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Supporting Online Material for

Five Rules for the Evolution of Cooperation

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Five rules for the evolution of cooperation
Supporting Online Material

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The standard payoff matrix between cooperators, C, and defectors, D, is given by

$$\begin{array}{cc} & \begin{array}{cc} C & D \end{array} \\ \begin{array}{c} C \\ D \end{array} & \begin{pmatrix} b-c & -c \\ b & 0 \end{pmatrix} \end{array} \tag{1}$$

The entries in the payoff matrix refer to the 'row player'. For each interaction, a cooperator pays a cost, c. Interacting with a cooperator leads to a benefit, b. Thus, the payoff for C versus C is $b-c$; the payoff for C versus D is $-c$; the payoff for D versus C is b; the payoff for D versus D is 0. Usually, we assume that $b > c$, otherwise the payoff for two cooperators is less than the payoff for two defectors, and cooperation becomes nonsensical. I will now discuss how to derive the five 2×2 matrices of Table 1.

1. Kin selection

A simple way to study games between relatives was proposed by Maynard Smith for the Hawk-Dove game (S1). I will use this method to analyze the interaction between cooperators and defectors. Consider a population where the average relatedness between individuals is given by r, which is a number between 0 and 1. The concept of inclusive fitness implies that the payoff received by a relative is added to my own payoff multiplied by r. Therefore, we obtain the modified matrix

$$\begin{array}{cc} & \begin{array}{cc} C & D \end{array} \\ \begin{array}{c} C \\ D \end{array} & \begin{pmatrix} (b-c)(1+r) & br-c \\ b-rc & 0 \end{pmatrix} \end{array} \tag{2}$$

For this payoff matrix, cooperators dominate defectors if $b/c > 1/r$. In this case, cooperators are also evolutionarily stable (ESS), risk-dominant (RD) and advantageous (AD); see main text for the definition of ESS, RD and AD.

Another method to describe games among relatives was proposed by Grafen (S2) also in the context of the Hawk Dove game. Let us assume that interactions are more likely between relatives. Each individual has a fraction, r, of its interactions with its own relatives, who use the same strategy, and a fraction $1 - r$ with random individuals from the population, who could use the same or a different strategy. Let x denote the frequency of cooperators. The frequency of defectors is given by $1 - x$. The fitness of a cooperator is $F_C(x) = r(b-c) + (1-r)[(b-c)x - c(1-x)]$. The fitness of a defector is $F_D(x) = (1-r)bx$. These linear fitness function can be described by the payoff matrix

$$\begin{array}{cc} & \begin{array}{cc} C & D \end{array} \\ \begin{array}{c} C \\ D \end{array} & \begin{pmatrix} F_C(1) & F_C(0) \\ F_D(1) & F_D(0) \end{pmatrix} \end{array} = \begin{array}{cc} & \begin{array}{cc} C & D \end{array} \\ \begin{array}{c} C \\ D \end{array} & \begin{pmatrix} b-c & br-c \\ b(1-r) & 0 \end{pmatrix} \end{array} \tag{3}$$

Again we find that cooperators dominate defectors if $b/c > 1/r$. Therefore, both approaches give the same answer, which turns out to be Hamilton's rule (S3). Note that the exact population genetics of sexually reproducing, diploid individuals require more complicated calculations (S4).

2. Direct reciprocity

In order to derive a necessary condition for the evolution of cooperation in the repeated Prisoner's Dilemma, we can study the interaction between 'always-defect' (ALLD) and tit-for-tat (TFT). If TFT cannot hold itself against ALLD then no cooperative strategy can. TFT starts with cooperation and then does whatever the opponent has done in the previous move. We ignore erroneous moves. In this setting, TFT playing ALLD will cooperate in the first round and defect afterwards. Therefore, the payoff for TFT versus ALLD is $-c$. The payoff for ALLD versus TFT is b. Only the first round leads to a payoff, while all subsequent rounds consist of mutual defection and produce zero payoff for both players. The payoff for ALLD versus ALLD is 0. The payoff for TFT versus TFT is $(b-c)/(1-w)$. The parameter w denotes the probability of playing another round between the same two players. The average number of rounds is given by $1/(1-w)$. Hence, we obtain the payoff matrix

$$\begin{array}{cc} & \begin{array}{cc} C & D \end{array} \\ \begin{array}{c} C \\ D \end{array} & \begin{pmatrix} (b-c)/(1-w) & -c \\ b & 0 \end{pmatrix} \end{array} \tag{4}$$

From this matrix we immediately obtain the three conditions for ESS, RD and AD that are shown in Table 1. For cooperators (using TFT) to be ESS in comparison with ALLD, we need $b/c > 1/w$. Slightly more stringent conditions are required for cooperators to be RD or AD. Note that ALLD is always an ESS, and hence cooperators cannot dominate defectors in the framework of direct reciprocity.

