

Evolution of contingent altruism when cooperation is expensive

Ross A. Hammond^a, Robert Axelrod^{b,*}

^aDepartment of Political Science, University of Michigan, Ann Arbor, MI 48104, USA

^bFord School of Public Policy, University of Michigan, Ann Arbor, MI 48104, USA

Available online 19 January 2006

Abstract

The ubiquity of cooperation has motivated a major research program over the last 50 years to discover ever more minimal conditions for the evolution of altruism. One important line of work is based on favoritism toward those who appear to be close relatives. Another important line is based on continuing interactions, whether between individuals (e.g., reciprocity) or between lines of descent in a viscous population. Here, we use an agent-based model to demonstrate a new mechanism that combines both lines of work to show when and how favoritism toward apparently similar others can evolve in the first place. The mechanism is the joint operation of viscosity and of tags (heritable, observable, and initially arbitrary characteristics), which serve as weak and potentially deceptive indicators of relatedness. Although tags are insufficient to support cooperation alone, we show that this joint mechanism vastly increases the range of environments in which contingent altruism can evolve in viscous populations. Even though our model is quite simple, the subtle dynamics underlying our results are not tractable using formal analytic tools (such as analysis of evolutionarily stable strategies), but are amenable to agent-based simulation.

© 2005 Elsevier Inc. All rights reserved.

Keywords: Viscous population; Hamilton's rule; Evolutionarily stable strategy (ESS); Evolution of cooperation; Reciprocity; Kin recognition; Armpit effect; Prisoner's dilemma

The ubiquity of cooperation suggests that its requirements must be fairly minimal. Thus, discovering ever more minimal conditions for the evolution of cooperation has been a major research program for the last 50 years. One line of work uses strategies biased in favor of cooperation with those who appear to be close relatives—a bias which is assumed to have already evolved. The most demanding member of this category is kin selection, when based on directly estimated relatedness (Hamilton, 1964). Riolo et al. (2001) show that even a tag (i.e., a heritable, observable, and initially arbitrary characteristic) which serves as a weak and potentially deceptive indicator of relatedness can support the evolution of cooperation, if bias in favor of similar others is assumed. We show that *without* a pre-evolved bias in favor of similar others, tags alone may not be sufficient to sustain widespread cooperation.

A second line of work assumes continuing interaction, either between individuals or lines of descent. Continuing

interaction between pairs of individuals who can make their behavior contingent on the outcome of their previous interactions can support the evolution of cooperation, for example through reciprocity (Axelrod and Hamilton, 1981; Axelrod, 1984). Cooperation between lines of descent can sometimes be supported by population viscosity (Epstein, 1998; Hamilton, 1964; Koella, 2000; Le Galliard et al., 2003; van Baalen and Rand, 1998). Although viscosity facilitates cooperation by creating positive correlations of relatedness between neighbors (Nakamaru et al., 1997; Nowak and May, 1992; Pollack, 1989; West et al., 2002; Wilson et al., 1992), it can also inhibit cooperation by intensifying competition between neighbors for scarce resources (Nakamaru et al., 1997; West et al., 2002; Wilson et al., 1992).

We demonstrate a new mechanism that combines tags and viscosity to show how even a weak and possibly deceptive indicator of relatedness can account for (rather than assume) the evolution of bias toward apparently similar others, known as the “armpit effect” (Dawkins, 1976; Lacy and Sherman, 1983). Surprisingly, such a bias

*Corresponding author.

E-mail address: raxelrod@gmail.com (R. Axelrod).

does not become widespread without viscosity. We also show how tags and viscosity together can support the evolution of contingent altruism even when cooperation is expensive.

To model this mechanism, we combine a population structure governed by viscosity with strategies that can allow altruism to be contingent on the tags of others. The novel aspect of this combination is that strategies *coevolve* with the tags on which they are contingent, while the social environment of each individual is also evolving. This co-evolution is not included in previous theories of kin recognition (Crozier, 1986; Reeve, 1989; Ratnieks, 1991; Frank, 1998; Agrawal, 2001; Lehmann and Perrin, 2002; but see also Hochberg et al., 2003).

