



Contents lists available at ScienceDirect

Journal of Theoretical Biology

journal homepage: www.elsevier.com/locate/jtbi

The volunteer's dilemma and the optimal size of a social group

Marco Archetti *

Department of Organismic and Evolutionary Biology, Harvard University, 26 Oxford Street, Cambridge, MA 02138-2902, USA

ARTICLE INFO

Article history:

Received 1 May 2009

Received in revised form

10 August 2009

Accepted 17 August 2009

Available online 22 August 2009

Keywords:

Volunteer's dilemma

Social dilemma

Social evolution

Cooperation

Group size

Public good

Inclusive fitness

ABSTRACT

If one or few individuals are enough to perform an action that produces a collective good and if this action has a cost, living in group can be beneficial because the cost can be shared with other individuals. Without coordination, however, the production of a collective good by the contribution of one or few individuals is inefficient and can be modelled as a volunteer's dilemma. In the volunteer's dilemma the individuals that pay the cost for the production of the collective good benefit from their action if nobody else volunteers, but the cost is wasted if too many individuals volunteer. Increasing group size reduces the need of volunteering for each member of the group; the overall benefit for the group, however, decreases too because the larger the group is, the less likely it is that the collective good is produced. This problem persists even with a high degree of relatedness between group members; an optimal, intermediate group size exists that maximizes the probability to produce the collective good.

© 2009 Elsevier Ltd. All rights reserved.

1. Introduction

Imagine the following social dilemma (Diekmann, 1985): N individuals are sentenced to jail for 10 years unless at least one of them volunteer to confess; in this case the one that confesses (the volunteer) is imprisoned for one year, and the others are released. Therefore, a collective good is produced if and only if *at least one* player volunteers to pay a cost. Volunteering produces a common good, but the action is costly to the volunteer himself; the volunteer benefits from his action if nobody else volunteers, but the cost of his action is in vain if someone else volunteers; this is the dilemma. The production of a collective good by the contribution of a single volunteer is inefficient without a coordination mechanism for selecting who volunteers. What is the optimal strategy for an individual? And does it lead to an optimal result for the group?

I analyse a model of the volunteer's dilemma extending it to cases of relatedness between group members and to situations in which more than one volunteer is necessary to produce the collective good. I show that at equilibrium cheating remains at an intermediate frequency. The dilemma is not why cheaters do not invade, but how to increase the probability that the collective good is produced.

2. The volunteer's dilemma

2.1. 2 players

Two individuals observe a predator approaching and must decide, separately and without coordination, whether to give the alarm, which would spoil the predator's ambush. An alarm call would be beneficial for both individuals because it would deter the predator from this and future attacks; each player, however, prefers that it is the other player to report the presence of the predator, because giving the alarm has a cost $c > 0$; if one gives the alarm he has a payoff $1 - c$ and the one who does not has a payoff 1; if nobody gives the alarm, the predator attacks and both suffer a damage $a > c$ (and have a payoff $1 - a$).

This 2-player game is equivalent to the game of chicken (Rapoport and Chammah, 1966), also called hawk–dove (Maynard Smith and Price, 1973) or snowdrift (Sugden, 1986): with the two pure strategies *Volunteer* (V) and *Ignore* (I) it has two asymmetric pure-strategy equilibria in which only one player gives the alarm, but they require coordination: it only works if the players decide in advance who is going to volunteer and when. The game has also a symmetric mixed-strategy equilibrium, which does not require coordination, in which the probability of ignoring the predator is $\gamma = c/a$.

2.2. N players

The game becomes a volunteer's dilemma (Diekmann, 1985) if we increase the number of players. The volunteer's dilemma is different from an N -player chicken game with pairwise

* Tel.: +16174968146.

E-mail address: archetti@fas.harvard.edu

interactions (Taylor, 1987); it is, in effect, chicken with collective interactions. Note also that the term “volunteer” has been used by Hauert et al. (2002) in a different context for non-mandatory public goods games, which is different from the scenario described here.

