

COEXISTENCE OF COOPERATION AND DEFECTION IN PUBLIC GOODS GAMES

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The production of public goods by the contribution of individual volunteers is a social dilemma because an individual that does not volunteer can benefit from the public good produced by the contributions of others. Therefore it is generally believed that public goods can be produced only in the presence of repeated interactions (which allow reciprocation, reputation effects and punishment) or relatedness (kin selection). Cooperation, however, often occurs in the absence of iterations and relatedness. We show that when the production of a public good is a Volunteer's Dilemma, in which a fixed number of cooperators is necessary to produce the public good, cooperators and defectors persist in a mixed equilibrium, without iterations and without relatedness. This mixed equilibrium is absent in the N-person Prisoner's Dilemma, in which the public good is a linear function of the individual contributions. We also show that the Prisoner's Dilemma and the Volunteer's Dilemma are the two opposite extremes of a general public goods game, and that all intermediate cases can have a mixed equilibrium like the Volunteer's Dilemma. The coexistence of cooperators and defectors, therefore, is a typical outcome of most social dilemmas, which requires neither relatedness nor iterations.

KEY WORDS: Cooperation, game theory, mixed equilibrium, prisoner's dilemma, public good, volunteer's dilemma.

The production of a public good that depends on the costly contribution of a number of individuals is a social dilemma because everybody relies on someone else. Imagine a group of individuals witnessing a crime: each can volunteer to pay a small contribution to call the police; if nobody volunteers everybody pays a higher cost because the criminal remains at large. Clearly it is better to volunteer if nobody else does it, but everybody prefers that it is someone else who pays the contribution. The dilemma is that, if the decision is simultaneous, it can happen that one volunteers in vain, or that nobody volunteers because everybody thinks that someone else is doing it. A similar dilemma occurs in animal groups, for example when

individuals must decide whether to raise the alarm against a predator.

Other situations require more than one volunteer to produce the public good. Public goods games are common in biology at all levels of organization, from the capture and sharing of large preys by groups of predators (Packer et al. 1990; Stander 1991; Creel 1997; Bednarz 1988) and cooperative nesting and breeding in birds (Rabenold 1984) to the production of replication enzymes in viruses (Turner and Chao 2003), adhesive polymers in bacteria (Rainey and Rainey 2003) or invertase in yeast (Gore et al. 2009), or the formation of fruiting bodies in social amoebas (Bonner 2008); in the social sciences, typical examples are voting,

the production of open-source software, or refraining from downloading music from the internet (Palfrey and Rosenthal 1984; Myatt and Wallace 2009).

The problem with the production of public goods (Olson 1965) is that, if contributing is costly, volunteers have a lower fitness than individuals that do not contribute; therefore an individual would rather avoid the cost of volunteering and exploit the public goods produced by others; someone must volunteer, however, otherwise the public good is not produced and everybody pays a cost higher than that of volunteering. Hence the social dilemma (Dawes 1980), which leads to the celebrated “tragedy of the commons” (Hardin 1968).

In evolutionary biology it is generally believed (Rankin et al. 2007) that cooperation in public goods games is only possible in the presence of some form of assortment, which can be due to repeated interactions (which allow reciprocation, reputation effects and punishment; Axelrod and Hamilton 1981) or relatedness (kin selection; Hamilton 1964). Our scope here is to show that, instead, assortment is necessary only if the public good is modeled as an N-person Prisoner’s Dilemma (NPD).

It seems such common wisdom in the evolutionary biology literature to equate public goods games with the NPD, that in most papers the two terms are used interchangeably, without realizing the profound implications of this assumption. A recent review on public goods games in evolutionary biology (Rankin et al. 2007) for example states that “the tragedy of the commons in evolutionary biology encompasses what social scientists call a public good game, or an NPD.” Compare this statement with the following, taken from a review of public goods games in the social sciences (Kollock, 1998): “A common misunderstanding is the assumption that all N-person dilemmas have the structure of an NPD.” In fact it is understood, at least in game theory in economics, that the NPD is only a special case of public goods games; yet the misunderstanding persists in evolutionary biology.

So what is an NPD? The name originated in the social sciences (Hamburger 1973; Fox and Guyer 1978), when game theorists begun to be interested in the N-person version of the Prisoner’s Dilemma (Tucker 1950; Luce and Raiffa 1957). The game is usually described as follows: individuals can be cooperators (volunteers) or defectors; cooperators pay a contribution c , whereas defectors do not; all contributions are put together, multiplied by a factor, and then redistributed to all individuals (both cooperators and defectors). The NPD therefore (at least in the common sense used in evolutionary theory) is an N-person game in which the public good is a linear function of the individual contributions. This assumption of linearity, apparently innocuous, is usually taken for granted; only recently Frank (2010) pointed out that nonlinearity has had very little attention in studies of public goods and might be potentially important. As we will show, this has indeed deep implications.

