

## Reply to McNally and Tanner: Generosity evolves when cooperative decisions must be made under uncertainty

We thank McNally and Tanner (1) for their considered critique of our article (2). Our article addressed the puzzle of why humans, in one-shot interactions, often choose to incur costs to allocate benefits to others, with no possibility of recouping these losses (i.e., “irrational” generosity) (2). This empirical pattern challenges standard models of economic and evolutionary rationality, and has prompted the development of ever-more-cumbersome explanations (e.g., group selection, gene–culture coevolution, cultural group selection)—models fragily dependent on many hard-to-verify assumptions. In our article, we demonstrated that the well-documented selective regime of direct reciprocity produces agents willing to cooperate in apparently one-shot encounters, when the cognitive problem of discriminating one-shot from repeated encounters under uncertainty has been incorporated into the analysis (as, realistically, it must be). This is a parsimonious solution to the puzzle that flows naturally out of well-understood selection pressures.

McNally and Tanner (1) voice the reasonable concern that our results may not generalize widely because we did not model hesitant or forgiving strategies. A hesitantly cooperative strategy initially defects but may cooperate if the interaction continues. A forgiving cooperative strategy will switch to cooperation if its partner ceases defection. In contrast, the cooperative strategies we modeled cooperate initially, and the defecting strategy defects forever. The crux of their concern is that the magnitude of the effects we observed might be reduced had we instead made the defection strategy hesitantly cooperative. We concur that the fitness differential between initial cooperation and defection might be smaller in such a model. Importantly, however, the direction of selection would be the same, just with reduced

strength. Hence, the effects would not be eliminated and the generality of our results would be unchanged.

Indeed, the joint space of possible strategies and parameters is vast. So, to derive conclusions that were as general and transparent as possible, we selected cooperative strategies that are well understood and directly relevant to our question. Hesitant strategies, in contrast, introduce aspects of cooperation beyond the empirical issue we were addressing: the human propensity to be generous with a novel partner on the first move in a situation that appears to be one-shot. In such situations, a hesitant strategy—unlike humans—would not be generous on the first move and could thus not plausibly model the actual behavior we sought to understand. All strategies explored in game theory, including tit for tat, hesitant, and forgiving strategies, are far too simple to capture human cooperative psychology, but we think our results nonetheless generalize to all fundamentally cooperative strategies because uncertainty is a reliable feature of realistic ecologies. Although their details differ, these cooperative strategies are designed to extract the benefits of cooperation by selectively cooperating with other cooperative strategies and avoiding noncooperative strategies. Because uncertainty exists in the detection of one-shots (or last moves, or games with definite expected lengths), when cooperation yields gains in trade, selection should generally favor generosity. Forgiving, hesitant, or not, a psychology that is generous in the absence of anticipated payoffs is anything but Machiavellian.

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1. McNally L, Tanner CJ (2011) Flexible strategies, forgiveness, and the evolution of generosity in one-shot encounters. *Proc Natl Acad Sci USA* 108:E971.
2. Delton AW, Krasnow MM, Cosmides L, Tooby J (2011) Evolution of direct reciprocity under uncertainty can explain human generosity in one-shot encounters. *Proc Natl Acad Sci USA* 108:13335–13340.

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