With N players the payoffs of the two pure strategies *Volunteer* (W_V) and *Ignore* (W_I) are

$$W_V = 1 - c$$

$$W_I = \gamma^{N-1}(1 - a) + (1 - \gamma^{N-1})$$

and the fitness of the mixed strategy is

$$W_{MIX} = \gamma W_I + (1 - \gamma) W_V$$

The mixed-strategy equilibrium can be found by equating the fitness of the two pure strategies, which gives

$$\gamma_{eq} = (c/a)^{1/(N-1)}$$

The probability of ignoring the predator therefore increases with N : when there are more players, each relies more on somebody else giving the alarm. It is also intuitive that the probability of ignoring the predator increases with c (the cost of the alarm) and decreases with a (the cost paid if nobody gives the alarm).

It is perhaps less intuitive that the probability that *nobody* gives the alarm, also *increases* with N . Because $\gamma_{eq} = (c/a)^{1/(N-1)}$ then $\gamma_{eq}^{N-1} = c/a$, and $\gamma_{eq}^N = \gamma_{eq} c/a$, which is increasing in N (because γ_{eq} is increasing in N). If $a = 1$ and $c = 0.3$, for example, the probability that nobody gives the alarm with $N=2$ is $\gamma_{eq}^2 = 0.09$; with $N = 10$, the probability rises to $\gamma_{eq}^{10} = 0.26$ and with $N = 50$ to $\gamma_{eq}^{50} = 0.29$. Therefore the more individuals observe the predator, the *less* likely it is that someone will give the alarm. Increasing group size does not lead to a benefit for the group.

2.3. N players with relatedness

Individuals in a group are often genetically related. Does relatedness affect the volunteer's dilemma? If r is the average relatedness with other members of the group, and

$$f_i = \binom{N-1}{i} \gamma^i (1-\gamma)^{N-1-i}$$

is the probability that i of the other $N-1$ individuals (other than self) do not volunteer, the inclusive fitness of *Volunteer* is

$$W_V = \underbrace{\gamma^{N-1}(1-c)}_{\text{nobody volunteers}} + \underbrace{(1-\gamma^{N-1})(1-c)}_{\text{somebody volunteers}} + r \left\{ \underbrace{\gamma^{N-1}(N-1)(1-c)}_{\text{nobody volunteers}} + \sum_{i=0}^{N-2} f_i \left[\underbrace{(N-1-i)(1-c)}_{\text{volunteer}} + \underbrace{i(1)}_{\text{ignore}} \right] \right\}_{\text{somebody volunteers}}$$

because *Volunteer* has a direct payoff $(1-c)$ irrespective of the probability that someone else reports the predator; in addition, if nobody of the other $N-1$ members of the group (whose average relatedness to the focal individual is r) reports the predator, which happens with probability γ^{N-1} , their payoff is 1; if i of these $N-1$ individuals ignore the predator, instead, which happens with

probability f_i , the payoff for those $(N-1-i)$ who report it is $(1-c)$ and the payoff for the i who ignore it is 1.

The inclusive fitness of *Ignore* is

$$W_I = \underbrace{\gamma^{N-1}(1-a)}_{\text{nobody volunteers}} + \underbrace{(1-\gamma^{N-1})}_{\text{somebody volunteers}} + r \left\{ \underbrace{\gamma^{N-1}(N-1)(1-a)}_{\text{nobody volunteers}} + \sum_{i=0}^{N-2} f_i \left[\underbrace{(N-1-i)(1-c)}_{\text{volunteer}} + \underbrace{i(1)}_{\text{ignore}} \right] \right\}_{\text{somebody volunteers}}$$

because *Ignore* has a direct payoff 1 if somebody else reports the predator, which happens with probability $(1-\gamma)^{N-1}$, and $(1-a)$ if nobody else reports it, which happens with probability γ^{N-1} ; in addition, if nobody of the other $N-1$ members of the group (whose average relatedness to the focal individual is r) reports the predator, which happens with probability γ^{N-1} , their payoff is $(1-a)$. If i of these $N-1$ individuals ignore the predator, instead, which happens with probability f_i , the payoff for those $(N-1-i)$ who report it is $(1-c)$ and the payoff for the i who ignore it is 1.

The mixed equilibrium, found by equating W_V and W_I , is

$$\gamma_{eq} = \left\{ \frac{c}{a[1+r(N-1)]} \right\}^{1/(N-1)}$$

Again, the probability of ignoring the predator γ_{eq} increases with N . The probability γ_{eq}^N that nobody reports the predator, however, now decreases with N over a certain threshold if the cost a for the group does not depend on N (Fig. 1).

