ON THE EVOLUTION OF ALTRUISTIC COOPERATION

Ilan Eshel Department of Statistics School of Mathematics Tel Aviv University Israel Daphna Weinshall Center of Biological Information Processing MIT, Cambridge MA 02139, USA Uzi Motro Department of Statistics and Genetics The Hebrew University of Jerusalem, Israel

Cooperation is a sort of behavior that, if followed by all participants of a game, increases the payoff of each. Altruistic behavior is such that, if followed by one individual alone, it decreases its own payoff but helps the other. Altruistic cooperation is the combination of both. For example, so is the first strategy of each player in the two-player game with the following payoff matrix:

(.9;.9)	(.0;1.0)
(1.0;.1)	(.1;.2)

Best known is the symmetric case of altruistic cooperation, in a two player game, generally referred to as the prisoner's dilemma. This is a two-player game characterized by the following payoff matrix:

(x_1,x_1)	(x_3, x_2)
(x_2,x_3)	(x_4, x_4)

where $x_2 > x_1 > x_4 > x_3$ and $x_1 + x_4 > x_2 + x_3$.

As we see (having $x_1 > x_4$), both players will gain by agreement to choose the first strategy (which we call *cooperation*). Yet, regardless of what one player does, it is always advantageous for the other player to choose the second strategy (say *defection*). A seemingly strange result is that non-cooperation (with the payoff x_4 for each player) is the only Nash solution of the game (or the only ESS in its population version). Even more interesting is the finding that (at least for a certain range of parameters x_1, \ldots, x_4) humans, and perhaps animals, tend to cooperate in such situations, thus behaving in a non-rational way from the viewpoint of individual maximization of the payoff (Axelrod, 1980 and many references there).

Cooperation in situations of the prisoner's dilemma type can, therefore, be treated as a special case of altruism. As such, one can attempt to explain their evolution on the basis of kin selection (Hamilton 1964; see also a general representation of Matessi in this volume). Many experiments and observations of human behavior have established, however, that

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In this presentation, we maintain that the model of a repeated game under the same condition (as suggested by Rapoport, 1967, and widely employed since its inclusion by Axelrod and by Axelrod and Hamilton) is insufficient to analyze the situation of longlasting cooperation among individuals in natural populations. Indeed, such a situation is characterized not only by repeated encounters but also by the diverse, random feature of such encounters. We see that this second characteristic, hitherto neglected, is crucial for the evolution of cooperative behavior.

In a previous work (Eshel and Motro, 1981) we considered the importance of such a structure for the evolution of cooperation among relatives. Assuming a relatedness 0 < r < 1 between two individuals, it is the Hamiltonian prediction (Hamilton, 1964; see also Matessi, this volume) that natural selection, operating to maximize one's inclusive fitness, will favor the level r of self-sacrifice, namely, altruistic behavior in such situations where the ratio between donor risk and recipient benefit is not higher than r. But if this is true, then the death of one's relative means more than the loss of a fraction r of one's genes but also (and maybe not less important) a loss of a potential helper, determined to help because of the same, apparently symmetric, kin-selection argument. A level of self-sacrifice r^* , higher than the relatedness r is, thus, established in the population. But this, in return, even increases the importance of a relative as a potential helper and the process magnifies itself. It is shown, however, that the process does converge to a stable (ESS) level of altruistic self-sacrifice, which may be significantly higher then the original level of relatedness. Moreover, more than one possible ESS level of altruism can be established with the result of a reciprocal-like behavior (Eshel and Motro, 1981).

In this representation we take over the same basic idea in order to study the evolution of altruistic cooperation among non-relatives in situations of the prisoner's dilemma type.

Following previous models (Rapoport, 1967, and later), we assume that the two participants of an encounter have, at any given time, regardless of past events, a probability p > 0 for a future encounter, provided both survive the present one. We assume, however, that the outcome of the encounter is the participants survival probability at the end of the encounter. Moreover, this outcome depends not only on the participants' strategies but also on the specific conditions of the encounter, which are known to the participants (and therefore, can affect their behavior at the time of the encounter). The outcome of an encounter is, therefore, given by the matrix

	Cooperate	Defect
Cooperate	(X_1, X_1)	(X_{3}, X_{2})
Defect	(X_2, X_3)	(X_{4}, X_{4})

where the survival probabilities X_1, \ldots, X_4 are random variables with $X_1 > X_4$ (which is

the definition of cooperation).

