

Tel: +43 2236 807 342 Fax: +43 2236 71313 E-mail: publications@iiasa.ac.at

Web: www.iiasa.ac.at

Interim Report

IR-10-028

Freedom, enforcement, and the social dilemma of strong altruism

Hannelore De Silva (hannelore.desilva@wu.ac.at) Christoph Hauert (christoph.hauert@math.ubc.ca) Arne Traulsen (traulsen@evolbio.mpg.de) Karl Sigmund (ksigmund@iiasa.ac.at)

Approved by

Ulf Dieckmann Program Leader, EEP

June 2011

Freedom, enforcement, and the social dilemma of strong altruism

Hannelore Brandt ¹, Christoph Hauert ^{2,3}, Arne Traulsen ⁴, & Karl Sigmund ^{5,6}

Vienna University of Economics and Business Administration, A-1090 Vienna, Austria
 Program for Evolutionary Dynamics, Harvard University,

 One Brattle Square, Cambridge, MA 02138, USA

 ³Department of Mathematics, University of British Columbia,

 1984 Mathematics Road, Vancouver B.C. Canada V6T 1Z2
 ⁴ Max-Planck-Institute for Evolutionary Biology, 24306 Plön, Germany
 ⁵ Faculty of Mathematics, University of Vienna, A-1090 Vienna, Austria
 ⁶ International Institute for Applied Systems Analysis, A-2361 Laxenburg, Austria

November 22, 2007

Corresponding author:

Hannelore Brandt

Vienna University of Economics and Business Administration, A-1090 Vienna, Austria e-mail: hannelore.brandt@wu-wien.ac.at, phone: +43 1 31336 5017, fax: +43 1 3100 580

Abstract

Cooperation in joint enterprises poses a social dilemma. How can altruistic behaviour be sustained if selfish alternatives provide a higher payoff? This social dilemma can be overcome by the threat of sanctions. But a sanctioning system is itself a public good and poses a second-order social dilemma. In this paper, we show by means of deterministic and stochastic evolutionary game theory that imitation-driven evolution can lead to the emergence of cooperation based on punishment, provided the participation in the joint enterprise is not compulsory. This surprising result – cooperation can be enforced if participation is voluntary – holds even in the case of 'strong altruism', when the benefits of a player's contribution are reaped by the other participants only.

Keywords: evolutionary game theory; public goods games; cooperation; costly punishment; social dilemma; strong altruism; voluntary interactions;

JEL Classification code: C73

1 Introduction

Team efforts and other instances of 'public good games' display a social dilemma, since each participant is better off by not contributing to the public good. If players maximise their utility in a rational way, or if they simply imitate their successful co-players, they will all end up by not contributing, and hence by failing to obtain a collective benefit (Samuelson 1954, Hardin 1968). It is only through positive or negative incentives directed selectively toward specific individuals in the team (e.g. by imposing sanctions on cheaters or dispensing rewards to contributors) that the joint effort can be maintained in the long run (Olson 1965, Ostrom 1990).

But how can the sanctioning system be sustained? It is itself a public good (Yamagishi 1986). This creates a 'second order social dilemma'. by appealing to localised interactions (Brandt et al 2003, Nakamaru and Iwasa 2005), group selection (Boyd et al 2003), or the effects of reputation (Sigmund et al 2001, Hauert et al 2004) and conformism (Henrich and Boyd 2001), the stability of a well-established system of incentives can be explained under appropriate conditions. However, the emergence of such a system has long been considered an open problem (Hammerstein 2003, Gardner and West 2004, Colman 2006, see also Fowler 2005a).

A series of papers (Fowler 2005b, Brandt et al 2006, Hauert et al 2007, Boyd and Mathew 2007, Hauert et al 2008) has recently attempted to provide a solution by considering team efforts which are non-compulsory. If players can decide whether to participate in a joint enterprise or abstain from it, then costly punishment can emerge and prevail for most of the time, even if the population is well-mixed. If the same public good game is compulsory, punishers fail to invade and defection dominates.

Roughly speaking, the joint enterprise is a venture. It succeeds if most players contribute, but not if most players cheat. The availability of punishment turns this venture into a game of cops and robbers. If the game is compulsory, robbers win. But if the game is voluntary, cops win.