If the cost a of failing to produce the collective good is shared among the members of the group (for example $a = \alpha^N$, with $\alpha < 1$; Fig. 1), however, in most cases γ_{eq}^N increases for very low values of N , then decreases, reaches a minimum and then increases again. While the magnitude of a strongly affects the optimal group size, relatedness does not, unless it is very low (Fig. 1). Therefore there is an optimal, intermediate value of N for which the probability that nobody reports the predator is minimized. The optimal group size for the production of the collective good (the highest probability that *someone* gives the alarm) will be this value of N if defense against predators is the only determinant of fitness. Changing the parameter a does not change this effect; the equilibrium value of N adapts to the value of a and, as a result, although γ changes with a , individual fitness always increases with group size, irrespective of the shape of a .

2.4. More than one volunteer needed

If $k (> 1)$ volunteers are necessary to produce the collective good, the fitness functions become

$$W_V = \sum_{i=0}^{N-1} f_i (1 - a_V) - c + r \left\{ \sum_{i=0}^{N-1} f_i \left[\underbrace{(N-1-i)(1-a_V-c)}_{\text{volunteer}} + \underbrace{i(1-a_V)}_{\text{ignore}} \right] \right\}_{\text{kin}}$$

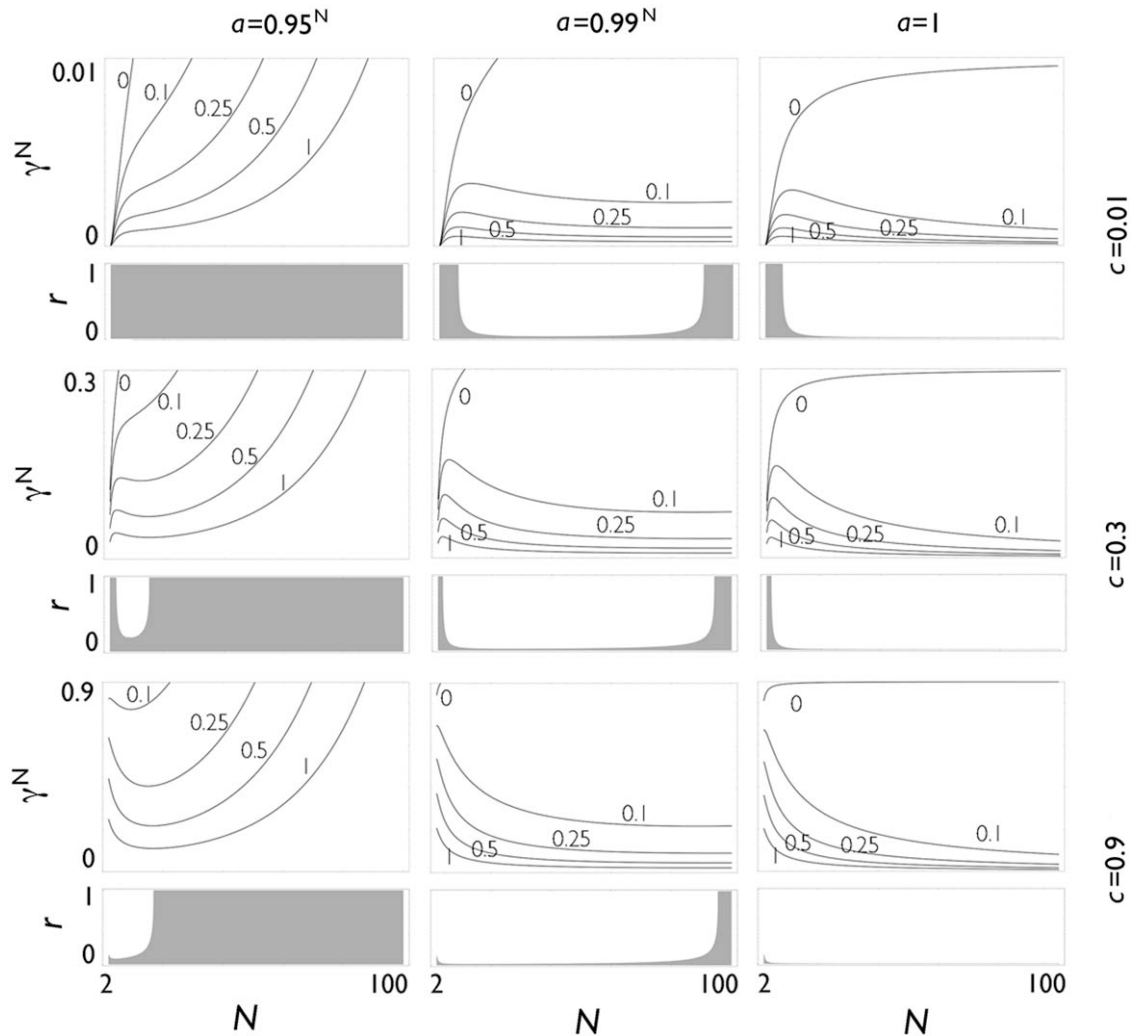


Fig. 1. The probability that nobody volunteers may increase with group size. Each panel is drawn for a combination of values of a (the cost if nobody volunteers) and c (the cost of volunteering) and shows on top the values of γ^N (the probability that nobody volunteers) for different values of r (the average relatedness between group members) as a function of N ; on the bottom the values of N and r for which γ^N increases with population size N (the area in grey). Note that the lines are drawn as continuous but they exist only for discrete, integer values of N ; $k = 1$.

$$W_I = \underbrace{\sum_{i=0}^{N-1} f_i(1 - a_i)}_{\text{self}} + r \left\{ \underbrace{\sum_{i=0}^{N-1} f_i \left[(N-1-i)(1-a_i-c) + i(1-a_i) \right]}_{\text{volunteer}} \right\}$$

