LETTER

REPLY TO LEIMAR AND HAMMERSTEIN:

Limited gene flow leads to individuals being related within groups

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The aim of our paper (1) is to evaluate whether all impactful published models where altruism evolves (or can evolve under some range of model parameter values) are based on a life cycle with local reproduction and local interactions leading to interacting individuals being genetically related. In their response (2), Leimar and Hammerstein imply that we should not have included their 2001 paper (3) in our analysis because "the evolutionary stability of the standing strategy, which [they] investigated, does not depend on relatedness...." They are correct that the evolutionary stability of the standing strategy does not hinge on relatedness. However, some other results of their paper depend on relatedness, and this they do not acknowledge.

Leimar and Hammerstein's (3) paper investigates the evolution of conditional helping through indirect reciprocity strategies in an island model of population structure. Because interactions occur within islands, individuals will be related (i.e., $r > 0$), and kin selection will operate when dispersal is limited (see figure 1 of ref. 1). However, when the authors discuss the role of limited dispersal on the equilibrium frequency of evolving strategies (figure 2 b and c of ref. 3), they attribute the observed difference to drift: "with more gene flow between social groups, as in figure 2c, cooperative image-scoring strategies seem not to evolve at all. Thus, when the influence of genetic drift is reduced, cooperative image scoring becomes rare over the long term." This is incorrect. Relatedness covaries with gene flow (4), and it is relatedness, not genetic drift, which accounts for the observed differences in the simulations of figure 2 b and c in ref. 3. Genetic drift alone would produce the opposite result, with less cooperation in figure 2b than in figure 2c in ref. 3, since drift increases with gene flow in island models (equation 2.7 of ref. 4). This is why their paper was included in our analysis, in particular, in SI Appendix, table S4 of ref. 1.

We take this opportunity to mention that the original caption for SI Appendix, table S4 of ref. 1 is unfortunately ambiguous because it may be read as if altruism evolved under all conditions and variants of the models included in this table. However, in some of the models (e.g., ref. 3), the evolving phenotype can be either altruistic or cooperative depending on specific parameter settings (as acknowledged in our main text, ref. 1, pp. 28895–28896). Thus, the caption for SI Appendix, table S4 of ref. 1 should read "Impactful papers presenting evolutionary models where the evolving trait is altruistic under some parameter values, and where the authors attribute the evolution of this trait to a mechanism other than kin selection (column 1)."

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The authors declare no competing interest.

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