The importance of selection rate

in the evolution of cooperation

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Abstract

How cooperation emerges in human societies is still a puzzle. Evolutionary game theory has been the standard framework to address this issue. In most models, every individual plays with all others, and then reproduce and die according to what they earn. This amounts to assuming that selection takes place at a slow pace with respect to the interaction time scale. We show that, quite generally, if selection speeds up, the evolution outcome changes dramatically. Thus, in games such as Harmony, where cooperation is the only equilibrium and the only rational outcome, rapid selection leads to dominance of defectors. Similar non trivial phenomena arise in other binary games and even in more complicated settings such as the Ultimatum game. We conclude that the rate of selection is a key element to understand and model the emergence of cooperation, and one that has so far been overlooked.

Keywords   Selection Rate, Cooperation, Evolution, Game Theory

Short Title   Selection Rate and Evolution of Cooperation

1 Introduction

A fundamental, profound and broad-ranging unsolved question is how cooperation among animals and humans has evolved (Darwin, 1871; Maynard-Smith & Szathmáry, 1995; Pennisi, 2005). From the point of view of natural selection, the question to be answered is why cooperation may be a better strategy for survival or reproduction than a more selfish behavior. For this reason evolutionary game theory has been the mathematical framework that has provided the deepest insights into this issue (Axelrod & Hamilton, 1981; Gintis, 2000; Nowak & Sigmund, 2004). Simple games such as the Prisoner's Dilemma (Axelrod & Hamilton, 1981), the Snowdrift game (Sugden, 1986) or the Stag-Hunt game (Skyrms, 2003) have been the subject of intense experimental and theoretical work along this line (Camerer, 2003). One of the main achievements of this approach has been to show that the emergence of cooperation is sensitive to whether populations are well-mixed, such as in replicator dynamics evolution (Taylor & Jonker, 1978; Hofbauer & Sigmund, 1998; Gintis, 2000), or spatially structured (Nowak & May, 1992; Doebeli & Knowlton, 1998; Page, Nowak & Sigmund, 2000; Hauert & Doebeli, 2004). Co-evolution of agents and networks (Eguíluz et al., 2005; Zimmermann & Eguíluz, 2005) and finite population effects (Nowak et al., 2004) are also relevant factors to take into account inasmuch as they may enhance or hinder cooperation. However, none of these approaches has considered the influence of different selection rates so far, surely because ever since Darwin it has been acknowledged that natural selection acts at a very slow pace. Nevertheless, recent experiments show that this may not always be the case (Hendry & Kinnison, 1999; Hendry et al., 2000; Yoshida et al., 2003): under certain circumstances (e.g. strong predation or captive breeding) evolution selects for a new trait in just a few generations.

Generally, research on evolutionary game theory is based on a population of individuals or agents that interact by playing a game. In the absence of spatial structure, it is posited that every agent plays the game against every other one, and then reproduction proceeds according to the payoffs earned during the game stage. For large populations, this amounts to saying that every player gains the payoff of the game averaged in the current distribution of strategies. In terms of time scales, such an evolution corresponds to a regime in

which selection takes place at a much slower rate than the interaction between agents. However, these two time scales need not be different in general and, in fact, for many specific applications they can arguably be of the same order (Hendry & Kinnison, 1999; Hendry et al., 2000; Yoshida et al., 2003).

Our main aim in this work is to show that the pace at which selection acts on the population is crucial for the appearance and stability of cooperation. Even in non-dilemma games such as Harmony (Litch, 1999), where cooperation is the only possible rational outcome, defectors may be selected for if population renewal is very rapid. Similar results hold true for several others games, thus pointing out the necessity to include a discussion on the rate of selection, compared to the rate of interaction, in any study about cooperation or any other situation modelled by evolutionary games.