The importance of linearity is easily understood if we consider another type of public goods game, the Volunteer’s Dilemma (VD; Diekmann 1985). In the VD individuals can volunteer to pay a small cost c (strategy *Volunteer*) or avoid to pay the cost (strategy *Ignore*); the public good is produced if and only if a certain number of individuals play *Volunteer* (i.e., the public good is a step function of the individual contributions); if the public good is produced, each individual in the group has a benefit $b > c$; if the public good is not produced, the benefit is 0. The VD can be thought of as the N-person version of the game of Chicken (or Hawk-Dove, or Snowdrift); it has been discussed in the social sciences (Palfrey and Rosenthal 1984; Diekmann 1985), but virtually ignored in evolutionary biology (until Archetti 2009a,b). The VD is a social dilemma like the NPD; it has a Pareto-deficient equilibrium in which nobody contributes; unlike the NPD, however, the VD has also a stable mixed equilibrium in which cooperators and defectors coexist (Archetti 2009a,b). That the VD has a mixed equilibrium can be seen easily in the simplest version of the game, in which one volunteer is sufficient to produce the public good: the payoffs of the two pure strategies *Volunteer* (V) and *Ignore* (I) in this case are $W_V = b - c$ and $W_I = (1 - \phi^{N-1})(0) + [1 - (1 - \phi)^{N-1}]b$, where N is the number of individuals in the group and ϕ is the frequency of the strategy *Volunteer*. The game has a stable mixed equilibrium at $\phi_{eq} = 1 - (c/b)^{1/(N-1)}$ (Archetti 2009a,b).

When more than one volunteer is necessary to produce the public good the situation is more complex. Our scope is to understand the production of public goods in one-shot, N-person games in social dilemmas that are intermediate between the NPD and the VD, that is situations in which the public good is intermediate between the linear (NPD) and the step (VD) function. Our contention is that the VD and the NPD are two extreme, opposite, cases of a general public goods game and that a mixed equilibrium exists not only in the VD, but in all public goods games except the NPD. Therefore the production of public goods is generally possible simply due to the strategic nature of the interactions, even without iterations and relatedness.

The Model

The payoffs of the two strategies *Volunteer* and *Ignore* can be written as

$$W_V = \sum_{j=0}^{N-1} f_j B_V(j) - c$$

$$W_I = \sum_{j=0}^{N-1} f_j B_I(j),$$

where

$$f_j = \binom{N-1}{j} \phi^j (1 - \phi)^{N-1-j}$$

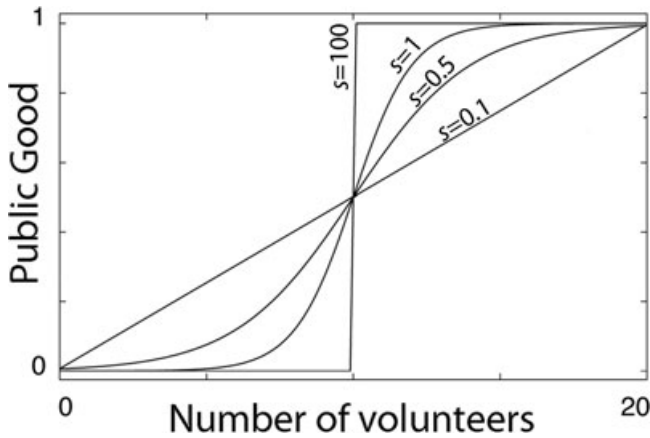


Figure 1. Public goods as a function of the number of volunteers. The steepness of the curve is defined by s ; the inflection point is at k ; in this examples $k = 10$ and group size is $N = 20$. The public good is $B_x(j) = b[\beta_x(j) - \beta_x(0)]/[\beta_x(N) - \beta_x(0)]$ where $x = I, V$ and $\beta_I(j) = \beta_V(j - 1) = 1/(1 + e^{-s(j-k)})$ (see Appendix 1); $b = 1$. The Prisoner’s Dilemma corresponds to $s \rightarrow 0$ (the public good is a linear function of the number of volunteers); the Volunteer’s Dilemma corresponds to $s \rightarrow \infty$ (the public good is a Heaviside step function of the number of volunteers; approximated here by $s = 100$). The domain of the B function are the nonnegative integers $[0, N]$; the continuous solid lines are only for visualization.

is the probability that j of the other $N-1$ individuals (other than self) play *Volunteer*; $B_V(j)$ and $B_I(j)$ are the benefits due to the public good for the two strategies *Volunteer* and *Ignore*, ϕ is the frequency of the strategy *Volunteer*, and c is the cost of volunteering.

We use a very general function for the public good (Fig. 1, Appendices 1 and 2), which only assumes that these benefits are strictly increasing functions of j ; changing the position of the inflection point (k) and the steepness (s) at the inflection point (i.e., the synergistic effects of volunteering), allows us to recover the NPD and the VD as special cases: the NPD corresponds to $s \rightarrow 0$ (in this limit case the public good is a linear function of the individual contributions, Appendix 2); the VD corresponds to $s \rightarrow \infty$ (in this limit case the public good is a step function of the individual contributions) (Fig. 1). The NPD and the VD, therefore, are the two extreme versions of this general public goods game.

