

option of not donating. We therefore question their mechanism for maintaining cooperation without reciprocity.

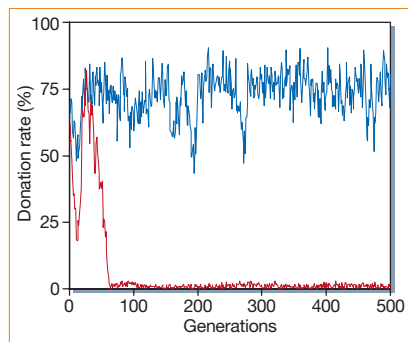
What makes cooperation so challenging for theorists is explaining how it can persist in the face of more exploitative strategies. In the system of Riolo *et al.*, clusters of cooperating agents with similar tags arise intermittently, only to be undermined by agents that reduce their tolerance level,  $T$ , such that they accept more donations than they offer. However, there is a limit to such cheating imposed by the minimum  $T=0$ . This means that when individuals with identical tags interact, they must always donate. A striking characteristic of Riolo and colleagues' simulations was the formation, through differential reproduction, of clusters of agents with identical tags. Most individuals in their simulations (up to 97% of the population<sup>4</sup>) were therefore ultimately constrained to cooperate.

To investigate what would happen if agents were given the option of declining to donate to any other agents, even those with identical tags, we replicated Riolo and colleagues' simulations with one simple modification: we allowed tolerance to evolve to below zero. Agents with negative  $T$  values would not donate to any other agent, although, by setting the minimum boundary for  $T$  at  $-10^{-6}$ , we ensured that all positive mutational changes converted  $T$  back to the cooperative region. We found that introducing the realistic option of non-donation had a catastrophic effect on cooperation (Fig. 1).

Why do we not find the high degree of cooperation reported by Riolo *et al.*? Once the constraint that identical tags must cooperate has been removed, agents interacting with others bearing the same tag face the classical 'prisoner's dilemma' — they can do well by cooperating, but they can do even better by accepting donations without donating. Thus, mutants that fail to donate, even to those with identical tags, will tend to invade, destroying cooperation.

Cooperation under the original conditions of Riolo *et al.* operates through a process of 'like helping like'<sup>5</sup> — agents sharing any particular tag also share the rule of donating to each other, so a form of kin selection<sup>6</sup> can support cooperation. However, agents can have identical tags without having a recent common ancestor, so in our modified system they can share tags without sharing the rule for cooperating. Because tag similarity is no longer a reliable guide to behaviour, the system of 'like helping like' breaks down. Whereas the problematic 'green beard' effect<sup>7</sup> depends on a link between altruism and a particular trait, the system of Riolo *et al.* depends on a link between altruism and similarity. Allowing similar individuals not to donate caused cooperation to be restricted in our system, even without any mechanism for cheating through faking tags<sup>5</sup>.

Cooperation based on similarity there-



**Figure 1** Population dynamics for the first 500 generations of a typical run of Riolo and colleagues' model<sup>1</sup>, in which individuals with identical tags must donate (blue), and our modified model in which individuals with identical tags may or may not donate (red). All parameter values were the same as for Fig. 1 of ref. 4. In 30 runs of our modified model, each for 30,000 generations, the overall mean donation rate was 1.48% (s.e.m. 0.031%), in comparison with Riolo *et al.*'s 73.6%.

fore turns out to be a rule that was built into the model rather than an inference that can be drawn from it. Nevertheless, we believe that possible mechanisms by which cooperation can arise without reciprocity merit further attention<sup>8</sup>, and the role of signals in such systems will be an important consideration.

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*Riolo et al. reply* — Roberts and Sherratt argue that if agents with identical tags are allowed a choice of behaviour, then tag similarity can no longer be a reliable guide to behaviour and so similarity does not breed cooperation. Although they are correct in noting that in our model<sup>1</sup> an agent will always donate when it meets another with an identical tag, we do not believe that their basic claim is correct.

We have replicated the results of Roberts and Sherratt and have run a generalized model that includes theirs as one extreme and our original model as another (details are available from R.L.R.). We find that if mutations are not biased as strongly

towards 'never donate', as in their version of the model, similarity can indeed breed cooperation. Whether it does, and to what extent, depends on several factors, including the rate at which 'never donate' agents are created, the number of pairings, the cost/benefit ratio of donations and the particular adaptive mechanisms in the model. If unconditional defection is introduced by adding a binary trait that controls whether agents never donate, or donate using tags and tolerance, we find that cooperation also emerges, but again the extent of cooperation depends on many factors.

We believe that the difference has not been fully understood between the stability of cooperation within any particular tag group and the rate of cooperation across a population consisting of diverse tags with changing frequencies over time. There is no dispute that particular cooperative tag groups are invadable<sup>1,2</sup>. However, as one tag group is invaded and thus dies off, another tag group with more reliable cooperators can flourish and become dominant, resulting in the cycles of cooperation and tag dominance noted previously<sup>1,3</sup>.

Roberts and Sherratt claim that cooperation based on similarity was built into our model. It was not, which is why, under some parameter settings (few pairings or high cost of donation), cooperative periods are rare and short-lived, resulting in very low overall donation rates<sup>1</sup>. Nevertheless, the level of cooperation for other parameter settings is substantial, with the overall rate of cooperation depending on the relative dynamics of invasion, resistance and emergence of dominant groups.

Many factors could affect the dynamics generated by tag-based mechanisms. For instance, tags that are easy to copy might lead to high rates of invasion, whereas other tags, such as language or accent, might be difficult to copy<sup>3</sup>. Our model could also be extended to study how a tag mechanism acts in conjunction with other mechanisms known to affect the emergence of cooperation. For example, territorial distribution of agents might favour 'speciation' into self-enforcing stereotypes<sup>3</sup>. Further investigation is needed to understand fully the range of mechanisms that can produce cooperation without reciprocity. Our results show that, under some conditions, tag mechanisms are one viable approach.

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