I assume that the same collective good is produced when at least some individuals volunteer, that is

$$a_i = \begin{cases} 0 & \text{if } (N-1) - i \geq k \\ a & \text{if } (N-1) - i < k \end{cases}$$

$$a_v = \begin{cases} 0 & \text{if } (N-1) - i \geq k - 1 \\ a & \text{if } (N-1) - i < k - 1 \end{cases}$$

where i is the number of individuals that do not volunteer and $(N-1)$ is the number of other individuals (apart from the focal individual); therefore $(N-1)-i$ is the number of volunteers apart from the focal individual (who can be a volunteer or not); the cost a is the same for focal volunteers and focal non-volunteers, but while volunteers pay it only when $(N-1)-i < k-1$ (because they do volunteer and only need $k-1$ other volunteers), non-volunteers pay it when $(N-1)-i < k$, because they need k others to volunteer.

The mixed equilibrium (γ_{eq}) can be found, as before, by equating the payoffs (but in this case the results are found numerically). The probability that nobody volunteers, in this case, is

$$\pi = \sum_{i=N-k+1}^N \binom{N}{i} \gamma_{eq}^i (1 - \gamma_{eq})^{N-i}$$

Fig. 2 shows that the highest probability that nobody volunteers (π) and therefore the worst outcome for the group, occurs at intermediate values of k (the number of volunteers needed to produce the common good). Fitness is also reduced at intermediate values of k , at least for low values of relatedness, while with high relatedness it has a minimum at high values of k (Fig. 3). This is because the probability that the number of necessary volunteers in not reached increases with k , while the probability that there are already enough volunteers decreases with k . Note also that, with low relatedness, small changes in the magnitude of c can lead to a drastic change in the production of the collective good (Figs. 2–3).

3. Discussion

Social dilemmas (Hardin, 1968; Dawes, 1980) are situations in which the optimal strategy of an individual contrasts with the