The calculations for exploring the interactions of larger sets of probabilistic strategies of the repeated Prisoner's Dilemma in the presence of noise (S5) are more complicated (S6, S7). Often there are cycles between ALLD, TFT and unconditional cooperators (ALLC) (S8). The point is that $b/c > 1/w$ is a necessary condition for the evolution of cooperation. This argument is related to the Folk theorem which states that certain trigger strategies can achieve cooperation if there are enough rounds of the repeated Prisoner's Dilemma (S9, S10).

3. Indirect reciprocity

Indirect reciprocity describes the interaction between a donor and a recipient. The donor can either cooperate or defect. The basic idea of indirect reciprocity is that cooperation increases ones own reputation, while defection reduces it. The fundamental question is whether natural selection can lead to strategies that base their decision to cooperate (at least to some extent) on the reputation of the recipient.

A strategy for indirect reciprocity consists of an action rule and an assessment norm. The action rule determines whether to cooperate or to defect in a particular situation depending on the recipient's reputation (image score) and ones own. The assessment norm determines how to evaluate an interaction between two other people as an observer. Most analytic calculations of indirect reciprocity assume binary image scores: the reputation of someone is either 'good' or 'bad'. Nobody so far has succeeded to formulate an exact analysis for the realistic situation where the image scores are more gradual and different people have different image scores of the same person as a consequence of private and incomplete information.

In order to derive a necessary condition for the evolution of cooperation by indirect reciprocity, let us study the interaction between the two basic strategies: (i) defectors and (ii) cooperators who cooperate unless they know the reputation of the other person to indicate a defector. The parameter q denotes the probability to know the reputation of another person. A cooperator always helps another cooperator. A cooperator helps a defector with probability $1-q$. Defectors never help. Hence, we obtain the payoff matrix

$$\begin{array}{cc} & \begin{array}{cc} C & D \end{array} \\ \begin{array}{c} C \\ D \end{array} & \begin{pmatrix} b-c & -c(1-q) \\ b(1-q) & 0 \end{pmatrix} \end{array} \tag{5}$$

We have assumed that in a pairwise interaction both individuals are donor and recipient. If only one of them is donor and the other recipient, then all entries are multiplied by 1/2, which makes no difference. Note that the payoff matrices (4) and (5) are identical (up to a factor) if we set $w=q$. Hence, indirect reciprocity leads to the same three conditions for ESS, RD and AD as direct reciprocity with q instead of w (see Table 1).

4. Network reciprocity

Spatial games can lead to cooperation in the absence of any strategic complexity (S11): unconditional cooperators can coexist with and sometimes outcompete unconditional defectors. This effect is called 'spatial reciprocity'. Spatial games are usually played on regular lattices such as square, triangular or hexagonal lattices. Network reciprocity is a generalization of spatial reciprocity to graphs. Individuals occupy the vertices of a graph. The edges denotes who interacts with whom. In principle, there can be two different graphs. The 'interaction graph' determines who plays with whom. The 'replacement graph' determines who competes with whom for reproduction, which can be genetic or cultural. Here we assume that the interaction and replacement graphs are identical. Evolutionary graph theory (S12) is a general approach to study the effect of population structure or social networks on evolutionary dynamics.

We consider a 'two coloring' of the graph: each vertex can be either a cooperator or a defector. A cooperator pays a cost, c, for each neighbor to receive a benefit, b. Defectors pay no cost and distribute no benefits. According to this simple rule the payoff, P, for each individual is evaluated. The fitness of an individual is given by $1-\omega+\omega P$ where $\omega \in [0,1]$ denotes the intensity of selection. Weak selection means that ω is much smaller than 1. Evolutionary updating works as follows: in each time step a random individual is chosen to die; the neighbors compete for the empty site proportional to their fitness.

We want to calculate the 'fixation probabilities', ρ_C, that a single cooperator starting in a random position on the graph takes over an entire population of defectors, and ρ_D, that a single defector starting in a random position on the graph takes over an entire population of cooperators. The fixation probability of a neutral mutant is $1/N$ where N is the population size. If $\rho_C > 1/N$ then selection favors the fixation of cooperators; in this case cooperation is an advantageous strategy (AD).

For regular graphs, where each individual has exactly k neighbors, a calculation using pair-approximation (S13) leads to a surprisingly simple result: if $b/c > k$ then $\rho_C > 1/N > \rho_D$ for weak selection and large N. Numerical simulations show that this result is also an excellent approximation for non-regular graphs such as random graphs and scale free networks (S13).

The pair approximation calculation (for $k \geq 3$) also leads to a deterministic differential equation which describes how the expected frequency of cooperators (and defectors) changes over time (S14). This differential equation turns out to be a standard replicator equation (S15,S16) with a modified payoff matrix. For the interaction between cooperators and defectors on a graph with average degree k this modified payoff matrix is of the form

$$\begin{array}{cc} & \begin{array}{cc} C & D \end{array} \\ \begin{array}{c} C \\ D \end{array} & \begin{pmatrix} b-c & H-c \\ b-H & 0 \end{pmatrix} \end{array} \tag{6}$$

where

$$H = \frac{(b-c)k - 2c}{(k+1)(k-2)}.$$

It is easy to see that the payoff matrix (6) leads to the condition $b/c > k$ for cooperators to dominate defectors. In this case, cooperators are also ESS, RD and AD.

