"Why cooperation is not running away"

Review

In this paper, the authors present a model of the coevolution of cooperation and partner choice. They find that when partner choice is an unconditional trait (individuals accept a partner based only on their cooperation level), cooperation evolves to the point where its costs erode all of its benefits (analogous to the runaway process in sexual selection). At this point, cooperation and choosiness yield the same mean fitness as not cooperating at all. In contrast, when partner choice is a reaction norm, the evolved norm is (roughly) an increasing function of individual cooperativeness; i.e., more cooperative individuals are choosier and demand more cooperative partners. In this case, the level of cooperation does not escalate to erode all the benefits; rather, when partner switching is relatively cost free (a "fluid market"), the evolved level of cooperation is close to the Pareto optimal point where mean payoff is maximized. When partner switching has a higher opportunity cost, the level of cooperation is lower than the Pareto optimal value due to these costs.

I found the model and results quite interesting and thought provoking. I think its quite clear that behavioral feedbacks (assortment or reciprocity defined in a general way) can generate cooperation (even Pareto optimal levels), but a crucial point is in describing which mechanisms are more (or less) plausible and providing concise evolutionary accounts of how such mechanisms might evolve. This paper provides a very nice demonstration of how partner choice can be such a mechanism where the crucial part of the mechanism is a reaction norm. Also, I really liked the connection to runaway sexual selection and the idea that assortment might limit the runaway process. I suspect such a limitation could even make the runaway process a more plausible mechanism, particularly given the lack of evidence for good genes mechanisms.

My main critiques are relatively minor. First, I think that the emphasis in the Abstract, Introduction, and elsewhere in how the paper looks at the quantitative level of cooperation instead of just whether cooperation is possible (e.g., lines 61–63) is unnecessary; its true that some models have used discrete strategies (cooperate or not or "all-or-nothing") but others have used continuous ones and even the discrete strategy models can provide results on the precise level of cooperation evolved. Its also not clear, as claimed on lines 94–95, that other models lack diminishing returns of cooperation. However, the main point that these other models neither focus on the runaway process due to competitive altruism nor find a way to inhibit it without adding additional costs remains. Thus, I suggest that the authors simply point to this result as the main feature/point of the paper rather than that the paper looks at the quantitative level of cooperation (which of course it does, but this isn't the differentiating feature of the paper).

Second, the paper points to a few previous papers for inspiration, such as the ones by Debove et al (2015) and McNamara et al (2008). These papers essentially provide much of the framework for the current paper where the McNamara et al sets up the coevolution of cooperation and choosiness and the Debove et al papers look at cooperation in another game, the ultimatum game, using a similar partner choice mechanism. I think the authors could do more in the discussion to talk about the connection between these prior works and the current paper. In particular, they can highlight how the Debove et al. papers find similar results about Pareto optimality and market fluidity for the ultimatum game. Also I'm not sure the stuff about the McNamara et al paper starting on line 417 is exactly right; McNamara et al do show (or claim at least) that in the prisoner's dilemma game with linear costs the Pareto-optimal investment evolves. While they do use accelerating costs, its only in the snowdrift game. The authors provide data in the SI for why the McNamara et al model might not obtain Pareto-optimal investment, essentially mutation load is costly, but this is really

about how mutation load may be less efficient that phenotypic plasticity. Here, the authors could strength that analysis by looking at lower and higher values of σ_{mut}; they should be able to reduce the relative effect of the load and get closer to Pareto-optimal investment. More generally, its not entirely clear (to me at least) why McNamara et al get Pareto-optimal investment in the prisoner's dilemma at all with linear benefits and costs, which would seems to me to generate a runaway process even with linkage between cooperation and choosiness.

Finally, I'm a little unclear about a piece of the partner choice mechanism that is described in more detail in the SI of Debove et al (2015 Proc B). The ODE described there, above equation (1) in the SI, is purely linear in fraction of individuals in a pair and solitary. However, this doesn't seem to me to fit a mass-action kinetic where two solitary individuals must interact to become a pair and this should occur at rate proportional to S_i^2. I don't know how this changes the partner choice model and whether it changes results about the role of β/τ in controlling "market fluidity", but I suggest that the authors address this point.

Finally, I have a few specific comments below.

Specific Comments

- Line 121: I'm not sure I quite get how choosiness is best when β/τ is high. When its high, the pool of unpaired individuals is very small, so there are few individuals to choose from. In contrast, when β/τ is low, the pool of unpaired individuals is large and choosiness should yield better returns. Maybe the authors could address what's wrong with this intuition.
- Line 360: "analytically": more precisely, "numerically" since the solutions are not analytical.
- Line 398: "effective units of selection". Cite Akçay and Van Cleve (2012) here who discuss levels of selection and assortment explicitly.
- Line 485–486. The paper here presents a continuous prisoners dilemma. The relevant difference with the paper here is simply the mechanism of conditional behavior.
- Line 496: Akçay and Van Cleve (2012) actually do not show that relatedness is required for socially optimal cooperation levels in general; rather they find this for a specific preference function. Its really an open question worth exploring how the preference mechanism in that paper can or cannot generate socially optimal behavior.