Allowing such co-evolution means that the reliability of both tags and proximity as indicators of relatedness varies endogenously in the model. In other words, *history matters*—the “fitness” of a given type of individual depends on the history of evolution as reflected in its current social environment. This represents an important category of real biological dynamics, for example in sessile cnidarians (Grosberg and Quinn, 1989; Grafen, 1990).

The co-evolution of strategies and tags also means that many common analytic techniques cannot be applied to the model. For example, evolutionarily stable strategy (ESS) techniques generally rely on mean-field, pair-wise, class-based, or neighborhood approximations to assess the “fitness” of categories of individuals (e.g., Taylor and Frank, 1996; Proulx, 2000). In our model, these approximations are not sufficient since an assessment of “fitness” at any particular time depends not just on the characteristics of an individual, but also on events distant in time and space that helped determine the individual’s current social environment. Estimation techniques used for analytic approximation of dynamics under viscosity (e.g. van Baalen and Rand, 1998; van Baalen and Jansen, 2002) are also insufficient, since they apply to strategies of altruism that are neither pair-wise nor contingent. We will also show that the spatial dynamics we discover in our model are subtle enough to make any pair-based approximation inadequate. Therefore, we will use an agent-based simulation to study all but our simplest models. This simulation technique allows us to explore the entire dynamic history of many populations, and to account for the co-evolution of heritable tags, strategies based on those tags, and population structure.

Any explanation for the evolution of cooperation requires both environmental beneficence and individual capability. The beneficence of the environment is determined not only by the magnitude of the cost (i.e. the expense) that must be borne to provide a given benefit to another, but also by the correlation pattern of who interacts with whom. An individual’s capabilities are measured in part by how refined is its ability to detect and exploit meaningful cues in its social and physical environment. To explore the potential for the evolution of altruistic strategies and cooperative behavior under a range

of environmental beneficence and individual capability, we employ a sequence of models using the common paradigm of asexual reproduction based on degree of success in pairwise Prisoner’s Dilemmas (Axelrod and Hamilton, 1981; Axelrod, 1984; Epstein, 1998; Koella, 2000; Le Galliard et al., 2003; Riolo et al., 2001).

We start with a Null Model with no individual ability to exploit cues, and no structure in the environment. The Null Model thereby rules out any strategy based on kinship or reciprocity. Each individual is either an altruist who always cooperates or an egoist who never cooperates. Without any pattern of who interacts with whom, individuals simply meet at random. As expected, these conditions are not sufficient to attain the emergence of cooperation.

We next consider a Viscosity Model that adds some structure to the environment by giving each individual a specific location and making interaction and reproduction local. We show that viscosity can be sufficient for the emergence and maintenance of cooperation, but only if the level of viscosity is very high, and if the environment is benign enough to allow a given benefit to be provided at relatively low cost.

We call our third model the Tag Model. Instead of viscosity, this model gives each individual the capacity to detect and condition its behavior on a tag that provides only rudimentary information about the other’s phenotype. The tag takes the form of a single heritable trait which we call “color”. Since there is no linkage between color and strategy, observing whether another individual has one’s own color provides no direct information about the unobservable traits that determine the other’s strategy. With the ability to distinguish among only four colors, the tags provide a weak and possibly deceptive indicator of relatedness. We show that without a built-in bias, discrimination based on such a tag is not sufficient to support cooperation. The reason is that even the weak cue about relatedness that such a tag may provide is undermined as soon as a line of unrelated “cheaters” evolves the same tag, a possibility not always included in previous models of altruism based on tags (e.g. Traulsen and Claussen, 2004).