The generalized model is intractable analytically, therefore we start by using the step function (the $s \rightarrow \infty$ limit; the VD) as an approximation; we will show later that the results obtained using the step function are similar to the results obtained using a smooth function, even if the smooth function is very shallow (small s). If we assume that $s \rightarrow \infty$, the public good b is produced if and only if at least k individuals volunteer

$$B_I(j) = \begin{cases} b & \text{if } j \geq k \\ 0 & \text{if } j < k \end{cases}$$

$$B_V(j) = \begin{cases} b & \text{if } j \geq k - 1 \\ 0 & \text{if } j < k - 1 \end{cases}$$

We assume a large, well-mixed, asexual population in which all individuals play the public goods game in groups of N individuals formed at random; after payoffs are assigned the groups are dissolved and all individuals reproduce with a probability proportional to their relative fitness; the new generation replaces the parent generation; population size is constant. This system can be studied by considering the replication dynamics of the two pure strategies *Volunteer* and *Ignore*

$$d\phi/dt = \phi(1 - \phi)(W_V - W_I) \tag{1}$$

The same dynamics can be considered when the system contains a finite number of mixed strategies (see Appendix 3). Beside the trivial $\phi_{eq1} = 1$ (unstable) and $\phi_{eq0} = 0$ (stable) fixed points, the system can have a stable and an unstable equilibrium, denoted by $\phi_{eq}^{(u)}$ and $\phi_{eq}^{(s)}$ ($0 < \phi_{eq}^{(u)} < \phi_{eq}^{(s)} < 1$) which can be found (see Appendix 4) from

$$\binom{N-1}{k-1} \phi^{k-1} (1 - \phi)^{N-k} = \frac{c}{b} \tag{2}$$

The probability that at least k individuals volunteer (and therefore the public good is produced) is

$$\sum_{j=k}^N \binom{N}{j} \phi^{(s)j} (1 - \phi^{(s)})^{N-j}$$

This result is valid both for the case of mixed-strategy mixed equilibrium (a monomorphic population in which each individual plays *Volunteer* with probability ϕ and *Ignore* with probability $1 - \phi$) and for the pure-strategy mixed equilibrium (a polymorphic population in which ϕ is the frequency of individuals playing *Volunteer* and $1 - \phi$ is the frequency of individuals playing *Ignore*).

The stable equilibrium and the resulting public good are shown in Figure 2, which also shows the equilibria obtained using the smooth function: it is clear that even for an extremely shallow smooth function (small s) the results are very similar to the ones obtained with the step function (approximated in Fig. 2 by $s = 100$), unless the cost of volunteering (c) is relatively high (in which case the mixed equilibrium disappears). The reason is that both the step function and the smooth functions for the public good produce smooth payoffs as a function of ϕ and the position of the mixed equilibrium is only marginally affected by the steepness of the public goods function (unless k is very close to 1 or to N).

This solution requires a numerical approach to find the equilibria, which is not practical for large group sizes. We also provide an approximation that allows to calculate analytically the equilibrium for large groups ($N \gg 1$) (see Appendix 5); in this case, again, the difference between the step function and the smooth

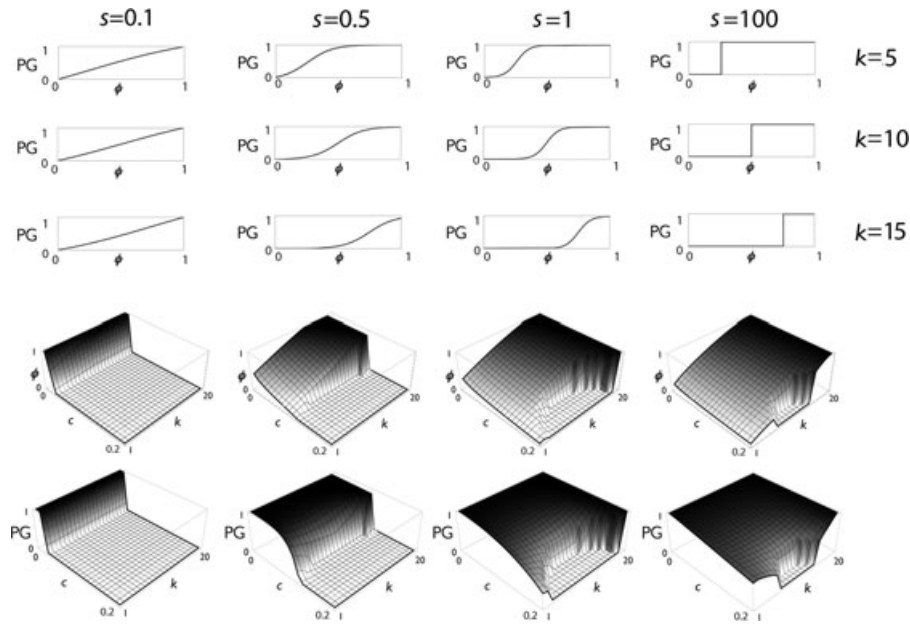


Figure 2. Top: The public good (PG) as a function of the fraction of volunteers (ϕ) for different values of k (the position of the inflection point) and s (the steepness of the curve). $N = 20$; $b = 1$; the public good function is shown in Figure 1 and described in Appendix 1. Bottom: The probability of volunteering at equilibrium (ϕ ; the stable equilibrium $\phi_{eq}^{(s)}$) and the probability that the public good is produced at equilibrium (PG) as a function of k and of the cost of volunteering (c).