2 Setting: Dynamics and games

When selection acts at a much slower rate than interaction, a widely used tool to analyze frequency-dependent selection without mutation is replicator dynamics (Taylor & Jonker, 1978; Hofbauer & Sigmund, 1998; Gintis, 2000). Replicator dynamics assumes a well-mixed population where all agents interact before selection, with a per capita growth rate of each strategy proportional to its fitness (the payoff earned in a round of games between selection events). However, as stated in the previous section, we aim to understand the effects of different selection rates. To this end, we introduce the following new dynamics: There is a population with N players. A pair of individuals is randomly selected for playing, earning each one an amount of fitness according to the rules of the payoff matrix of the game. This game act is repeated s times, choosing a new random pair of players in each occasion.

After every s games, selection takes place. Following Nowak et al. (2004), we have chosen Moran dynamics (Moran, 1962) to model selection in a finite population. One individual among the population of N players is chosen for reproduction proportionally to its fitness, and its offspring replaces a randomly chosen individual. As the fitness of all players is set to zero before the following round of s games, the overall result

is that all players have been replaced by one descendant, but the player selected for reproduction has had a reproductive advantage of doubling its offspring at the expense of the randomly selected player. It is worth noting that the population size N is therefore constant along the evolution.

The parameter s controls the time scales of the model, i.e. reflects the relation between the rate of selection and the rate of interaction. For $s \ll N$ selection is very fast and very few individuals interact between selection events. Higher values of s represent proportionally slower rates of selection. Thus, when $s \gg N$ selection is very slow and population is effectively well-mixed.

It only remains to specify the games we will be studying in this paper, namely binary games. These have been widely used in evolutionary game theory, because of their simplicity and amenability for both analytical treatment and computer simulation. A symmetrical binary game is completely defined by its 2×2 payoff matrix (or normal form, see e.g. Gintis (2000))

$$
\begin{array}{cc}
 & \begin{array}{cc} C & \quad D \end{array} \\
\begin{array}{c} C \\ D \end{array} & \left(\begin{array}{cc} a & c \\ b & d \end{array} \right),
\end{array}
\tag{1}
$$

whose rows give the payoff obtained by each strategy when confronted to all others including itself. When interpreted as a model for the emergence of cooperation, C and D denote, respectively, the strategies "cooperate" and "defect". Different kinds of games have been defined according to the relations between the four coefficients of the matrix (Rapoport & Guyer, 1966).

3   Results

The dynamics we introduced in the previous section can be studied analytically and exactly in the following manner: Let us denote by $0 \leq n \leq N$ the number of cooperators present in the population. We calculate the probability x_n of ending up in state $n = N$ (i.e., all players cooperate) when starting in state $n < N$. For $s = 1$ and $s \to \infty$, we obtain an exact, analytical expression for x_n. For arbitrary values of s, such a closed form

cannot be found; however, it is possible to carry out a combinatorial analysis of the possible combinations

of rounds and evaluate, numerically but exactly, x_n. See appendix A for the detailed mathematics.

As our first and most striking example of the influence of the selection rate, we will start by considering

the Harmony game (Litch, 1999), determined by $a > c > b > d$. The *only* Nash equilibrium of this game

is (C, C), as it is obvious from the payoffs: The best option for both players is to cooperate, which yields

the maximum payoff for each one. When this game is framed in our dynamical model, Fig. 1a shows that

the rationally expected outcome, namely that the final population consists entirely of cooperators, is not

achieved for small and moderate values of the selection rate parameter s. For the smallest values, only when

starting from a population largely formed by cooperators there is some chance of reaching full cooperation;

most of the times, defectors will eventually prevail and invade the whole population. This counterintuitive

result may arise even for values of s comparable to the population size, by choosing suitable payoffs (not

shown). Interestingly, the main result that defection is selected for small values of s does not depend on the

population size N; only details such as the shape of the curves (cf. Fig. 1b) are modified by N.