Finally, we consider the Viscosity and Tag Model, combining the conditions in which viscosity provides structure to the interactions, and in which an individual can condition its behavior on the other’s tag. We show that under these conditions, cooperation can emerge and be maintained even when it is quite costly, when viscosity is not total, or when the only capability is the ability to distinguish a few types of an arbitrary trait that is not linked to strategy. We also show that altruists can not only invade a population of egoists, but can eventually dominate such a population as well.

We now implement each of these four models and compare their performance. Although our first model can be approximated analytically, our final model is not analytically tractable. We therefore formulate the four models as a sequence of agent-based simulations, starting with the Null Model.

In the simulation of the Null Model, the lack of environmental structure means interaction is strictly at random. Likewise, the lack of individual capacity for contingent behavior means that only two strategies are possible: being an altruist who always cooperates or an egoist who never cooperates. The simulation begins with an empty environment. Each time period consists of four stages: immigration, interaction, reproduction, and death.

1. A single immigrant with a random strategy enters.
2. Each agent achieves a potential to reproduce, Z . At the beginning of each period an agent has the same initial $Z = Z_0$. Each agent is paired with another agent chosen at random to interact in a one-move Prisoner's Dilemma. Thus, on average, an agent will play two such games each period: once through its own pairing, and once by another agent's pairing. Altruists give help and pay a cost, c , for each donation. Egoists do not give help. Receiving help has a benefit, b . For altruists, the average potential to reproduce is $\bar{Z}_A = Z_0 + 2(bp - c)$ and for egoists it is $\bar{Z}_E = Z_0 + 2bp$, where p is the proportion of altruists in the population. In the simulation, the standard values of these parameters are $Z_0 = 12\%$, $c = 1\%$, $b = 3\%$.
3. Each agent is chosen in a random order and given a chance to reproduce with probability equal to its Z , provided that the population is below the environment's carrying capacity of 2500. Reproduction is asexual and consists of creating an offspring who receives the strategy of its parent, with a mutation rate $m = 0.5\%$.
4. Each agent has a 10% chance of dying, making room for future offspring.

This first model, with no viscosity, can be estimated analytically by calculating the expected number of new altruists (N_A) and new egoists (N_E) each round and solving for the condition in which proportions of each strategy in the population are stable. For example, the total number of new altruists in each round, N_A , includes un-mutated offspring of altruists, mutated offspring of egoists, and a 50% chance that the immigrant for the round is an altruist. Given a mutation rate of m , an immigration rate of i , and a proportion of altruists p this gives:

$$N_A = \bar{Z}_A p(1 - m) + \bar{Z}_E(1 - p)m + i/2.$$

Likewise,

$$N_E = \bar{Z}_E(1 - p)(1 - m) + \bar{Z}_A p m + i/2.$$

The simulation and the analytic approximation agree that with the given parameters, the proportion of altruists falls to just less than 5% (Table 1 row a). The failure of cooperation is not surprising since there is nothing to counter the fact that an egoist always tends to have more offspring than an altruist.

We now add some structure to the population by localizing interaction and reproduction to create a Viscosity Model. As in the Null Model, agents are either altruists

Table 1

Population structure, environmental austerity, and individual capability all affect whether altruism can emerge and be maintained

	% Altruists	% Donations
a. Null model	4.6 ± 0.3	4.6 ± 0.3
b. Viscosity model	74.4 ± 1.2	75.3 ± 1.1
c. High cost	13.7 ± 1.2	14.0 ± 1.2
d. Low viscosity	43.9 ± 2.5	44.4 ± 2.5
e. Tags model	22.0 ± 1.8	14.5 ± 0.7
f. Viscosity and tags model	89.0 ± 0.7	74.2 ± 0.5
g. High cost	68.0 ± 1.5	56.1 ± 1.2
h. Low viscosity	78.4 ± 1.2	57.5 ± 0.9
i. Weakened indicator of relatedness	86.8 ± 0.6	78.1 ± 0.5
j. Inaccurate perception	88.0 ± 0.6	69.1 ± 0.5
k. All egoist start	90.7 ± 0.5	77.1 ± 0.8