Assume further, that if player I is absent at a situation of a potential encounter (i.e., if he died at some previous encounter) then the survival probability of player I is equal to the one he had without cooperation, namely X_4 . Let the vector $\underline{X} = (X_1, \ldots, X_4)$ have a four dimensional continuous distribution $F(\underline{x})$ with a positive density over some convex set which intersects the two following sets of parameters:

$$D = \{ \underline{x} \mid x_3 < x_4 < x_1 < x_2 ; x_2 + x_3 < x_1 + x_4 \}$$

$$S = \{ x \mid x_1 > x_2 ; x_3 > x_4 \}$$

Note that while D stands for encounters of the prisoner's dilemma type, S stands for encounters in which cooperation is of a direct advantage to both participants. (This is the case in many daily situations in which defection may be harmful to the defector as it is to its potential collaborator. Indeed, no explanation for the evolution of cooperation in a such situation is needed. We want to explain the evolution of cooperation on D or on a subset of it, but for this end, the very existence of the positive measure set S is needed.) Finally, we assume that at any encounter, both participants are able to assess the values of x_1, \ldots, x_4 . Their behavior is affected by the realization of these values but not by past events.

A strategy of player i (i = 1, 2) is, therefore, a probability $\Gamma_i = \Gamma_i(\underline{x})$ to cooperate under the condition \underline{x} . The a priori survival proability $s_1 = s_1(\Gamma_1, \Gamma_2)$ of player I through one encounter in which player II is present is, therefore,

$$s_1(\Gamma_1,\Gamma_2) = \iiint_{\Omega} \left\{ \Gamma_1\Gamma_2x_1 + \Gamma_1(1-\Gamma_2)x_2 + (1-\Gamma_1)\Gamma_2x_3 + (1-\Gamma_1)(1-\Gamma_2)x_4 \right\} dF(\underline{x})$$

where $\Gamma_i = \Gamma_i(\underline{x})$. The survival probability of player II is, then, $s_2(\Gamma_1, \Gamma_2) = s_1(\Gamma_2, \Gamma_1)$.

The one-event survival probability of each participant with the absence of the other is $\lambda = EX_4$.

By straightforward calculation, one can see that the survival probability of player I through the whole sequence of encounters is

$$V(\Gamma_1,\Gamma_2) = \frac{1-p}{1-ps_1s_2} + \frac{p(1-s_1s_2)}{1-ps_1s_2} \cdot \frac{s_1(1-s_2)}{1-s_1s_2} \cdot \frac{1-p}{1-\lambda p} = \frac{q}{1-\lambda p} (1+\psi(s_1,s_2))$$

where

$$\psi(s_1,s_2)=\frac{s_1-\lambda}{1-ps_1s_2}$$

 ψ (and therefore V) is indeed an increasing function of s_1 . Moreover, as long as Γ_1 is close to Γ_2 and both determine the positive probability of cooperation on some nondegenerate range, it can be shown that $s_1 > \lambda$ and then ψ (and therefore V) is also an increasing function of s_2 . Hence, in order to increase one's own viability V, one must seek to increase not only one's own survival probability s_1 , but also the survival probability s_2 of one's potential collaborator. The problem is, indeed, that by increasing the one, one inevitably decreases the other.

More specifically, player I can change only his own strategy Γ_1 . Assume that all individuals in the population choose the same strategy Γ , and let $\Gamma(\underline{x}) < 1$ for some $\underline{x} \in \Omega$. Assume that by increasing his probability of cooperation by $\delta > 0$ over a measure- ε vicinity

of \underline{x} , player I decreases s_1 by θ_1 and increases s_2 by θ_2 (as long as player II sticks to Γ). The viability of player I thus increases by $\theta_1 \frac{\partial \psi}{\partial s_2} - \theta_1 \frac{\partial \psi}{\partial s_1}$. If this value is non-positive for all $\underline{x} \in \Omega$ and for all δ and ϵ sufficiently small, then we say that Γ is stable against an increased tendency to cooperate. In the same way one defines stability against a decreased tendency to cooperate. A Nash solution of the game is a strategy that is stable against both an increased and a decreased tendency to cooperate. By combining arguments of game theory and measure theory one can prove (Eshel and Weinshall, 1988)

Proposition.

(*)

- (i) The supergame, as defined above has infinitely many Nash solutions.
- (ii) For any distribution of parameters F (satisfying the conditions mentioned above), there is a positive value $x_0 > 0$ such that if

 $\frac{x_4 - x_3}{x_2 - x_4} < x_0$

.

then any Nash solution of the supergame determines full cooperation in a situation determined by the payoff vector $\underline{x} = (x_1, x_2, x_3, x_4)$.

Note that the range

$$G_{x_0} = \left\{ \underline{x} \mid \frac{x_4 - x_3}{x_2 - x_4} < x_0 \right\}$$

of full cooperation always intersects the range D of the prisoner's dilemma encounters and the intersection $D \cap G_{x_0}$ is always of a positive measure. More specifically, the proposition ascertains cooperation in those situations of the prisoner's dilemma type in which the ratio between one's loss $x_4 - x_3$ and opponents gain $x_2 - x_4$ due to one's exclusive shift to cooperative behavior is bounded by a certain value x_0 .

This prediction of the model is in agreement with the laboratory results and observation of human behavior (Axelrod, 1980, and references there).

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