This effect is due to a rock-paper-scissors type of cycle between contributing, defecting and abstaining. Players who do not participate in the joint enterprise can rely on some autarkic income instead. We shall assume that their income is lower than the payoff obtained from a joint effort if all contribute, but higher than if no one contributes. (Only with this assumption does the joint effort turn into a venture.) In a finite population, cooperation evolves time and again, although it will then be quickly subverted by defection, which in turn gives way to non-participation (Hauert et al 2002a,b, Semmann et al 2004). If costly punishment

of defectors is included in the game, then one of the upsurges of cooperation will lead to a population dominated by punishers, and such a regime will last considerably longer before defectors invade again. Cooperation safeguarded by the costly punishment of defectors dominates most of the time.

This model has been based on the classical 'public good game' used in many theoretical and experimental investigations (Boyd and Richerson 1992, Camerer 2003, Fehr and Gächter 2000, 2002, Hauert et al 2005, Brandt et al 2003, Nakamaru and Iwasa 2004). It suffers from a weakness which makes it less convincing than it could be. Indeed, whenever the interacting groups are very small (as happens if most players tend not to participate in the joint effort), the social dilemma disappears; it only re-appears when the game attracts sufficiently many participants. In a frequently used terminology, cooperation in such a public good game is 'weakly altruistic', because cooperators receive a return from their own contribution (Kerr and Godfrey-Smith 2002, Fletcher and Zwick 2004, 2007, see also Wilson 1990 for a related notion).

In this note, we show that the same result – in compulsory games, robbers win; in optional games cops do – holds also for 'strong altruism', and more precisely even in the 'others-only' case, i.e. when *no* part of the benefit returns to the contributor. It is always better, in that case, not to contribute. Nevertheless, cooperation based on costly punishment emerges, if players can choose not to participate. If the game is compulsory, defectors will win.

According to the 'weak altruism' model, players have to decide whether or not to contribute an amount c, knowing that the joint contributions will be multiplied by a factor r>1 and then divided equally among all S participants. Rational players understand that if they invest an amount c, their personal return is rc/S. If the group size S is larger than r, their return is smaller than their investment, and hence they are better off by not contributing. In that case, we encounter the usual social dilemma: a group of selfish income maximisers will forego a benefit, by failing to earn (r-1)c each. The proverbial 'invisible hand' fails to work. However, if the group size S is smaller than r, selfish players will contribute, since the return from their personal investment c is larger than their investment. In that case, the social dilemma has disappeared.

In all the models of voluntary public good games mentioned so far, it has been assumed that a random sample of the population of size N is faced with the decision whether or not to participate in a public good game of the 'weakly altruistic' type described above. If most players tend not to participate, the resulting teams will mostly have a small size S, and therefore the social dilemma will not hold. (This effect of population size is well-known, see eg. Pepper 2000). Small won-

der, then, that cooperation emerges in such a situation. A well-meaning colleague even called it a 'sleight of hand'.

In the 'strong altruism' variant considered here, players have to decide whether or not to contribute an amount c, knowing that it will be multiplied by a factor r>1 and then divided equally among all the *other* members of the group. A player's contribution benefits the *others only*. The social dilemma always holds, in this case, no matter whether the group is large or small. We shall show that nevertheless, a rock-paper-scissor cycle leading to cooperation still emerges, and that the population will be dominated by players who punish defectors. This is a striking instance of the general phenomenon that complex dynamics can play an important role even in very simple types of economic models (see eg Kirman et al 2004).

The idea of considering a public good game of 'others only' type is not new. It was used in Yamagishi 1986, a brilliant forerunner to Fehr and Gächter 2000. Yamagishi's motivation was interesting: he made 'public good game' experiments using small groups (the small size is almost a necessity, due to practical reasons), but he wanted to address the issue of public goods in very large groups. Since in large groups, the effect of an individual decision is almost negligible, Yamagishi opted for a treatment which excludes any return from the own contribution.

In this paper, we investigate the evolutionary dynamics of voluntary public good games with punishment, using for the public good the 'others-only' variant \mathbf{OO} rather than the 'self-returning' (or 'self-beneficial') variant \mathbf{SR} . We consider the evolutionary dynamics in well mixed populations which can either be infinite (in which case we analyse the replicator dynamics, see Hofbauer-Sigmund 1998), or of a finite size M (in which we case we use the Moran process, see Nowak 2005, Nowak et al. 2004, Imhof et al. 2005). We will show that for finite populations, voluntary participation is just as efficient for 'strong altruism' as for 'weak altruism'. Thus even if the social dilemma holds consistently, cooperation based on costly punishment emerges.