Population viscosity (i.e. causing all interactions to be local rather than random) is sufficient for the dominance of the altruist strategy (row a versus b). Viscosity does not sustain cooperation in an austere environment where the cost of helping is 2/3 rather than 1/3 of the benefit of receiving help (b, c, and Fig. 1). In addition, the viscosity itself must be high because if only half the interactions are random rather than local, altruism no longer dominates the population (b, d). The ability to detect phenotypic similarity of tags is not sufficient by itself (e), but does allow the evolution of altruism in a viscous population to emerge (f), even when the environment that is austere (c, g) or the viscosity is low (d, h). Moreover, in a viscous population, tags can support altruism even with weakened individual capability to distinguish only two rather than four tags (i) or 10% of the perceptions of tag similarity are inaccurate (j). Altruists can also invade (by mutation) an initially full lattice populated entirely by egoists, without the need for immigration (k). All models are run to stability and use standard parameters unless otherwise indicated. Standard parameters are: 1% as the cost of giving help (relative to 3% as the benefit from receiving help), 4 colors of tags, 0.5% mutation rate per trait, 1 immigrant per time period, 50 × 50 lattice size. Each case is replicated 10 times. Data are averaged over the last 100 periods in runs of 2000 periods. The range shown is plus or minus the standard error. The first column gives the percentage of the population that uses an altruist strategy (either contingent or pure). The second column shows the percentage of behavioral choices that are donations.

or egoists and interact in one-move Prisoner's Dilemmas. However, agents are now situated in a space of 50 × 50 sites, with wrap-around borders so that each site has exactly four adjacent neighbors. Instead of choosing pairs of interacting agents at random, each pair of adjacent agents interacts (with both given a chance to donate). Reproduction and death are as before, except that offspring are created only if they can be placed in an empty site adjacent to the parent. This creates competition for a scarce resource, namely space for offspring.¹ Simulation results show that the Viscosity Model supports the evolution of cooperation if the environment is sufficiently benign in terms of a low cost/benefit ratio (Table 1 rows a and b, and Fig. 1 line a). This result is generally consistent with previous work showing that the cooperation-enhancing effects of viscosity can overcome the cooperation-retarding effects of crowding only when

¹For a similar model with tags, but without local competition, see (Axelrod et al., 2004).

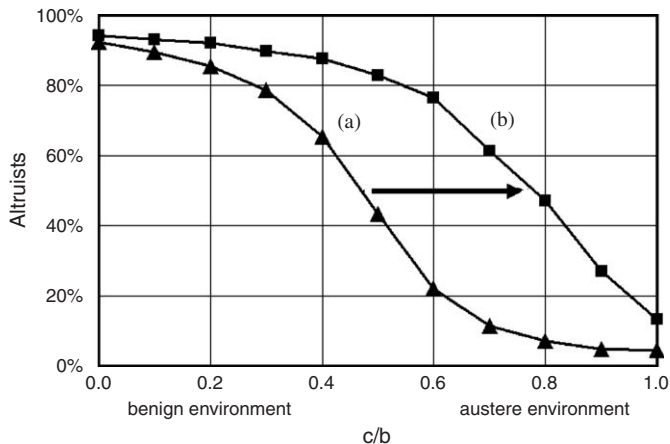


Fig. 1. Altruism as a function of environmental austerity measured in terms of the ratio of cost (c) to benefit (b), with viscosity alone (line a) and with both viscosity and tags (line b). Adding tags to viscosity allows a given level of altruism to be maintained in more austere environments. For example, the arrow indicates that the addition of tags allows altruists to be sustained at 50% of the population in a substantially more austere environment.