function is negligible; indeed it becomes less important for large N (Fig. 3). For large N the equilibrium can be estimated simply by the k/N ratio (see Appendix 5)

$$\phi^* = \frac{k - 1}{N - 1}.$$

It is interesting that a similar convergence effect also occurs in other N -person games with a threshold (Pacheco et al. 2009; Souza et al. 2009) (results not shown here). If $N \rightarrow \infty$, $\phi_{eq}^{(u)}$ and $\phi_{eq}^{(s)}$ converge to ϕ^* , and random fluctuations could move the population above $\phi_{eq}^{(u)}$, which would then cause the population to move to the $\phi = 0$ state; in other words, at the $N \rightarrow \infty$ limit, while the mixed equilibrium remains stable to the invasion of rare mutants, it is vulnerable to relatively small stochastic fluctuations. This convergence effect is probably relevant only for microbes, in which group size (N ; not the population size) can be very large (Appendix 5).

Discussion

The problem of cooperation in public goods games has been traditionally investigated by studying the NPD, and it is generally believed that the maintenance of cooperation in this case requires some form of assortment due to either relatedness or repeated interactions (which allow reciprocation, reputation effects or punishment). We have shown that the NPD is only a very specific, extreme, case of public goods game, and that most social dilemmas can be approximated, instead, by the VD, a well-known game

in economics, but neglected in evolutionary biology, in which the public good is produced if a fixed number of individuals volunteer to pay a cost.

First, by studying the evolutionary dynamics, and using approximations for large group sizes, we found a general solution for the VD. Then, using numerical calculations, we showed that the VD is a good approximation of any public goods games in which the public good is a nonlinear function of the number of cooperators; the NPD is an extreme case in which the public good is a linear function. Our main result, therefore, is valid for most social dilemmas: cooperation and defection persist at equilibrium if the cost of volunteering is not too high; the public good is produced in the absence of iterations, relatedness, or external enforcement.

The fact that assortment (including genetic assortment, that is relatedness; Queller 1985; Fletcher and Doebeli 2009) is not necessary for the existence of cooperation in a one-shot game might seem surprising (Hauert et al. (2006) also find coexistence, but their game is not properly a social dilemma because it alternates periodically between an NPD and a game with no conflict). One could suspect that some form of assortment, although not explicitly modeled, is embedded in the model in a more subtle way; this usually happens because of the way groups are formed or because of limited dispersal in a topologically structured populations (see for example Grafen 2007; Grafen and Archetti 2008). This, however, is not the case in our framework; our result derives simply from strategic considerations: in the VD if nobody volunteers the public good is not produced, so it pays to volunteer; but