In the usual scenarios, it is well-known that while weakly altruistic traits can increase, strongly altruistic traits cannot. Our paper shows, in contrast, that strongly altruistic traits can spread if players can inflict costly punishment on defectors *and* if they can choose not to participate in the team effort. In a sense to be explained later, the mechanism works even better than for weak altruism.

2 The model

We consider a well-mixed population, which is either infinite or of finite size M. From time to time, a random sample of size N is presented with the opportunity to participate in a 'public good game'. Those who decline (the non-participants) receive a fixed payoff σ which corresponds to an autarkic income. Those who participate have to decide whether to contribute a fixed amount c. In the 'self-returning' case \mathbf{SR} , the contribution will be multiplied by a factor r and the resulting 'public good' will be shared equally among all participants of the game; in the 'others-only' case \mathbf{OO} , it will be shared among all the other participants of the game. (We note that in this case, if there are only two participants, we obtain a classical Prisonners' Dilemma scenario, which can be interpreted as a donation game: namely whether or not to provide a benefit b = rc to the co-player at a cost c to oneself, with r > 1).

In both types of public good games, the participants obtain their share irrespective of whether they contributed or not (the public good, in this sense, is non-excludable). If only one player in the sample decides to participate, we shall assume that the public good game cannot take place. Such a player obtains the same payoff σ as a non-participant. In addition, participants in the game can also punish the cheaters in their group. Thus we consider four strategies: (1) non-participants; (2) cooperators, who participate and contribute, but do not punish; (3) defectors, who participate, but neither contribute nor punish; and (4) punishers, who participate, contribute, and punish the defectors in their group. We denote the relative frequencies of cooperators, defectors, non-participants and punishers in the infinite population by x, y, z and w, and their numbers in the finite population by x, y, z and w, respectively (with x + y + z + w = M, and x + y + z + w = 1). Their frequencies in a given random sample of size N are denoted by N_x, N_y, N_z and N_w respectively (with $N_x + N_y + N_z + N_w = N$, and $N_x + N_y + N_w = S$ the number of participants in the public good game).

Following the usual models, we shall assume that each punisher imposes a fine on each defector; such punishment costs γ to the punisher and β to the punished player, so that punishers have to pay γN_y and defectors βN_w . The total payoff is the sum of a public good term and a punishment term.

3 The infinite population case

Let us assume first that the population size is infinite. Each players' payoff is the sum of a public good term (which is σ if the player does not participate in the joint effort) and a punishment term (which is 0 for non-participants and cooperators). The expected punishment terms are easily seen to be $-\beta w(N-1)$ for the defectors and $-\gamma y(N-1)$ for the punishers.

As shown in Brandt et al 2006, the payoff stemming from the public good is given in the **SR** case by

$$\sigma z^{N-1} + rc(x+w)F_N(z)$$

for the defectors, and

$$\sigma z^{N-1} + c(r-1)(1-z^{N-1}) - rcyF_N(z)$$

for the cooperators and the punishers, with

$$F_N(z) = \frac{1}{1-z} (1 - \frac{1-z^N}{N(1-z)}).$$

The payoff for non-participants is σ . As shown in the appendix, the payoff stemming from the public good in the **OO** case is

$$\sigma z^{N-1} + (1 - z^{N-1}) \frac{rc(x+w)}{1-z}$$

for a defector. Cooperators and punishers obtain from the public good the same term, reduced by $c(1-z^{N-1})$ (this is the cost of contributing, given that there is at least one co-player).

Let us now consider the replicator dynamics for the **OO**-case. After removing the common term σz^{N-1} from all payoffs, we obtain for the expected payoff values of non-participants, defectors, cooperators and punishers

$$P_z = (1 - z^{N-1})\sigma$$

$$P_y = (1 - z^{N-1})(rc\frac{x+w}{1-z}) - \beta w(N-1)$$

$$P_x = (1 - z^{N-1})(rc\frac{x+w}{1-z} - c)$$

$$P_w = (1 - z^{N-1})(rc\frac{x+w}{1-z} - c) - \gamma y(N-1)$$

In the interior of the simplex S_4 there is no fixed point since $P_w < P_x$. hence all orbits converge to the boundary (see Hofbauer and Sigmund 1998). On the face w=0, we find a rock-paper-scissors game, as in the **SR** case: non-participants are dominated by cooperators who are dominated by defectors who are dominated by non-participants. In the interior of this face there is no fixed point, since $P_x < P_y$; all orbits are homoclinic orbits, converging to the non-participant state z=1 if time converges to $\pm \infty$ (see Fig.1). This contrasts with the **SR** case, where the face w=0 is filled with periodic orbits for r>2 (see also the corresponding phase portraits in Brandt et al 2006).