the environment is sufficiently benign (van Baalen and Rand, 1998), although the full dynamics of the simulation are difficult to capture using analytic techniques for reasons discussed above. Next, we return to the Null Model and instead of adding population structure, we enhance the agents themselves. In particular, we give an agent the capacity to condition its behavior on an observable characteristic of the agent with whom it is interacting. Wanting to make this capacity quite limited, we create a Tag Model in which an agent can distinguish among only four “colors” of a single heritable tag. We limit the usefulness of the tag by assigning colors at random to the immigrants. Most important, the individual’s tag is not linked to its strategy. Without such linkage, an observed tag provides only a weak, and possibly even deceptive, indicator of relatedness. Previous work has shown that such tags can support cooperation if individuals are assumed to favor automatically those who are similar to their own type (Riolo et al., 2001).

In the Tag Model, we do not make this assumption—instead, we allow strategies that preferentially favor similar others and those that do not. In the Tag Model, an agent has both a tag, and a strategy that can take account of another’s tag. This means that each individual agent now has three heritable traits, each with an independent mutation rate of 0.5%. The first trait specifies which of the four colors of tag the agent has. The second and third traits specify the agent’s strategy. The second trait specifies whether the agent cooperates or not when meeting another agent of its own color. The third trait specifies whether the agent cooperates or not when meeting an agent of a *different* color. Together, the second and third traits specify one of four possible strategies—including pure altruism (cooperate with all others) and contingent altruism

(cooperate with only those who share your color). Since the tags and strategies are not linked and only tags are observable, the model allows for the possibility of “cheaters” who receive help from others of the same color while providing help to no one at all. Without a pre-evolved bias in favor of similar others, we find that tags alone are insufficient to sustain high levels of cooperation: with a cost/benefit ratio of one-third, only 22% of agents are altruists of either type (Table 1 row e). Moreover, the bias *assumed* in previous work on tags (Riolo et al., 2001) and the “armpit effect” (Lacy and Sherman, 1983) does not evolve in the Tag Model, where it occurs in less than one-fifth of the population.

Our final model, the Viscosity and Tag Model, achieves high levels of cooperation by the mechanism of combining environmental structure and individual capacity. Fig. 1 shows that adding tags to viscosity increases the level of cooperation at any given level of environmental austerity, and that tags allow a given level of altruism to be maintained in more austere environments. For example, when viscosity alone is present, the cost per donation can be no greater than 47% of the benefit in order to support altruism in at least half the population. With the addition of tags, the same level of altruism can be supported when the cost per donation is as high as 78% of the benefit. In an austere environment where the cost of cooperation is two-thirds (rather than one-third) of the benefit, the ability to discriminate based on tags can even be necessary for the maintenance of cooperation (Table 1 rows c vs. g).

The success of altruism in the Viscosity and Tag Model is robust to a wide range of other parameter changes and variations in the model. With the standard parameters, 89% of the population are altruists (Table 1 row f). When any of the following demographic parameters are either halved or doubled, at least 83% of the population are altruists: lattice width (which governs maximum population size), and the rates of immigration, mutation, and mortality.² Altruism is also robust to lower levels of viscosity (Table 1 rows h vs. d) and to weaker indicators of relatedness (row i). Altruism is just as dominant in a variant of the model in which an agent can distinguish all four colors (rather than just distinguishing between its own color and all other colors). Surprisingly, the results are also not very sensitive to the possibility that an agent will occasionally misperceive whether the other agent in the interaction has the same color (row j). Most importantly, altruists even invade and dominate a population of egoists without the benefit of immigration or an initially empty lattice (row k).