[Figure 1 here]

In the preceding paragraph we have chosen the Harmony game to discuss the effect of the rate of se-

lection, but this effect is very general and appears in many other games. To see this, consider the example

of the Stag-Hunt game (Skyrms, 2003), with payoffs $a > c > d > b$. This is the paradigmatic situation

of a 2×2 game with two Nash equilibria in pure strategies, one Pareto-dominant (Gintis, 2000) (C, C), in

which players maximize their payoffs, and the other risk-dominant (Gintis, 2000) (D, D), in which players

minimize the possible damage resulting from a defection of the partner. Which of these equilibria is selected

has been the subject of a long argument in the past, and rationales for both of them can be provided. As Fig.

2 shows, results for small s are completely different from those obtained for larger values. Indeed, we see

that for $s = 1$, all agents become defectors except for initial densities of cooperators close to 1. However,

for values of $s \gtrsim N$ the resulting curve is quasi-symmetrical, reflecting a much more balanced competition

between both strategies.

[Figure 2 here]

Yet another example of the importance of the selection rate is provided by the Snowdrift game (Sugden, 1986), defined by the payoffs $c > a > b > d$. Also known as Chicken or Hawk-Dove, it is a dilemma game not unrelated to, but different from, the Prisoner's dilemma. Fig. 3 shows that for small values of s defectors are selected for almost any initial fraction of cooperators. When s increases, we observe an intermediate regime where both full cooperation and full defection have a nonzero probability, which, interestingly, is almost independent of the initial population. And, for large enough s, full cooperation is almost always achieved.

[Figure 3 here]

Finally, we show for completeness the results for the most ubiquitous game in studies about the evolution of cooperation: the Prisoner's Dilemma (Axelrod & Hamilton, 1981), with payoffs $c > a > d > b$. As is well known, in this game the rational choice is to defect. The effect of a small number of games, shown in Fig. 4, is to bias the game even more towards defection. In any case, the initial density of cooperators must be very large for cooperation to have some chance of becoming the selected strategy, but for small values of s this requirement is most severe. Therefore, the parameter s does not change the qualitative behavior of the Prisoner's Dilemma, alhtough once again low s works against cooperation.

[Figure 4 here]

Similar results are to be found in almost any binary game. Indeed, it can be shown that D strategists are selected for when the payoffs satisfy $b < c$ in the extreme case $s = 1$, irrespective of a, d, or the population size N (cf. Eq. (9) in appendix A). Larger s values can not be analyzed in such a simple manner and, in particular, the corresponding results depend on all four parameters of the payoff matrix.

The reason for this dramatic influence of the parameter s resides in the resulting fitness distribution over the population. For large values of s ($s \gtrsim N$), most agents have played between selection events, and as a

consequence most of the population has nonzero payoff, which in turn implies a nonzero probability of being selected for reproductive advantage. On the contrary, with small s ($s \ll N$) the distribution concentrates on the few players that have actually played, these ones being the only candidates for selection. This results in a completely different probabilistic scenario, with the consequences reflected in the results above.

As a specific example, consider the Stag-Hunt game shown in Fig. 2, for the particular initial number of cooperators $n = N/2$. With values of $s \gtrsim 100$, the payoffs are distributed to a large set of pairs of players, with approximate frequencies of $1/4$ (C, C), $1/4$ (D, D) and $1/2$ (C, D) or (D, C). Given that the payoff matrix fulfills $a + b = c + d$, both strategies collect a practically equal amount of fitness, thus with no reproductive advantage for any strategy and then $x_n \approx 0.5$. However, considering the case of $s \ll 100$, only a few pairs are selected to play. With pairs (C, C) or (D, D), the reproductive advantage is obviously the same, as only one strategy receives all the fitness. But pairs (C, D) or (D, C) will draw a strong advantage to defectors, given the relation $b/c = 1/5$, which in the end causes $x_n \approx 0$. Results for other games can be understood in a similar way.