It is easy to see that punishers dominate non-participants, and that punishers and defectors form a bistable system if $c+\gamma < \beta(N-1)$. The edge of cooperators and punishers (y=z=0) consists of fixed points, those with

$$w > \frac{c}{\beta(N-1)}$$

are saturated and hence Nash-equilibria. Depending on the initial condition, orbits in the interior of the simplex converge either to the segment of Nash-equilibria or to the state consisting only of non-participants.

Altogether, this system has a remarkable similarity which the replicator system for **SR** originally proposed by Fowler 2005b (and criticised by Brandt et al 2006), provided Fowler's second-order punishment term is neglected.

4 Finite populations

We now turn to finite populations of size M. As learning rule, we shall use the familiar Moran process: we assume that occasionally, players can update their strategy by copying the strategy of a 'model', namely a player chosen at random with a probability which is proportional to that player's fitness. This fitness in turn is assumed to be a convex combination (1-s)B+sP, where B is a 'baseline fitness' (the same for all players), P is the payoff (which depends on the strategy, and the state of the population), and $0 \le s \le 1$ measures the 'strength of selection', i.e. the importance of the game for overall fitness. (We shall always assume s small enough to avoid negative fitness values.) This learning rule corresponds to a Markov process. The process has four absorbing states, namely the homogeneous

states: if all players use the same strategy, imitation leads to nothing new. Hence we assume that with a small 'mutation probability' μ , players chose a strategy at random, rather than imitate another player. This yields an irreducible Markov chain with a unique stationary distribution. (We emphasize that the terms 'selection' and 'mutation' are used for convenience only, and do not imply a genetic transmission of strategies.)

In the limiting case of small mutation rates $\mu << M^{-2}$, we can assume that the population consists, most of the time, of one type only. Mutants occur rarely, and will be eliminated, or have reached fixation, before the next mutation occurs. Hence we can study this limiting case by an embedded Markov chain with four states only. These are the four homogenous states, with the population consisting of only cooperators, only defectors, only non-participants or only punishers, respectively. It is now easy to compute the transition probabilities. For instance, ρ_{xy} denotes the probability that a mutant defector can invade a population of cooperators and reach fixation. The corresponding stationary distribution $(\pi_x, \pi_y, \pi_z, \pi_w)$ describes how often (on average) the population is dominated by cooperators, defectors etc.

The transition probabilities are given by formulas of the type

$$\rho_{xy} = \left[1 + \sum_{k=1}^{M-1} \prod_{X=1}^{k} \frac{1 - s + sP_{XY}}{1 - s + sP_{YX}}\right]^{-1}$$

where P_{XY} denotes the payoff obtained by a cooperator in a population consisting of X cooperators and Y = M - X defectors (see Nowak 2005). Hence all that remains is to compute these expressions. Again, these payoffs consist of two terms: the contribution from the public good round, and those from the punishment round.

Clearly, if there are W punishers and Y defectors (with W+Y=M), the former must pay $\gamma Y(N-1)/(M-1)$ and the latter $\beta W(N-1)/(M-1)$ on average.

The payoff obtained from the public good term has been computed in (Hauert at al 2007) for the **SR**-case. We now compute it for the **OO**-case. In a population consisting of X cooperators and Y = M - X defectors, a co-operator obtains

$$\frac{cr(X-1)}{M-1} - c.$$

Defectors in a population of Y defectors and X = M - Y cooperators (or pun-

ishers) obtain from the public good

$$\frac{cr(M-Y)}{M-1}.$$

The probability to be the only participant in the sample is

$$\frac{\binom{Z}{N-1}}{\binom{M-1}{N-1}} = \frac{Z_{N-1}}{(M-1)_{N-1}}$$

where $Z_k := Z(Z-1)...(Z-k+1)$. Hence in a population with Z non-participants, if the rest is composed only of punishers (or of cooperators), the participants obtain from the public good

$$\sigma \frac{Z_{N-1}}{(M-1)_{N-1}} + c(r-1)(1 - \frac{Z_{N-1}}{(M-1)_{N-1}})$$

In a population consisting only of punishers and cooperators, the public good term of the payoff is

$$\frac{rc(N-1)}{N-1} - c = c(r-1).$$

We can now compute the stationary distributions. As shown in Figs 2 and 3, the outcome is clear: in the compulsory case, defectors take over; in the optional case, punishers dominate. The result are derived for the limiting case of very small mutation rates ($\mu << M^{-2}$), but computer simulations show that they are valid for larger mutation rates too. In interactive computer simulations