5. Group selection

Many models of group selection have been proposed over the years (S17-S29). It is difficult to formulate a model which is so simple that it can be studied analytically. One such model is the following (S30). A population is subdivided into m groups. The maximum size of a group is n. Individuals interact with others in the same group. Cooperators pay a cost c for each other member of the group to receive a benefit b. Defectors pay no costs and distribute no benefits. The fitness of an individual is $1 - \omega + \omega P$, where P is the payoff and ω the intensity of selection. At each time step, an individual from the entire population is chosen for reproduction proportional to fitness. The offspring is added to the same group. If the group reaches the maximum size, it can split into two groups with a certain probability, p. In this case, a randomly selected group dies to prevent the population from exploding. The maximum population size is mn. With probability $1 - p$ the group does not divide. In this case, a random individual of that group is chosen to die.

For small p, the fixation probability of a single cooperator in the entire population is given by the fixation probability of a single cooperator in a group times the fixation probability of that group.

For the fixation probability of one cooperator in a group of $n-1$ defectors we obtain $\phi_C = [1/n][1-(b+cn-c)\omega/2]$. For the fixation probability of one cooperator group in a population of $m-1$ defector groups we obtain $\Phi_C = [1/m][1+(b-c)(m-1)\omega/2]$. Both results hold for weak selection (small ω). Note that the lower level selection within a group is frequency dependent and opposes cooperators, while the higher level selection between groups is constant and favors cooperators.

In the case of rare group splitting, the fixation probability of a single cooperator in the entire population, is given by the product $\rho_C = \phi_C \Phi_C$. It is easy to see that $\rho_C > 1/(nm)$ leads to $b/c > 1 + [n/(m-2)]$. If this inequality holds, then cooperators are advantageous (and defectors disadvantageous) once both levels of selection are combined.

For a large number of groups, $m \gg 1$, we obtain the simplified condition $b/c > 1+n/m$. The benefit to cost ratio of the altruistic act must exceed one plus the ratio of group size over the number of groups. The model can also be extended to include migration, which can be seen as 'noise' of group selection. In this case, the relevant criterion is $b/c > 1+\mu+n/m$, where μ is the average number of migrants accepted over the life-time of a group (S30).

Now comes a surprising move that allows us to reduce the evolutionary dynamics on two levels of selection to a single two-person game on one level of selection. The payoff matrix that describes the interactions within a group is given by

$$\begin{array}{cc} & \begin{array}{cc} C & D \end{array} \\ \begin{array}{c} C \\ D \end{array} & \begin{pmatrix} b-c & -c \\ b & 0 \end{pmatrix} \end{array} \tag{7}$$

Between groups there is no game dynamical interaction in our model, but groups divide at rates that are proportional to the average fitness of individuals in that group. Therefore one can say that cooperator groups have a constant payoff $b-c$, while defector groups have a constant payoff 0. Hence, in a sense the following 'game' between groups is happening

$$\begin{array}{cc} & \begin{array}{cc} C & D \end{array} \\ \begin{array}{c} C \\ D \end{array} & \begin{pmatrix} b-c & b-c \\ 0 & 0 \end{pmatrix} \end{array} \tag{8}$$

Remember also that the 'fitness' of a group is $1-\omega+\omega P$ where P is its 'payoff'. We can now multiply the first matrix by the group size, n, and the second matrix by the number of groups, m, and add the two matrices. The result is

$$\begin{array}{cc} & \begin{array}{cc} C & D \end{array} \\ \begin{array}{c} C \\ D \end{array} & \begin{pmatrix} (b-c)(n+m) & bm - c(m+n) \\ bn & 0 \end{pmatrix} \end{array} \tag{9}$$

In this simple 2×2 game, cooperators dominate defectors if $b/c > 1 + (n/m)$. In this case, cooperators are also ESS, RD and AD.

Interestingly, the method also gives the right answer for two arbitrary payoff matrices describing the games on the two levels. The intuition for adding the two matrices multiplied with the respective population size is as follows. For fixation of a new strategy in a homogeneous population using the other strategy, first the game dynamics within one group (of size n) have to be won and then the game dynamics between m groups have to be won. For weak selection and large m and n, the overall fixation probability is the same as the fixation probability in the single game using the combined matrix (9) and population size, mn. The stochastic process on two levels can be studied by a standard replicator equation using the combined matrix.

Finally, note that payoff matrix (9) for group selection is structurally identical to the payoff matrix (3) for kin selection if we set $r = m/(m+n)$ pointing to yet another interesting relationship between kin selection and group selection (S31).

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