacting with others, and in a diversity of contexts, so this idea could link naturally to the existing work on the role of reputation in partner choice. Generalized positive or negative feelings toward potential partners could extend to other types of interaction, say with food types, and could stimulate renewed interest in the topic of the evolution of aesthetic sense in non-humans (17).

The rules for behavior during courtship are appropriately simple in this study, but there is clearly room for greater sophistication in the nature of the courtship (for example, with partners having control of the nature and investment in different stages of a courtship process) and in the strategies used (for example, in determining the timing of moving from the courtship phase to the main interaction stage). Also, these models generally assume that partnerships are formed randomly and that individuals can only enter into one partnership at a time. However social interactions in a diversity of taxa are more sophisticated than that and are increasingly well characterized in non-humans. Exploration of richer scenarios for initiating courtship with particular partners seems a fruitful source of further development.

Ethologists of the mid-twentieth century often focused on the cooperative aspects of courtship behavior, whereby sign stimuli would inhibit hostile or fearful reactions and facilitate coordination (18, 19). As behavioral ecology eclipsed classical ethology, these earlier views of courtship were largely replaced by a strategic framing that focused on information asymmetries, signaling, and mate assessment (20, 21). The analysis presented by Sadedin et al. moves us back toward these earlier views of courtship, and in doing so opens what we believe will be fruitful directions for further theoretical and empirical research.

1. D. Lack, Courtship feeding in birds. *Auk* **57**, 169–178 (1940).
2. M. Ayasse, Chemical ecology: Male orchid bees attract females with environmental-derived perfumes in courtship display. *Curr. Biol.* **33**, R405–R407 (2023).
3. E. Fitzgerald, *Let's Do It (Let's Fall in Love). Ella Fitzgerald Sings The Cole Porter Song Book*, Norman Grantz, producer (jazz record, Verve Records, New York, NY, 1956).
4. R. M. Cate, S. A. Lloyd, *Courtship* (SAGE Publications, 1992).
5. R. Dawkins, *The Selfish Gene* (Oxford University Press, 2016).
6. M. S. Sullivan, Mate choice as an information gathering process under time constraint: Implications for behaviour and signal design. *Anim. Behav.* **47**, 141–151 (1994).
7. C. A. Wachtmeister, M. Enquist, The evolution of female coyness-trading time for information. *Ethology* **105**, 983–992 (1999).
8. P. D. Sozou, R. M. Seymour, Costly but worthless gifts facilitate courtship. *Proc. R. Soc. B: Biol. Sci.* **272**, 1877–1884 (2005).
9. A. M. Spence, Time and communication in economic and social interaction. *Q. J. Econ.* **87**, 651–660 (1973).
10. L. A. Baxter, W. W. Wilmot, "Secret tests" social strategies for acquiring information about the state of the relationship. *Hum. Commun. Res.* **11**, 171–201 (1984).
11. C. Camerer, Gifts as economic signals and social symbols. *Am. J. Sociol.* **94**, S180–S214 (1988).
12. A. Farmer, A. W. Horowitz, The engagement game. *J. Popul. Econ.* **17**, 627–644 (2004).

13. D. G. E. A. Sadedin, J. Z. Susan, Leibo,, Emotions and courtship help bonded pairs cooperate, but emotional agents are vulnerable to deceit. *Proc. Natl. Acad. Sci. U.S.A.* **120**, e2308911120 (2023).
14. F. Aureli, C. M. Schaffner, Relationship assessment through emotional mediation. *Behaviour* **139**, 393–420 (2002).
15. R. Axelrod, W. D. Hamilton, The evolution of cooperation. *Science* **211**, 1390–1396 (1981).
16. R. Axelrod, R. Dawkins, *The Evolution of Cooperation, Revised Edition* (Basic Books, New York, NY, 2006).
17. R. O. Prum, *The Evolution of Beauty: How Darwin's Forgotten Theory of Mate Choice Shapes the Animal World–And Us* (Knopf Doubleday Publishing Group, 2017).
18. N. Tinbergen, *The Study of Instinct* (Pygmalion Press, an imprint of Plunkett Lake Press, 1951).
19. M. Bastock, *Courtship: An Ethological Study* (Routledge, 1967).
20. P. P. G. Bateson, *Mate Choice* (Cambridge University Press, 1983).
21. J. W. Bradbury *et al.*, *Principles of Animal Communication* (Sinauer Associates, Sunderland, MA, 1998), vol. 132.