(see for instance http://homepage.univie.ac.at/hannelore.brandt/simulations/ and http://www.people.fas.harvard.edu/ hauert/), it is possible to experiment with different parameter values (for $M, N, \sigma, r, c, \beta$ and γ) and with other learning processes, which provide convincing evidence that the outcome is robust. We note in particular that punishers are even more frequent for the strongly altruistic 'othersonly' scenario than for the weakly altruistic 'self-returning' variant. The reason behind this seems to be that the cooperators are less frequent in the **OO**-case (and each percent they lose is gained by the punishers). Why are they less frequent? In the **SR** case, cooperators can invade non-participants more easily, since they do get a return for their contribution. However, such an invasion has no lasting effect, because the cheaters can quickly replace the cooperators. All that these short episodes of cooperation without punishment achieve is that they stand in the way of the cooperation with punishment.

5 Discussion

Punishment of free riders is widespread in human societies (Henrich et al 2006, Sigmund 2007). The main result of our paper is that a public good game with punishment is much more likely to lead to a cooperative outcome if participation is voluntary, rather than compulsory. For the 'weakly altruistic' **SR** case, this is well established, see Hauert et al 2007 and 2008. But here, we show that it also holds in the 'strongly altruistic' **OO**-case, i.e. if the benefit of a contribution is exclusively directed at others.

The mechanism thus operates without a 'sleight of hand'. The fact that in sufficiently small groups playing the \mathbf{SR} public goods game, it is in the selfish interest of a player to contribute, is not essential. Even if the social dilemma is unmitigated, as in the \mathbf{OO} case, voluntary participation allows cooperators to emerge again and again from a population of non-participants. Indeed, if non-participants are frequent, the random samples of N players will provide only small groups willing to participate in the public goods game. In such small groups, it can happen by chance that most members contribute. These groups will have a high payoff and its members will be quickly imitated.

This is an instance of the well-known Simpson's paradox (see Sober and Wilson 1998): although within each group, free-riders do better than contributors, in can happen that on average, across the whole population, contributors do better than free-riders. A similar effect also holds in a model of Killingback et al (2006): in that scenario, the population is structured in groups of variable size, with dispersal between groups, whereas our model considers individual selection in a well-mixed population. For other investigations of the effect of finite population size and stochastic shocks, see e.g. (Peyton Young and Foster, 1995).

If the contributors are cooperators, imitation will lead to a regime dominated by cooperators. This will quickly be invaded by defectors, who in turn foster non-participation. But the resulting rock-paper-scissors cycle, which can be viewed as an extremely simple model of an endogenous business cycle (cf Dosi et al 2006), will eventually lead from non-participants to punishers (rather than non-punishing cooperators). In that case defectors will have a much harder time to come back.

In their lucid discussion of strong vs. weak altruism, Fletcher and Zwick 2007 argue that what counts for selection are fitness differences, i.e. relative fitnesses rather than absolute fitnesses (cf Hamilton 1975 and Wilson 1975). Although with weak altruism (which has been called 'benevolence' by Nunney 2000), a contribution directly benefits the contributor, it benefits the co-players just as well. Even if the return to the contributor exceeds the cost of the contribution, defectors in

the public goods group are still better off. In this sense, the difference between weak and strong altruism is less than may appear, despite the 'conventional wisdom' (Fletcher and Zwick 2007) stating that under the usual assumptions, weak altruism evolves and strong altruism does not.

In particular, while most models leading to cooperation assume weak altruism, Fletcher and Zwick 2004 have shown that strong altruism can prevail in public goods games of 'others-only' type if groups are randomly reassembled, not every generation, but every few generations. Our scenario emphasises a different, but related point. In voluntary public goods games with punishment, for strong and weak altruism alike, cooperation can emerge through individual selection.