4   Discussion and conclusion

Let us now summarize our main findings. We have shown that selection rate plays a crucial role in determining the fate of cooperation, by studying how evolutionary dynamics in a Moran setting depends on the number of times the game is played between selection events. We have seen that even in a game as simple as Harmony, where cooperating is the only rational outcome, rapid selection leads to the success of defectors. We have observed similar behavior in other examples such as the Snowdrift and the Stag-Hunt games. In binary games about cooperation situations (including Prisoner's Dilemma), we have found that rapid selection rates generally lead to the promotion of defectors. In other contexts the interpretation of the results would be different (such as a choice of the risk-dominant coordination option in the Stag-Hunt game) but the effect of the selection rate will undoubtedly be there. It is important to stress that the results are fully

analytic, involve no approximation, and apply to both finite and infinite populations.

Although in this paper we have worked only in the framework of binary games, we believe that our main claim, namely that different time scales for interaction and selection can modify the outcome of evolution, is relevant to evolutionary games in general. Consider, for instance, the Ultimatum game (Güth, Schmittberger & Schwarze, 1982; Fehr & Fischbacher, 2003), which is one of the most frequently used games in theoretical and experimental studies of cooperation. This game is much more complex than the previous binary games, as it asymmetrical, i.e. each individual of the pair of interacting players has a role, and there is a large number of strategies, not just two. In the Ultimatum game, under conditions of anonymity, two players are shown a sum of money. One of the players, the "proposer", is asked to offer an amount of this sum to the other, the "responder". The proposer can make only one offer, which the responder can accept or reject. If the offer is accepted, the money is shared accordingly (the proposer receives the rest of the money); if rejected, both players gain nothing. Since the game is played only once (no repeated interactions) and anonymously (no reputation gain), a self-interested responder will accept any amount of money offered whereas a self-interested proposer will offer the minimum possible amount which will be accepted. This is precisely the outcome predicted by the replicator dynamics in a well-mixed population: the final population will consist only of fully rational agents which offer the smallest possible amount and accept any amount (Page & Nowak, 2002). On the contrary, relaxing the assumption of a well-mixed population in favor of a dynamics that allows a faster selection rate changes this result absolutely. Proceeding similarly to the binary games of the previous section, pairs of players are randomly selected to interact, in series of s rounds between reproduction-selection events. Exhaustive simulations of different versions of the game with this kind of dynamics have shown that fair split becomes then the dominant strategy (Sánchez & Cuesta, 2005). An analytical study of this problem that confirms the simulation results is under way (Rodríguez, Cuesta & Sánchez, 2006).

Finally, the most important implication of our results is that, in studies about the emergence of cooperation, the rate of selection is an extremely influential parameter and very often leads to non-trivial, unexpected

outcomes. Of course, the scope of this result is not limited to cooperation among humans, as cooperative phenomena have been reported for many other species including bacteria (Griffin, West & Buckling, 2004). In fact, the research reported here stresses the importance of selection rates for evolutionary game theory, for all the situations it models (not only cooperation) and for evolutionary theory in general (Hendry & Kinnison, 1999; Hendry et al., 2000; Yoshida et al., 2003).

A Exact analytical results

In Moran dynamics, at each time step an individual is chosen for reproduction proportional to its fitness, and one identical offspring is produced that replaces another randomly chosen individual. In a population of N individuals where n are C strategists (cooperators) and $N - n$ are D strategists (defectors), we have a Markov process with a tridiagonal transition matrix (a birth-death process (Karlin & Taylor, 1975)) given by

$$P_{n,n+1} = \frac{N-n}{N} \left\langle \frac{W_n^C}{W_n^C + W_n^D} \right\rangle, \tag{2}$$

$$P_{n,n-1} = \frac{n}{N} \left\langle \frac{W_n^D}{W_n^C + W_n^D} \right\rangle, \tag{3}$$

and $P_{n,n} = 1 - P_{n,n+1} - P_{n,n-1}$, where W_n^α is the fitness earned by cooperators ($\alpha = $ C) or defectors ($\alpha = $ D) after s games, and $\langle \cdot \rangle$ denotes the average over realizations of the process. The dependence of the calculation on the selection rate, i.e., on s, enters only in these two quantities.