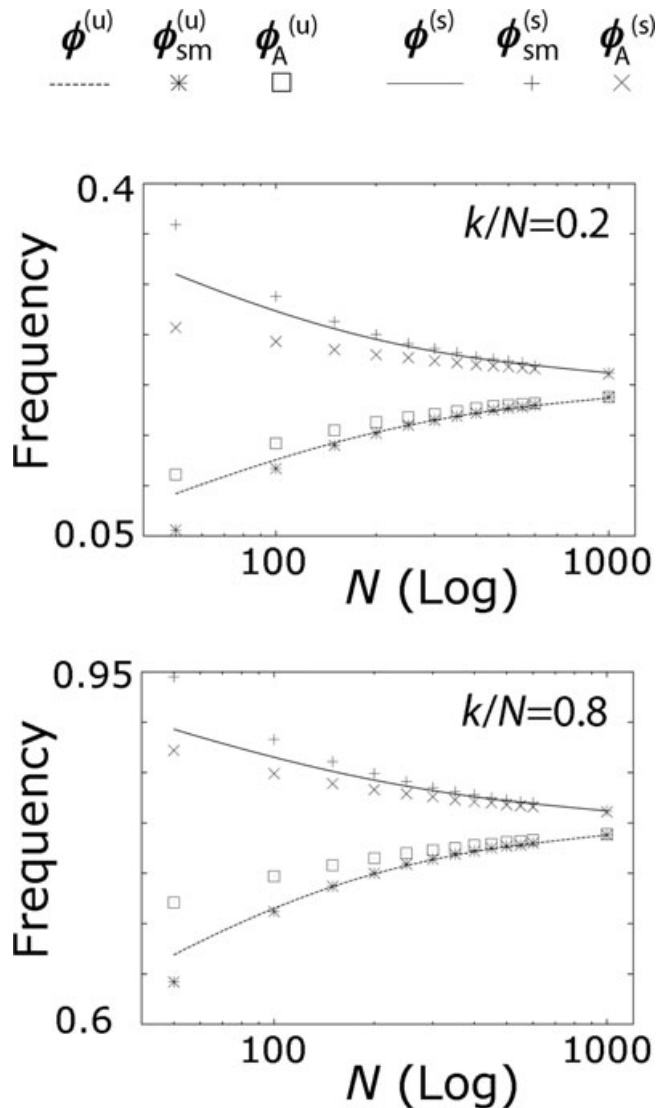


Figure 3. Differences between smooth and step functions and between exact and approximate results. The stable ($\phi^{(s)}$) and unstable ($\phi^{(u)}$) fixed points computed exactly by equation (2), according to the analytical approximation ($\phi_A^{(s)}$, $\phi_A^{(u)}$; see Appendix 3), and using the smooth payoff functions $B_I(j)$ and $B_V(j)$ defined in Fig. 1 (see also Appendix 1) ($\phi_{sm}^{(s)}$, $\phi_{sm}^{(u)}$) computed with $s = 0.5$; $c = 0.01$, $b = 0.5$.

if too many volunteer the cost of volunteering is wasted, so it pays not to; as a result the optimal strategy is to volunteer with a probability, that is we have a mixed equilibrium in which cooperation and defection coexist. In the VD, relatedness reduces the critical value of the cost of volunteering for which the mixed equilibrium exists; when the mixed equilibrium does exist, however, relatedness has a very small effect on the production of the public good (Archetti 2009a,b); a similar analysis could be extended to other public good functions and to other forms of assortment.

The mixed equilibrium disappears if the public good is a linear function of the individual contributions, that is if the game

is modeled as an NPD. This is a crucial point, because public goods in evolutionary biology have been usually modeled as an NPD. The NPD corresponds to our $s \rightarrow 0$, which does not have a mixed equilibrium: in this case only pure defection is stable, and to maintain cooperation assortment must play a role (in the form of genetic relatedness or repeated interactions). As we have seen, however, when the public good function deviates from the assumption of linearity of the NPD, public goods games resemble more a VD than an NPD: if the cost of volunteering is not too high there is a mixed equilibrium (in which cooperators and defectors coexist) in addition to the pure defection equilibrium. This mixed equilibrium is a natural outcome not only of the VD (in which the public good is a step function of the number of contributions) but also of all public goods games except the NPD (in which the public good is a linear function of the number of contributions). Cooperators and defectors, therefore, can persist at equilibrium, and the production of public goods requires neither relatedness nor iterations. Strategic behavior (Archetti 2009b, 2010) can improve the production of public goods in the absence of any form of assortment.

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Appendix 1

THE GENERALIZED PUBLIC GOODS GAME

The benefit $\beta_x(j)$ of the public good for an individual playing *Ignore* ($x = I$) and for an individual playing *Volunteer* ($x = V$) are

$$\beta_I(j) = \frac{1}{1 + e^{-s(j-k)}}$$

$$\beta_V(j) = \frac{1}{1 + e^{-s(j-k+1)}}$$

which are strictly increasing functions of j , the number of individuals that play *Volunteer* among the other $N - 1$ individuals in the group; the parameter k controls the position of the inflection point; the parameter s controls the steepness of the function at the inflection point (the synergistic effect of volunteering).

Our function therefore is a generalized sigmoid function. We use this function because it seems natural to assume that the public good is a saturating function of the number of cooperators (a few volunteers are necessary to produce the public good, but too many are unnecessary and inefficient). This kind of function has been documented in cooperative behavior in different species, for example for the capture and sharing of large preys by a group of individuals in lions (Packer et al. 1990; Stander 1991), wild dogs (Creel 1997), and hawks (Bednarz 1988) and for cooperative nesting and breeding in birds (Rabenold 1984). Clearly there are other possible similar functions we could use, but their behavior is virtually the same. Our function is attractive because it allows us to model many monotonic increasing functions, including increasing returns ($k \rightarrow N$) and diminishing returns ($k \rightarrow 0$) and it can be used to model the VD ($s \rightarrow \infty$) and the NPD ($s \rightarrow 0$). We have made experiments with more complex and implausible functions and we did not see any qualitative difference as long as the functions are monotonic and increasing.

Clearly $\beta_I(j) = \beta_V(j-1)$. To make the public good range between 0 (at $j = 0$) and b (at $j = N$) for any value of s , we transform these functions using a standard normalization

$$B_x(j) = b \frac{\beta_x(j) - \beta_x(0)}{\beta_x(N) - \beta_x(0)}$$

This transformation is irrelevant ($B \approx \beta$) unless $s \ll 1$, but it is useful because it allows to scale the public good function and keep it in the same range (between 0 and b) for any value of s (Appendix 2), which is useful when $s \ll 1$.

The payoffs of the two strategies *Ignore* and *Volunteer* can be written, respectively, as

$$W_I = \sum_{j=0}^{N-1} f_j B_I(j)$$

$$W_V = \sum_{j=0}^{N-1} f_j B_V(j) - c,$$

where

$$f_j = \binom{N-1}{j} \phi^j (1-\phi)^{N-1-j}$$

is the probability that j of the other $N - 1$ individuals (other than self) play *Volunteer*. This generalized public goods game

has the VD and the NPD as extreme opposite cases (see Fig. 1 and Appendix 2).