Acknowledgements: Part of this work is funded by EUROCORES TECT I-104 G15. We thank Martin Nowak for helpful discussions. C.H. is supported by the John Templeton Foundation and the NSF/NIH joint program in mathematical biology (NIH grant R01GM078986).

6 References

Boyd R and Richerson R J (1992) Punishment allows the evolution of cooperation (and anything else), in sizable groups, Ethology and Sociobiology 13, 171-195

Boyd, R., Gintis, H., Bowles, S., and Richerson, P. (2003) The evolution of altruistic punishment, Proc. Natl. Acad. Sci. USA 100, 3531–3535

R. Boyd and S. Mathew (2007) A Narrow Road to Cooperation, Science, 316: 18581859, 2007

Brandt, H., Hauert, C and Sigmund, K. (2003) Punishment and reputation in spatial public goods games, Proc. R. Soc. B 270, 1099-1104

Brandt, H., Hauert, C., and Sigmund, K. (2006), Punishing and abstaining for public goods, Proc. Natl. Acad. Sci. USA 103(2), 495–497

Camerer, C (2003) Behavioural game theory: experiments in strategic interactions, Princeton, Princeton UP

Colman, A. (2006), The puzzle of cooperation, Nature 440, 744–745

Dosi, G, Fagiolo, G and Roventini, A (2006) An evolutionary model of endogenous business cycles, Computational Economics, to appear

Fehr E and Gächter S (2000) Cooperation and Punishment in public goods experiments, Am. Econ. Rev. 90, 980-994

Fehr, E. and Gächter, S. (2002) Altruistic punishment in humans, Nature 415, 137–140

Fletcher, J A and Zwick, M (2004) Strong altruism can evolve in randomly formed groups, Journ. Theor. Biol. 228, 303-313

Fletcher J A and Zwick M (2007) The evolution of altruism: game theory in multilevel selection and inclusive fitness. Journ. Theor. Biol. 245, 26-36

Fowler, JH (2005a) The second-order free-rider problem solved? Nature 437, E8

Fowler, J. H. (2005b), Altruistic punishment and the origin of cooperation. Proc. Nat. Acad. Sci. USA 102(19), 7047–7049

Gardner. A and S.A. West (2004) Cooperation and punishment, especially in humans, American Naturalist 164, 753-764

Hamilton WD (1975) Innate social aptitudes of man: an approach from evolutionary genetics, in Fox R (ed) Biosocial Anthropology, Wiley, New York, 133-155

Hammerstein, P., ed. (2003) Genetic and cultural evolution of cooperation MIT Press, Cambridge MA

Hardin, G. (1968), The tragedy of the commons, Science 162, 1243–1248 (1968)

Hauert, C., De Monte, S, Hofbauer, J. and Sigmund, K (2002a) Volunteering as a Red Queen Mechanism for cooperation, Science 296, 1129-1132.

Hauert, C., De Monte, S, Hofbauer, J. and Sigmund, K (2002b) Replicator dynamics for optional public goods games, J. Theor. Biol 218, 187-194

Hauert C, Haiden N and Sigmund K (2004), The dynamics of public goods, Discrete and Continuous Dynamical Systems B, 4 575-585

Hauert, C, Traulsen, A, Nowak, MA, Brandt, H and Sigmund, K (2007) Between freedom and coercion: the emergence of altruistic punishment, Science 316, 1905-1907

Hauert, C, Traulsen, A, Nowak, MA, Brandt, H and Sigmund, K (2008) Public goods with abstaining in finite and infinite populations, submitted

Henrich, J. and Boyd, R. (2001), Why people punish defectors, J. theor. Biol. 208, 7989

Henrich, J. et al (2006) Costly punishment across human societies, Science 312, 1767-1770

Hofbauer, J. and Sigmund, K (1998), Evolutionary Games and Population Dynamics, Cambridge University Press

Imhof LA, Fudenberg D, Nowak MA (2005) Evolutionary cycles of cooperation and defection, Proc. Natl. Acad. Sci. USA 102, 10797-10800

Kerr B and Godfrey-Smith P (2002) Individualist and multi-level perspectives on selection in structured populations, Biology and Philosophy 17, 477-517

Killingback, T, Bieri, J and Flatt T (2006) Evolution in group-structured populations can solve the tragedy of the commons, Proc. Roy. Soc. B 273, 1477-1481