The simulation results also show that, with tags and viscosity, the most common strategy is contingent altruism (more than 76% of agents, compared to 25% if selection had been neutral) even though no bias toward similar others is built in to the model. Contingent altruism

²Data on these and other variants of the model are available at www.umich.edu/~axe/ExpensiveCooperation.htm

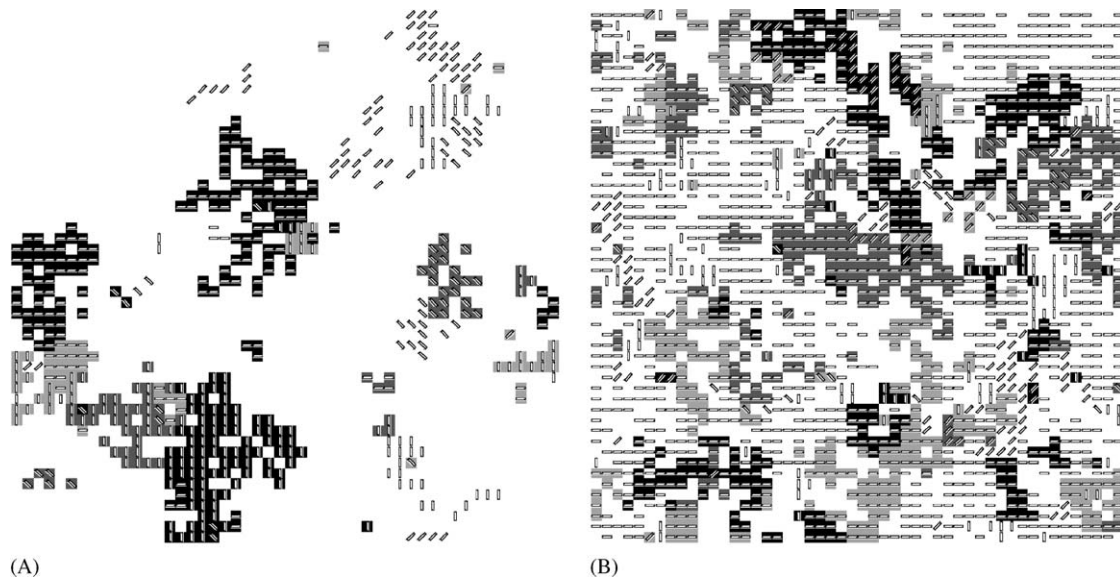


Fig. 2. A typical run of the viscosity and tag model after 100 periods (A) and 2000 periods (B). The four tag types are represented as shades of gray. In the early periods of the run (A), the scattered immigrants create regions of similar agents. By time (B), altruists dominate with an average of about 89% of the population in ten runs. Contingent altruists (shown here as horizontal lines) comprise on average about 76%, and pure altruists (vertical lines) another 13% of the population. Egoists (diagonal lines sloping up to the right), and the strategy of donating to dissimilar others (diagonal lines sloping down to the right) comprise only 9% and 2%, respectively. See text for explanation of the dynamics. A color movie of a typical run is available at umich.edu/~axe/vtmovie.htm

supports a high level of actual cooperative behavior (74% of interactions), because contingent altruists tend to have the same tag as most of their neighbors.

In the early periods of a typical run (Fig. 2a), the scattered immigrants create regions of similar agents. Once the space is nearly full (Fig. 2b), the dynamics are governed by what happens when regions with different attributes grow enough to become adjacent to each other. These dynamics can be analyzed in terms of regions of contiguous agents having the same color and strategy. The most important dynamic is that a region of contingent altruists will tend to expand at the expense of a region of a different color comprised of any one of the other three strategies. In this way, “cheaters” of one color are suppressed by contingent altruists of a different color, and egoists are kept in check.

To illustrate the advantage of contingent altruists over the other three competing strategies, consider the case of egoists. Contingent altruists have an advantage over egoists of any different color in competing for an empty space at the border between regions. The reason for this advantage is that a contingent altruist on the border will receive donations from others in its region, while egoists on the border do not receive any donation from other egoists. Fig. 3 shows a segment of the map that has only two kinds of agents: blue contingent altruists and red egoists. Let n be the number of neighbors who are an agent’s own color. For a blue contingent altruist, the potential to reproduce in this case is $Z_0 + n(b-c)$, while for a red egoist the potential to reproduce is simply Z_0 . So, given $n > 0$ and $b > c$, blues do