Appendix 2

THE GAME BECOMES AN NPD FOR $s \rightarrow 0$

If $s \ll 1$ the Taylor expansion of $B_x(j)$ yields

$$B_V(j - 1) = B_I(j) = bj/N + O(s^2)$$

Thus the payoffs for *Ignore* and *Volunteer* are respectively:

$$W_I = \sum_{j=0}^{N-1} f_j bj/N$$

$$W_V = \sum_{j=0}^{N-1} f_j b(j + 1)/N - c.$$

Therefore $W_I = b\phi(N - 1)/N$ and $W_V = b[\phi(N - 1) + 1]/N - c$ increase linearly with the frequency of volunteers ϕ ; $W_V < W_I$ for any ϕ if $b/N < c$ and $\phi_{eq0} = 0$ is the only stable equilibrium; it is trivial to show that it is Pareto-deficient if $b > c$. Thus in the $s \rightarrow 0$ limit (the public good is an increasing linear function of the individual contributions), the game is an NPD.

Appendix 3

EVOLUTIONARY DYNAMICS OF THE VD WITH MIXED STRATEGIES

In a large, well-mixed asexual population with pure strategies (*Ignore* or *Volunteer*) the replicator dynamics is

$$d\phi/dt = \phi(1 - \phi)(W_V - W_I). \tag{A1}$$

The situation is more complicated in the presence of mixed strategies. Let us assume that there are $M (\geq 2)$ different (mixing) strategies in the population. The dynamics of the system is

$$dp_{Q_i}/dt = p_{Q_i}(W(Q_i, p) - \bar{W}), \quad i = 1, \dots, M \tag{A2}$$

where p_{Q_i} is the frequency of strategy Q_i (playing strategy *Ignore* with probability q_i and strategy *Volunteer* with probability $1 - q_i$),

$$W(Q_i, p) = q_i W(I, p) + (1 - q_i)W(V, p)$$

is the payoff of Q_i in population $\mathbf{p} = (p_{Q_1}, p_{Q_2}, \dots, p_{Q_M})$, and the average payoff is

$$\bar{W} = \sum_i p_{Q_i} W(Q_i, p).$$

Treating the behavior of this system is hopeless in the general case. However we can consider a simplified model having characteristically the same dynamics. First let us assume that only

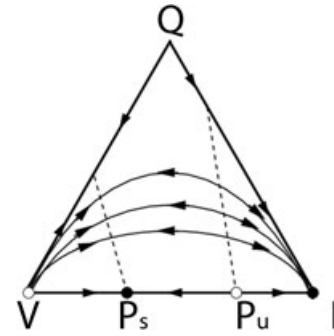


Figure A1. Evolutionary dynamics of the Volunteer's Dilemma. Dashed lines indicate the rest points, arrows indicates the direction of motion in the (V, I, Q) simplex. If the system is initially to the left of the line of rest points passing through P_u , the dynamics makes it evolve to the line of rest points passing through P_s . If the system is initially to the right of line of the rest points passing through P_u the dynamics makes it evolve to state I .

the two pure (*Volunteer* and *Ignore*) strategies are present in the population. Let us assume further that according to the replicator dynamics of these two strategies the system has inner stable and unstable fixed points denoted by p_u and p_s (we will see later that this is the situation in our case). Now assume that there is a third strategy in the population denoted by Q which is an arbitrary mixed strategy playing *Ignore* with probability q and *Volunteer* with probability $1 - q$. The replicator dynamics of this system is

$$\begin{cases} dp_I/dt = p_I(W(I, p) - \bar{W}) \\ dp_V/dt = p_V(W(V, p) - \bar{W}) \\ dp_Q/dt = p_Q(W(Q, p) - \bar{W}), \end{cases} \tag{A3}$$

where $W(I, p)$, $W(V, p)$, $W(Q, p)$ are the payoffs in population $\mathbf{p} = (p_I, p_V, p_Q)$. Because $W(Q, p) = qW(I, p) + (1 - q)W(V, p)$ it can be shown that there exist lines through P_u and P_s with the characteristics of $p_{Qq} + p_I = p_u$ or $p_{Qq} + p_I = p_s$ that are rest points of the dynamics. That is if the average probability of playing strategy *Ignore* is p_u or p_s then these states are neutrally stable in the direction of these lines (Fig. A1) (Hofbauer and Sigmund 1998). Moreover, it can be shown that

$$\frac{d}{dt} \left(\frac{p_Q}{p_I^q p_V^{1-q}} \right) = 0$$

that is $p_Q/(p_I^q p_V^{1-q})$ is a constant of motion (Hofbauer and Sigmund 1998). Consequently, the dynamics of system (A3) is qualitatively similar to the dynamics of the original two dimensional system (A1) (Fig. A1).