Kirman, A, Gallegatti M and Marsili P, eds. (2004) The Complex Dynamics of Economic Interaction, Springer Verlag, Heidelberg

Nakamaru, M. and Iwasa Y. (2005) The evolution of altruism by costly punishment in lattice-structured populations: score-dependent viability vs score-dependent fertility, Evol. Ecol. Res. 7, 853-870

Nowak MA, Sasaki A, Taylor C, Fudenberg D (2004). Emergence of cooperation and evolutionary stability in finite populations. Nature 428, 646-650

Nowak MA (2005) Evolutionary Dynamics, Harvard University Press, Harvard Mass

Nunney, L (2000) Altruism, benevolence and culture: commentary discussion of Sober and Wilson's 'Unto Others', J. Consciousness Stud. 7, 231-236

Olson M (1965) The Logic of Collective Action, Harvard UP, Cambridge, Mass

Ostrom, E (1990) Governing the Commons, Cambridge UP, New York

Pepper J W (2000) Relatedness in trait group models of social evolution, J Theor. Biol. 206, 355-368

Peyton Young, H and Foster, D (1995) Learning dynamics in games with stochastic perturbations, Games and Economic Behavior 11, 330-363

Samuelson, P A (1954) The pure Theory of Public Expenditure, Review of Economics and Statistics 36, 387-389

Semmann, D., Krambeck, H.-J., and Milinski, M. (2003), Volunteering leads to rock-paper-scissors dynamics in a public goods game, Nature 425, 390–393

Sigmund, K, Nowak M and Hauert C (2001) Reward and punishment, Proc Nat. Acad. Sci. U.S.A. 98, 10757-10762

Sigmund K (2007) Punish or perish? Retaliation and collaboration among humans, Trends in Evolution and Ecology...

Sober E and Wilson DS (1998) Unto Others. The Evolution and Psychology of Unselfish Behaviour, Harvard UP, Cambridge MA

Wilson D S (1990) Weak altruism, strong group selection, Oikos 59, 135-140 Wilson D S (1975) A theory of group selection, Proc Nat Acad Sci 72, 143-146

Yamagishi, T (1986) The provision of a sanctioning system as a public good, Journal of Personality and Social Psychology 51, 110-116

7 Figures

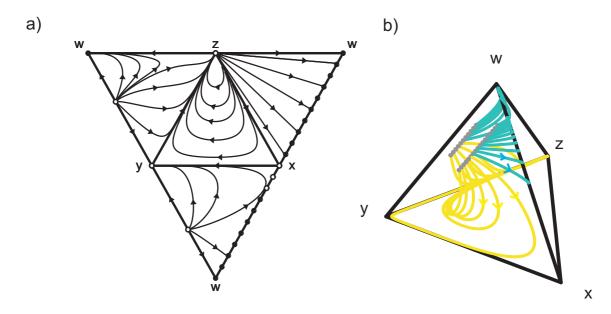


Figure 1: The replicator equation for the ${\bf OO}$ -case. Part a) shows the phase portrait on the boundary faces of the state space simplex S_4 . Part b) shows what happens in the interior of the simplex. Yellow orbits converge to the state z of only non-participants, blue orbits converge to a cooperative mixture of punishers w and cooperators x. The startpoints of the orbits are depicted in gray. Parameter values are $N=5, r=3, c=1, \beta=1.2, \gamma=1$ and $\sigma=1$.

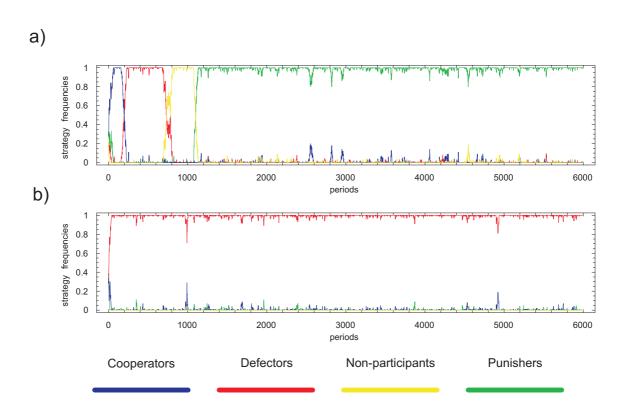


Figure 2: Time evolution of the frequencies in a finite population (a) if all four strategies are allowed and (b) if the game is compulsory, i.e. if there are no non-participants. We see that in the latter case, defectors quickly come to near-fixation; in the former case, a rock-paper-scissors type of cycle leads eventually to a cooperative regime dominated by punishers, which lasts for a long time. (It will eventually by subverted through random drift, in which case the oscillations start again). (Parameter values as in Fig.1 with $M=100, \mu=0.001, B=1, s=0.1$).