	CA	CA	E
CA	CA	CA ₂	E
	CA ₁		E ₁
CA	CA	E ₂	E

Fig. 3. A region of contingent altruists dominates a region of egoists of a different color. In this example, the contingent altruists have one color and the egoists have another. The four individuals labeled CA₁, CA₂, E₁, and E₂ are in competition to fill the empty space between them. CA₁ has two neighbors of its own type with whom it exchanges donations. The result is that CA₁’s potential to reproduce increases by $2(b-c)$, where b is the benefit from receiving a donation and c is the cost of giving a donation. The same is true for CA₂. In contrast, both E₁ and E₂ give no donations and receive none. The result is that their potential to reproduce is unchanged from its initial value. Since $b > c$, CA₁ and CA₂ have a better chance than E₁ or E₂ to have an offspring fill the empty cell between the regions. The result is that the contingent altruist region grows at the expense of the egoist region of a different color.

better than reds. The blues will therefore tend to expand into empty spaces between the regions, at the expense of the red egoists.

The example in Fig. 3 does not take into account “cheaters” in the form of agents who are blue but are egoists. A single mutant blue cheater in the region of blue contingent altruists would get $Z = Z_0 + nb$, and so cheaters would grow fastest of all at first. But as the number of individual blue egoist cheaters grows, they become a *region* of blue egoists—subject to being defeated by a region of contingent altruists of any other color, as shown in the figure.

An interesting result is that the most successful strategy in the Viscosity and Tag Model, contingent altruism, is not the strategy that maximizes “Darwinian fitness” (surviving offspring in the next generation). As noted above, the potential to reproduce for contingent altruists is $Z = Z_0 + n(b - c)$. For an agent with $n > 0$ same-color neighbors, an egoist strategy will achieve a strictly higher value of $Z = Z_0 + nb$. Thus, an individual egoist will on average produce more offspring than an individual contingent altruist in the same region. However, regions of contingent altruists tend to produce more offspring than do regions of egoists. This is because contingent altruists have, on average, more *grandchildren*, and so tend to have higher fitness in this sense (as in sex-ratio theories following Fisher, 1930).

In sum, our results show that contingent altruism (based on tags and viscosity together) can invade, spread, and can resist invasion even when cooperation is expensive and reciprocity is not possible. Thus, tags and viscosity together provide a powerful mechanism to overcome dilemmas of cooperation, supporting high levels of cooperation with minimal requirements. Although the combination of tags and viscosity is highly effective, we show that neither alone can evolve robust cooperation in austere environments. Tags alone are insufficient to sustain cooperation without a built-in bias in favor of similar others, and such a bias does not evolve without population viscosity. However, tags can add substantially to the level and robustness of the cooperation that emerges when viscosity *is* present. Ironically, then, tags are most effective in the evolution of cooperation when viscosity (another potential aid to cooperation) is also present. An important implication of tags is that “discrimination” in the form of bias in favor of similar others can actually promote cooperation. These results also suggest the potential for a feedback loop in which the emergence of even a small amount of bias increases the amount of altruism generated by a given level of viscosity, which in turn makes viscosity itself more valuable for the evolution of cooperation.

The authors thank Michael D. Cohen, Alan Grafen, John Holland, Richard Lenski, Scott Page, Carl Simon, Rick Riolo, Hans Christian Siller, Lars-Erik Cederman, J. M. G. van der Dennen, David Lazer, Robert Putnam, and Tarah M. Wheeler. For financial help, we thank the Intel Corporation, the National Science Foundation, and the Literature Science and Arts Enrichment Fund of The University of Michigan.