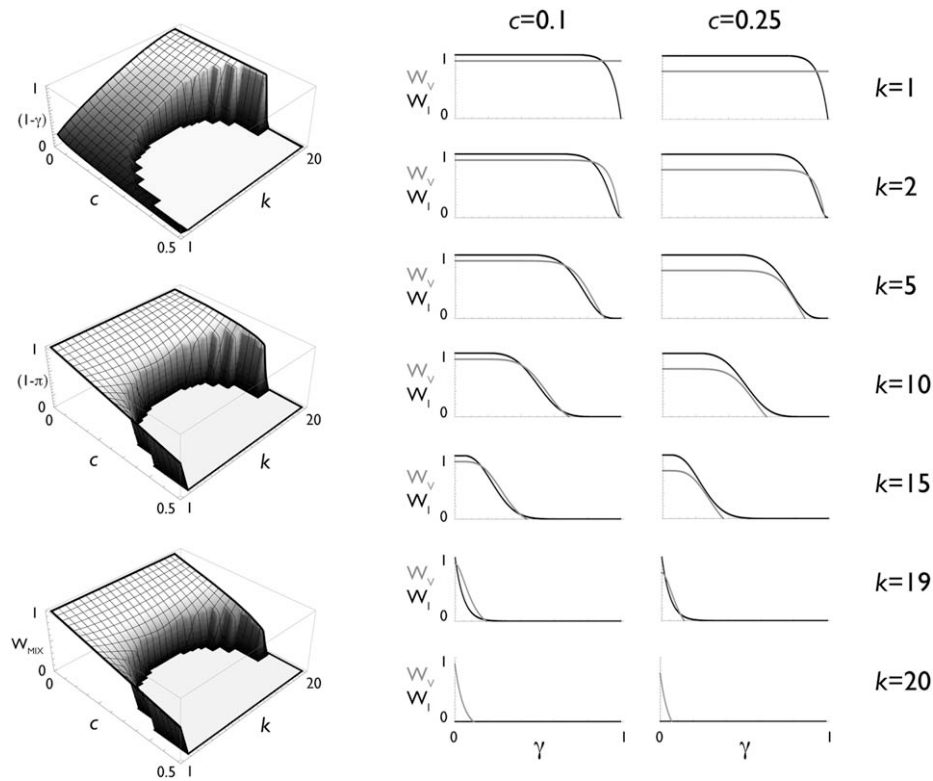


Fig. 2. Fitness and the collective good when more than one volunteer is needed. Left: the probability of volunteering $(1-\gamma)$, the probability that the collective good is produced $(1-\pi)$ and the fitness of the mixed equilibrium (W_{MIX}) as a function of k (the number of volunteers necessary to produce the common good) and c (the cost of volunteering), with no relatedness ($r = 0$); the population size (N) is 20 and the cost paid if nobody volunteers (a) is 1. Right: the fitness of the two pure strategies *Volunteer* (grey; W_V) and *Ignore* (black; W_I) as a function of γ (the probability of *Ignore*) for different values of k and c . Note that a mixed equilibrium exists only if W_V and W_I intersect; when this is the case, the higher equilibrium (lower γ) is stable (increasing γ reduces W_I , therefore *Ignore* does not invade; reducing γ reduces W_V , therefore *Volunteer* does not invade); the lower equilibrium (higher γ) is unstable (increasing γ increases W_I , therefore *Ignore* invades; reducing γ increases W_V , therefore *Volunteer* invades).

optimal result for the group, for example because an individual can exploit the benefits of living in a group without contributing to the costs. Social dilemmas may have a dominant strategy; the prisoner's dilemma (Tucker, 1950; Luce, and Raiffa 1957) and its N -person version are probably the most well-known cases. Other social dilemmas, however, do not have a dominant strategy; the volunteer's dilemma discussed here and the stag-hunt game (Pacheco et al., 2009) are two examples. It is misleading, therefore, to equate social dilemmas to the prisoner's dilemma.

3.1. Biological volunteer's dilemmas

The volunteer's dilemma I have described is relevant for cases in which one or few individuals are enough to perform a costly action that produces a collective good. It has been discussed in the social sciences (for the case of one volunteer: Diekmann, 1985), but it can be applied to many cases in biology.

In vertebrates, in groups that rely on alarm calls as a defense against predators, one or few individuals are enough to give the alarm, and giving the alarm may have non-negligible costs, for example because it increases the risk for the volunteer of being attacked by the predator (Searcy and Nowicki, 2005). The alarm produces a collective good but someone must volunteer to give it.

Replication enzymes produced by viruses co-infecting a cell (Turner and Chao, 2003), adhesive polymers produced by bacteria (Rainey and Rainey, 2003) and invertase produced by yeast (Gore et al., 2009) are also collective goods because they are produced outside the cell; they are costly to produce but must be produced by at least some of them.

En extreme case of volunteering can be found in the amoeba *Dictyostelium discoideum*: when facing starvation it differentiates

into a ball of spores, which reproduce, and a stalk, whose cells die. If one individual could avoid being in the stalk, it would have an advantage; however some individuals must volunteer to produce the stalk (Bonner, 1967). A similar situation occurs in *Myxococcus xanthus*, where cells become either spores or non-spores (Velicer et al., 2000).