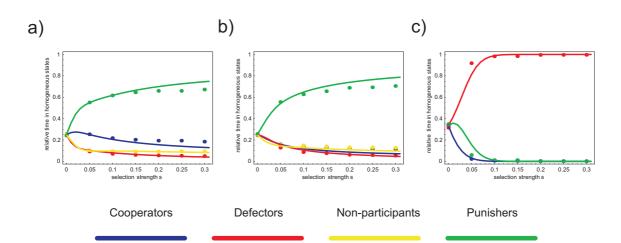


Figure 3: The frequencies of strategies in the stationary distribution, as a function of the selection strength s. (a) In the case of weak altruism, the punisher's strategy is the most frequent; (b) this also holds for strong altruism, with the additional feature that non-punishing cooperators are even less frequent; (c) if the game is compulsory (i.e. non-participants are excluded from the simulations), the defectors emerge as clear winners. This is shown here for the case of strong altruism, the weak-altruism case is similar. The lines describe the frequencies as computed in the limiting case $\mu \to 0$. The dots describe the results of numerical simulations averaged over 10^7 periods for $\mu = 0.001$. Parameter values are $N = 5, r = 3, c = 1, \beta = 1, \gamma = 0.3, \sigma = 1$ and B = 1.

8 Appendix

In the \mathbf{OO} case, the payoff from the public good can be computed as follows: The probability that a focal player has h co-players who participate is

$$\binom{N-1}{h}(1-z)^h z^{N-1-h}$$

for h = 0, ..., N - 1. The probability that m of these are contributing is

$$\binom{h}{m} \left(\frac{x+w}{1-z}\right)^m \left(\frac{y}{1-z}\right)^{h-m}$$

for m = 0, ..., h (if h > 0).

The focal player's expected gain stemming from his h co-participants is

$$\sum_{m=0}^{h} \frac{rcm}{h} \binom{h}{m} (\frac{x+w}{1-z})^m (\frac{y}{1-z})^{h-m} = \frac{rc(x+w)}{1-z}$$

which is independent of h (for h = 1, ..., N - 1).

Hence the payoff obtained from the public good is given by

$$\sigma z^{N-1} + \frac{rc(x+w)(1-z^{N-1})}{1-z}$$

for a defector. Cooperators and punishers obtain from the public good the same term, reduced by $c(1-z^{N-1})$.

We now compute the public good terms for the finite **OO**-case. In a population consisting of X cooperators and Y = M - X defectors, a co-operator obtains (if k is the number of other cooperators)

$$\sum_{k=0}^{N-1} H(k, N-1, X-1, M-1) \left(\frac{rck}{N-1} - c\right)$$

$$=\frac{rc}{N-1}\sum_{k=0}^{N-1}kH(k,N-1,X-1,M-1)-c\sum_{k=0}^{N-1}H(k,N-1,X-1,M-1)$$

Since the first sum is $(X-1)\frac{N-1}{M-1}$ and the second is 1, this yields

$$\frac{cr(X-1)}{M-1} - 1$$

Defectors in a population of Y defectors and X = M - Y cooperators or punishers obtain from the public good

$$\sum_{k=0}^{N-1} H(k, N-1, X, M-1) \left(\frac{rkc}{N-1}\right) = \frac{cr(M-Y)}{M-1}$$

The probability to be the only participant in the sample is

$$\frac{\binom{Z}{N-1}}{\binom{M-1}{N-1}} = \frac{Z_{N-1}}{(M-1)_{N-1}}$$

Hence in a population with Z non-participants, if the rest is composed only of punishers (or of cooperators), the participants obtain from the public good

$$\sigma \frac{Z_{N-1}}{(M-1)_{N-1}} + c(r-1)(1 - \frac{Z_{N-1}}{(M-1)_{N-1}})$$

In a population consisting only of punishers and cooperators, the public good term of the payoff is

$$\frac{rc(N-1)}{N-1} - c = c(r-1)$$