References

- Agrawal, A.F., 2001. Kin recognition and the evolution of altruism. *Proc. R. Soc. Lond. B* 268, 1099–1104.
- Axelrod, R., 1984. *The Evolution of Cooperation*. Basic Books, New York.
- Axelrod, R., Hamilton, W.D., 1981. The evolution of cooperation. *Science* 211, 1390–1396.
- Axelrod, R., Hammond, R.A., Grafen, A., 2004. Altruism via kin-selection strategies that rely on arbitrary tags with which they coevolve. *Evolution* 58, 1833–1838.
- Crozier, R.H., 1986. Genetic clonal recognition abilities in marine invertebrates must be maintained by selection for something else. *Evolution* 40, 1100–1101.
- Dawkins, R., 1976. *The Selfish Gene*. Oxford, New York.
- Epstein, J.M., 1998. Zones of cooperation in demographic Prisoner’s Dilemma. *Complexity* 4, 6–48.
- Fisher, R.A., 1930. *The Genetical Theory of Natural Selection*. Dover, New York.
- Grafen, A., 1990. Do animals really recognize kin? *Anim. Behav.* 39, 42–54.
- Grosberg, R.K., Quinn, J.F., 1989. The evolution of selective aggression conditioned on allorecognition specificity. *Evolution* 43, 504–515.
- Hamilton, W.D., 1964. The genetical evolution of social behaviour. I and II. *J. Theor. Biol.* 7, 1–52.
- Hochberg, M.E., Sinervo, B., Brown, S.P., 2003. Socially mediated selection. *Evolution* 57, 154–158.
- Koella, J.C., 2000. The spatial spread of altruism versus the evolutionary response of egoists. *Proc. R. Soc. Lond. B* 267, 1979–1985.
- Lacy, R.C., Sherman, P.W., 1983. Kin recognition by phenotype matching. *Am. Nat.* 121, 489–512.
- Le Galliard, J.F., Ferrière, R., Dieckmann, U., 2003. The adaptive dynamics of altruism in spatially heterogeneous populations. *Evolution* 57, 1–17.
- Lehmann, L., Perrin, N., 2002. Altruism, dispersal, and phenotype-matching kin recognition. *Am. Nat.* 159, 451–468.
- Nakamaru, M., Matsuda, H., Iwasa, Y., 1997. The evolution of cooperation in a lattice-structured population. *J. Theor. Biol.* 184, 65–81.
- Nowak, M.A., May, R.M., 1992. Evolutionary games and spatial chaos. *Nature* 359, 826–829.
- Pollack, G.B., 1989. Evolutionary stability on a viscous lattice. *Soc. Networks* 11, 175–212.
- Proulx, S.R., 2000. The ESS under spatial variation with applications to sex allocation. *Theor. Popul. Biol.* 58, 33–47.
- Ratnieks, F.L.W., 1991. The evolution of genetic odor-cue diversity in social Hymenoptera. *Am. Nat.* 137, 202–226.
- Reeve, H.K., 1989. The evolution of conspecific acceptance thresholds. *Am. Nat.* 133, 407–435.
- Riolo, R.L., Cohen, M.D., Axelrod, R., 2001. Evolution of cooperation without reciprocity. *Nature* 414, 441–443.
- Taylor, P.D., Frank, S.A., 1996. How to make a kin selection model. *J. Theor. Biol.* 180, 27–37.
- Traulsen, A., Claussen, J.C., 2004. Similarity-based cooperation and spatial segregation. *Phys. Rev. E* 70, 046128.
- van Baalen, M., Jansen, V.A.A., 2002. Common language or tower of babel? On the evolutionary dynamics of signals and their meanings. *Proc. R. Soc. Lond. B* 270 (1510), 69–76.
- van Baalen, M., Rand, D.A., 1998. The unit of selection in viscous populations and the evolution of altruism. *J. Theor. Biol.* 193, 631–648.
- West, S.A., Pen, I., Griffin, A.S., 2002. Conflict and cooperation: cooperation and competition between relatives. *Science* 296, 72–75.
- Wilson, D.S., Pollack, G.B., Dugatkin, L.A., 1992. Can altruism evolve in purely viscous populations? *Evol. Ecol.* 6, 331–341.