In general, in all these cases, each individual prefers to avoid the cost of volunteering and exploit the benefit of the common goods produced by others, but someone must volunteer and pay the cost of producing the common good. The volunteer benefits from his action if nobody else volunteers, but the cost he pays is wasted if someone else already volunteers.

3.2. The optimal group size for the production of collective goods

The more individuals are available to volunteer, the less likely it is that someone actually volunteers and the collective good is produced. This is the main result of the volunteer's dilemma. Increasing group size therefore does not lead to a beneficial effect for the group. This problem persists even in the presence of a high degree of relatedness between group members. An optimal, intermediate group size exists for which the probability that someone volunteers is maximized. This optimal group size, however, is unstable because fitness increases with group size and an individual will always find it profitable to join larger groups.

The fact that optimal group size is unstable and smaller than actual group size has been recognized before under different scenarios (for example: Sibly, 1983; Giraldeau and Cillis, 1985; Clark and Mangel, 1984; Pulliam and Caraco, 1984) but in all these cases there is an upper limit to the actual group size beyond which

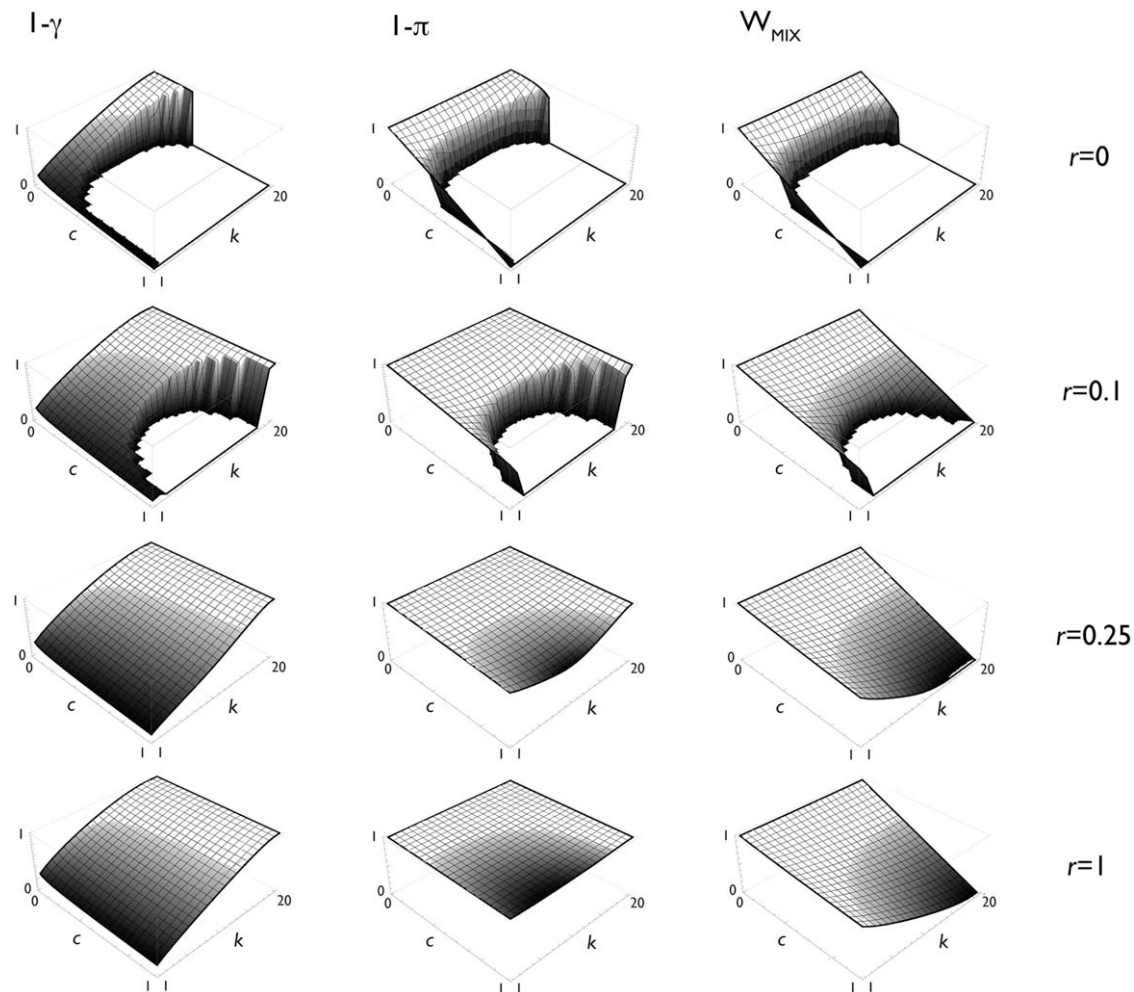


Fig. 3. Fitness and the collective good when more than one volunteer is needed, with relatedness. The probability of volunteering ($1-\gamma$), the probability that the collective good is produced ($1-\pi$) and the fitness of the mixed equilibrium (W_{MIX}) as a function of k (the number of volunteers necessary to produce the common good) and c (the cost of volunteering), with relatedness r ; the population size (N) is 20 and the cost paid if nobody volunteers (a) is 1.

it is no longer profitable to join a group. Competition for resources is the most obvious example: intermediate optima may occur when the direct benefits of group living (such as enhanced predator avoidance) increase rapidly in small groups but reach an asymptote in larger groups, while the direct costs (such as increased ectoparasitism and resource depletion) increase slowly in smaller groups, but rise rapidly in larger ones (Rannala and Brown, 1994). Even without density dependent effects on resources, a limited group size can be optimal when group members are related (Higashi and Yamamura, 1993).

The scenario described here, instead (the volunteer's dilemma) does not set, in principle, any limit to the size of a group. Here, in principle, groups always tend to become larger because individuals always benefit from joining a group. The dilemma is that the benefit for the group has a maximum at intermediate group size. A possible solution is clearly to limit group size to the optimal value. Individuals from outside the group will always find it profitable to enter a group, but resident individuals might adopt strategies to limit group size and exclude new individuals once the optimal group size has been reached.