This line of arguments remains valid if beside the pure strategies there are Q_1, Q_2, \dots, Q_{M-2} mixed strategies with frequency $p_{q_1}, p_{q_2}, \dots, p_{q_{M-2}}$. Thus the rest points are in the lines of

$$\sum_i p_{Q_i} q_i + p_I = p_u$$

and

$$\sum_i p_{Q_i} q_i + p_I = p_s$$

in the $M - 1$ dimensional simplex and $p_{Q_i} / (p_I^{q_i} p_V^{1-q_i})$ are constant of motion for every $i = 1, \dots, M - 2$. Thus, the dynamical behavior of system (A3) is topologically identical to the behavior of system (A1) if there are inner fixed points in this subsystem. According to these arguments, to study system (A2) it is sufficient to consider the system with only the pure strategies (A1).

Appendix 4

EQUILIBRIA OF THE VD

By substituting the benefit functions

$$B_I(j) = \begin{cases} b & \text{if } j \geq k \\ 0 & \text{if } j < k \end{cases}$$

$$B_V(j) = \begin{cases} b & \text{if } j \geq k - 1 \\ 0 & \text{if } j < k - 1 \end{cases}$$

into (A1) we get the replication dynamics

$$\frac{d\phi}{dt} = G(\phi) = \phi(1 - \phi) \left[b \binom{N-1}{k-1} \phi^{k-1} (1 - \phi)^{N-k} - c \right]. \tag{A4}$$

Beside the two trivial fixed points ($\phi_{eq0} = 0, \phi_{eq1} = 1$) the solutions of

$$\left[b \binom{N-1}{k-1} \phi^{k-1} (1 - \phi)^{N-k} - c \right] = 0$$

may give further nontrivial fixed points. Rearranging this equation, we look for the values of ϕ for which

$$F(\phi) = \binom{N-1}{k-1} \phi^{k-1} (1 - \phi)^{N-k} = \frac{c}{b}. \tag{A5}$$

First of all we note that (A5) reduces to $\phi_{eq} = 1 - (cb)^{1/(N-1)}$ if $k = 1$. If $k > 1$ it is easy to see that $F(0) = F(1) = 0$, and $F(\phi)$ is strictly monotone increasing if $\phi \in [0, \phi^*)$, monotone decreasing if $\phi \in [\phi^*, 1]$.

Thus at

$$\phi^* = (k - 1)/(N - 1)$$

$F(\phi^*)$ has a single positive maximum point in the $\phi \in [0, 1]$ interval. Consequently, depending on the parameters, (A5) has zero, one, or two solutions. Let us assume that (A5) has two solutions denoted by $\phi_{eq}^{(u)}$ and $\phi_{eq}^{(s)}$ ($\phi_{eq}^{(u)} < \phi^* < \phi_{eq}^{(s)}$). By deriving $G(\phi)$, it is easy to see that $G'(\phi_{eq}^{(u)}) > 0$ and $G'(\phi_{eq}^{(s)}) < 0$, thus $\phi_{eq}^{(u)}$ is an unstable fixed point whereas $\phi_{eq}^{(s)}$ is a stable fixed point of (A4).

It is important to determine the conditions when $\phi_{eq}^{(s)}$ exists, that is when (A5) has two solutions for ϕ . Otherwise the only stable fixed point of (A4) is ϕ_{eq0} , that is there is no volunteering at all at the evolutionary equilibrium. Equation (A5) has two solutions if the maximal value of $F(\phi^*)$ is greater than c/b .

Appendix 5

AN APPROXIMATE SOLUTION FOR LARGE GROUPS

A more convenient relationship can be considered in the $N, k \gg 1$ limit. By substituting ϕ^* into F , and using the Stirling series approximation for $n!$ ($\log n! \approx n \log n - n + 1/2 \log(2\pi n) + \dots$) we find that

$$F(\phi^*) \approx \sqrt{\frac{1}{2\pi} \frac{N-1}{(N-k)(k-1)}}$$

thus in the big N limit $\phi_{eq}^{(s)}$ exists if

$$\sqrt{\frac{2\pi(N-k)(k-1)}{N-1}} < \frac{b}{c}. \tag{A6}$$

This means that for a fixed k/N ($k/N \approx (k-1)/(N-1)$ in our limit) the critical b/c must increase with \sqrt{N} . It can be seen from (A6) that if k is fixed then the critical b/c must increase with $\sqrt{(N-k)/(N-1)}$. Because $\sqrt{(N-k)/(N-1)} < 1$, $\phi_{eq}^{(s)}$ exists if $b/c > \sqrt{2\pi(k-1)}$.