The solution to this birth-death process is obtained in a standard manner (Karlin & Taylor, 1975). Let us denote by x_n the probability of ending up in state $n = N$ when starting off from state n. Then we have

$$x_n = P_{n,n+1} x_{n+1} + P_{n,n} x_n + P_{n,n-1} x_{n-1} \tag{4}$$

with boundary conditions $x_0 = 0$, $x_N = 1$. The solution to this equation is given by

$$x_n = \frac{Q_n}{Q_N}, \qquad Q_n = 1 + \sum_{j=1}^{n-1} \prod_{i=1}^{j} \frac{P_{i,i-1}}{P_{i,i+1}} \quad (n > 1), \qquad Q_1 = 1. \tag{5}$$

When the ratio of the transition probabilities can be written as

$$\frac{P_{n,n-1}}{P_{n,n+1}} = \frac{\alpha n + \beta}{\alpha(n+1) + \gamma}, \qquad \alpha \neq 0, \tag{6}$$

equation (5) has the closed form

$$Q_n = \frac{\gamma}{\gamma - \beta} \left[1 - \binom{n + (\beta/\alpha)}{n} \binom{n + (\gamma/\alpha)}{n}^{-1} \right], \tag{7}$$

where the generalized binomial coefficient is defined as $\binom{x}{n} = x(x-1)\cdots(x-n+1)/n!$.

For the extreme case $s = 1$ there are two possible outcomes of the variable $W_n^{\mathrm{C}}/(W_n^{\mathrm{C}} + W_n^{\mathrm{D}})$, namely $2a/2a$, with probability $n(n-1)/N(N-1)$ (that of pairing two Cs), and $b/(b+c)$, with probability $2n(N-n)/N(N-1)$ (that of pairing a C and a D). Thus, we have

$$\left\langle \frac{W_n^{\mathrm{C}}}{W_n^{\mathrm{C}} + W_n^{\mathrm{D}}} \right\rangle = \frac{n}{N(N-1)} \left[\frac{c-b}{c+b}n + \frac{2b}{c+b}N - 1 \right]. \tag{8}$$

Using a similar reasoning for $W_n^{\mathrm{D}}/(W_n^{\mathrm{C}} + W_n^{\mathrm{D}})$ we end up with

$$\frac{P_{n,n-1}}{P_{n,n+1}} = \frac{(c-b)n + (c+b)N - c - b}{(c-b)n + 2bN - c - b}, \tag{9}$$

which has the form (6). Notice that if $b < c$ then $P_{n,n+1} < P_{n,n-1}$ regardless the values of a and d.

In the opposite limit $s \to \infty$ every player plays with every other an infinite number of times, so

$$\lim_{s\to\infty} \left\langle \frac{W_n^{\alpha}}{W_n^{\mathrm{C}} + W_n^{\mathrm{D}}} \right\rangle = \frac{\overline{W_n^{\alpha}}}{\overline{W_n^{\mathrm{C}}} + \overline{W_n^{\mathrm{D}}}}, \qquad \alpha = \mathrm{C, D}, \tag{10}$$

where $\overline{W_n^{\alpha}}$ denotes the payoff of α strategists when every player plays with every other once. Thus, in this case

$$\frac{P_{n,n-1}}{P_{n,n+1}} = \frac{(c-d)n + d(N-1)}{(a-b)n + bN - a}, \tag{11}$$

which has the form (6) only when $a + d = c + b$.

For other values of s, W_n^{C} and W_n^{D} can be computed through a combinatorial enumeration of all possible pairings, and the resulting exact expression (too cumbersome to be included here) can then be evaluated numerically.