3.3. Asymmetric equilibria

A possible solution to the volunteer's dilemma is to switch from a symmetric mixed equilibrium to an asymmetric equilibrium in

pure strategies in which only the necessary number of individuals volunteers every time and everybody is aware of it. If one volunteer is required, for example, and if individuals alternate perfectly, each pays the cost c only $1/N$ times and the inclusive fitness of individuals at this asymmetric equilibrium is $(1-c)/N+(N-1)/N+r(N-1)$, which is always higher than the fitness at the symmetric mixed equilibrium especially for low values of N and r . This solution, however, requires some kind of coordination. If asymmetries exist in the cost c , for example if some individuals pay a lower cost for volunteering, the player with the lowest cost will be the first to volunteer (for examples from the social sciences see Nalebuff and Bliss, 1984; Weesie, 1993).

In species that rely on alarm calls against predators, for example, living in groups of stable composition allows for the formation of a sentinel system, in which individuals can actually coordinate their vigilance. Florida scrub jays, (*Aphelocoma coerulescens coerulescens*), for example, live in family groups, and efficiently coordinate their vigilance against predators into a sentinel system, alternating bouts of watchfulness with little overlap (McGowan and Woolfenden, 1989; Bednekoff et al., 2008). In the Florida scrub jay, the presence of non-breeding helpers creates a clear asymmetry that favours the asymmetric equilibrium in which helpers are the ones that act as sentinels. Cooperative sentinel behaviour, however, does not seem to require clear asymmetries, as in the Arabian babbler (*Turdoides squamiceps*), which shows only very limited differences among group members in the rates of alarm calling (Wright et al., 2001). In meerkats

(*Suricata suricatta*) although individuals seldom take successive guarding bouts, there is no regular alternation; yet some coordination is achieved (Clutton-Brock, 1999).

3.4. Social dilemmas as volunteer's dilemmas

In the volunteer's dilemma each individual prefers to avoid the cost of volunteering and exploit the benefit of the collective goods produced by others, but someone must volunteer. The result is that each individual will volunteer with a certain probability. This probability decreases with group size and the probability that the collective good is produced also decreases with group size. The volunteer's dilemma, therefore, like the prisoner's dilemma, leads to a disappointing result for the society, although in the volunteer's dilemma cheating and cooperation coexist in a mixed equilibrium.