We can solve (A5) approximately if we consider the second-order approximation of the Taylor expansion of $F(\phi)$ around ϕ^* , that is if we consider

$$F(\phi) = F(\phi^*) + F'(\phi^*)(\phi - \phi^*) + \frac{1}{2} F''(\phi^*)(\phi - \phi^*)^2 + O(\phi^3).$$

Deriving and knowing that $F'(\phi^*) = 0$ equation (A5) simplifies to

$$\begin{aligned} \binom{N-1}{k-1} \phi^{*k-1} (1 - \phi^*)^{N-k} - \frac{1}{2} (N-1) \\ \binom{N-1}{k-1} \phi^{*k-2} (1 - \phi^*)^{N-k-1} (\phi - \phi^*)^2 = \frac{c}{b} \end{aligned}$$

Consequently

$$\begin{aligned} \phi_{eq}^{(s)} &= \phi^* + \sqrt{\frac{2\phi^*(1-\phi^*)}{N-1} \left[1 - \frac{c}{bF(\phi^*)} \right]} \\ \phi_{eq}^{(u)} &= \phi^* - \sqrt{\frac{2\phi^*(1-\phi^*)}{N-1} \left[1 - \frac{c}{bF(\phi^*)} \right]} \end{aligned} \tag{A7}$$

These forms give good approximation for both solutions. The approximation is reasonable even if N is only about 50 (relative error less than 10%); it can be shown easily that the second terms in equation (A7) tend to zero as N tends to infinity; therefore for large N , both $\phi_{eq}^{(u)}$ and $\phi_{eq}^{(s)}$ tend to $\phi^* = (k-1)/(N-1)$. When group size is very large, therefore, the equilibria can be computed simply

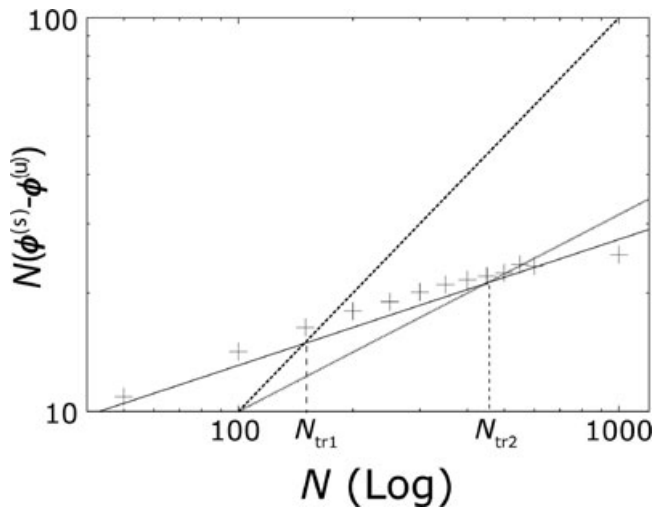


Figure A2. The vulnerability to fluctuations of cooperation as a function of group size. Exact values (+) and approximations of $N(\phi_{\text{eq}}^{(s)} - \phi_{\text{eq}}^{(u)})$: $N^{1/3}$ (solid line); $0.1 \cdot N$ (dashed line); $N^{1/2}$ (dotted line); N_{tr1} and N_{tr2} are the thresholds above which fluctuations can cause cooperation to collapse. $k/N = 0.2$; $c = 0.01$; $b = 0.5$.

by the k/N ratio, that is the probability of volunteering tends to be the same as the fraction of volunteers needed to produce the public good. It is interesting that a similar convergence effect also occurs in other N -person games (not shown here; see also Pacheco et al. 2009; Souza et al. 2009).

This convergence effect has another important consequence. If N is very large then $\phi_{\text{eq}}^{(u)}$ and $\phi_{\text{eq}}^{(s)}$ are close to each other, and fluctuations could move the population below $\phi_{\text{eq}}^{(u)}$, which will cause the population to move to the $\phi = 0$ state; in other words at

the large N limit cooperation is very vulnerable to random fluctuations. It is easy to see that at a stable mixed equilibrium, it would be enough to introduce $N(\phi_{\text{eq}}^{(s)} - \phi_{\text{eq}}^{(u)})$ noncooperative individuals to destabilize the system and lead the group to complete defection. We found that $N(\phi_{\text{eq}}^{(s)} - \phi_{\text{eq}}^{(u)})$ increases roughly as $N^{1/3}$, thus both if fluctuations are proportional to the population size N (a fixed ratio of individuals are dispersed) or proportional to $N^{1/2}$ (determined by many independent stochastic factors) they can be high enough to destabilize the cooperative state (Fig. A2).

Note that the mixed equilibrium remains stable to the invasion of rare mutants; this result only means that introducing a large number of cheaters may destabilize cooperation when N is large. Notice also that N is the group size, not the population size; therefore this effect is probably relevant only for microbes, where group size can be very large. Bacteria and other microorganisms exhibit a wide range of social behaviors ranging from dispersal to construction of biofilms, chemical warfare, and signaling (Crespi 2001; Velicer 2003; West and Buckling 2003) that rely on releasing products outside the cell, which are therefore public goods. Even in this case, it is not clear that cooperation will disappear with random large fluctuations, because N may decline (because of the lower production of public goods); if this reduction in N is quick, before ϕ can evolve to 0, then the system can go back to the basin of attraction of the stable equilibrium $\phi_{\text{eq}}^{(s)}$ (because at lower N $\phi_{\text{eq}}^{(u)}$ increases with N). In some cases, an external force may induce a reduction of N to prevent or react against destabilization; for example, in the squid-bacteria symbiosis, the squid reduces the size of the group of his bacterial symbionts every day by 95% (Nyholm and McFall-Ngai 2004), possibly as a way to restabilize bacterial cooperation.