Figure 1   Probability x_n of ending up with all cooperators starting from n cooperators, for different values

of s, in the Harmony game. a) For the smallest values of s, full cooperation is only reached if almost all

agents are initially cooperators. Values of s of the order of 10 show a behavior much more favorable to

cooperators. In this plot, the population size is $N = 100$. b) Taking a population of $N = 1000$, we observe

that the range of values of s for which defectors are selected does not depend on the population size, only the

shape of the curves does. Parameter choices are: Number of games between selection events, s, as indicated

in the plots; payoffs for the Harmony game, $a = 11$, $b = 2$, $c = 10$, $d = 1$. The dashed line corresponds to

a probability to reach full cooperation equal to the initial fraction of cooperators and is shown for reference.

Figure 2   Same as Fig. 1, for the Stag-Hunt game. The probability x_n of ending up with all cooperators when starting from n cooperators, is very low if s is small, and as s increases it tends to a quasi-symmetric distribution around $1/2$. Parameter choices are: Population, $N = 100$; number of games between selection events, s, as indicated in the plot; payoffs for the Stag-Hunt game, $a = 6, b = 1, c = 5, d = 2$.

Figure 3 Same as Fig. 1, for the Snowdrift game. The probability x_n of ending up with all cooperators starting from n cooperators is almost independent of n, except for very small or very large values. Small s values lead once again to selection of defectors, whereas cooperators prevail more often as s increases. Parameter choices are: Population, $N = 100$; number of games between selection events, s, as indicated in the plot; payoffs for the Snowdrift game, $a = 1$, $b = 0.35$, $c = 1.65$, $d = 0$.

Figure 4   Same as Fig. 1, for the Prisoner's Dilemma, but only the rightmost part of the n axis is shown (smallest n values have a negligible chance to give rise to cooperation). In this game, small values of s lead to an even larger possibility of defection. Parameter choices are: Population, $N = 100$; number of games between selection events, s, as indicated in the plot; payoffs for the Prisoner's Dilemma, $a = 1$, $b = 0$, $c = 1.2$, $d = 0.1$.

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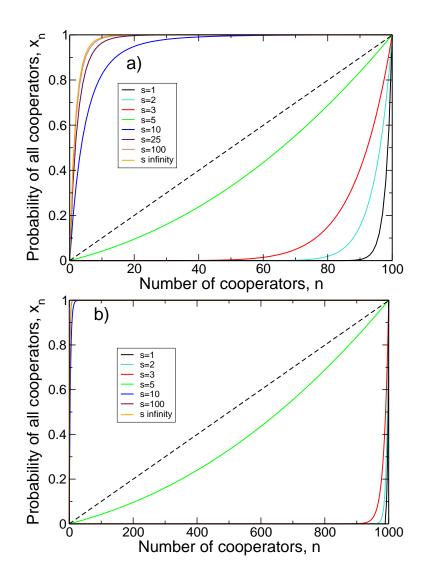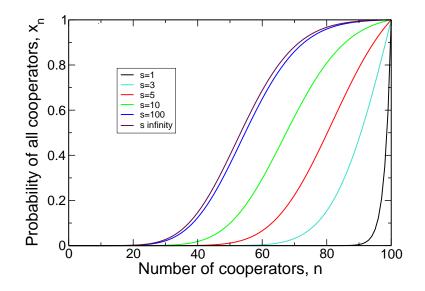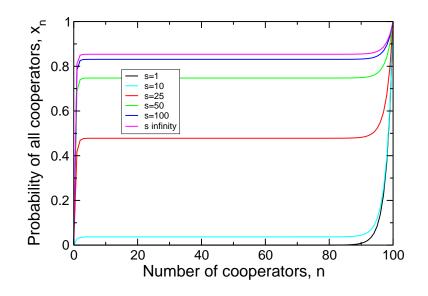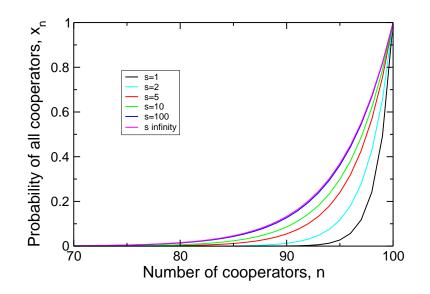
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