It is important to point out that volunteering does not require any relatedness nor reciprocation. Relatedness, as we have seen, affects the results but is by no means essential. In the extreme case of *Dictyostelium discoideum*, in which individuals that form the stalk die ($c=1$), a certain degree of relatedness is required. In general, however, volunteering does not require any relatedness. Reciprocation instead does not play any role, although it would be interesting to model an iterated version of the volunteer's dilemma and see what happens in the repeated game.

Social dilemmas are usually modelled as a prisoner's dilemma, in which it is always convenient to avoid the cost of cooperation. In a volunteer's dilemma, instead, avoiding volunteering pays only if others volunteer. In this case the relevant question is not "why do not cheaters invade?" but "how to increase the probability that the common good is produced?". This is a more practical question, for which more precise and practical answers can be found.

Acknowledgements

This work was supported by NSF grant SES-0750480.

References

- Bednekoff, P.A., Bowman, R., Woolfenden, G.E., 2008. Do conversational gutturals help Florida scrub-jays coordinate their sentinel behavior?. *Ethology* 114, 313–317.
- Bonner, J.T., 1967. *The Cellular Slime Molds*. Princeton University Press, Princeton.
- Clark, C.W., Mangel, M., 1984. Foraging and flocking strategies: information in an uncertain environment. *American Naturalist* 123, 626–641.
- Clutton-Brock, T.H., 1999. Selfish sentinels in cooperative mammals. *Science* 284, 1640–1999.
- Dawes, R.M., 1980. Social dilemmas. *Annual Review of Psychology* 31, 169–193.
- Diekmann, A., 1985. Volunteer's dilemma. *Journal of Conflict Resolution* 29, 605–610.
- Giraldeau, L.A., Cillis, D., 1985. Optimal group size can be stable. *Animal Behaviour* 33, 666–667.
- Gore, J., Youk, H., van Oudenaarden, A., 2009. Snowdrift game dynamics and facultative cheating in yeast. *Nature* 459, 253–256.
- Hardin, J., 1968. The tragedy of the commons. *Science* 162, 1243–1248.
- Hauert, C., De Monte, C., Hofbauer, J., Sigmund, K., 2002. Volunteering as red queen mechanism for cooperation in public goods games. *Science* 296, 1129–1132.
- Higashi, M., Yamamura, N., 1993. What determines animal group size? Insider-outsider conflict and its resolution. *American Naturalist* 142, 553–563.
- Luce, R.D., Raiffa, H., 1957. *Games and Decisions: Introduction and Critical Survey*. Wiley, New York.
- Maynard Smith, J., Price, G.R., 1973. The logic of animal conflict. *Nature* 246, 15–18.
- McGowan, K.J., Woolfenden, G.E., 1989. A sentinel system in the Florida scrub jay. *Animal Behaviour* 37, 1000–1006.
- Nalebuff, B., Bliss, C., 1984. Dragon-slaying and ballroom dancing, the private supply of a public good. *Journal of Public Economics* 25, 1–12.
- Pacheco, J.M., Santos, F.C., Souza, M.O., Skyrms, B., 2009. Evolutionary dynamics of collective action in N -person stag-hunt dilemmas. *Proceedings of the Royal Society B* 276, 315–321.
- Pulliam, H.R., Caraco, T., 1984. Living in groups, is there an optimal group size?. In: Krebs, J.R., Davies, N.B. (Eds.), *Behavioural Ecology, An Evolutionary Approach* second ed. Sunderland, Mass, Sinauer, pp. 122–147.
- Rainey, P.B., Rainey, K., 2003. Evolution of co-operation and conflict in experimental bacterial populations. *Nature* 425, 72–74.
- Rannala, B.H., Brown, C.R., 1994. Relatedness and conflict over optimal group size. *Trends in Ecology and Evolution* 9, 117–119.
- Rapoport, A., Chammah, A.M., 1966. The game of chicken. *American Behavioral Scientist* 10, 10–28.
- Searcy, W.A., Nowicki, S., 2005. *The Evolution of Animal Communication*. Princeton University Press, Princeton, NJ.
- Sibly, R.M., 1983. Optimal group size is unstable. *Animal Behaviour* 31, 947–948.
- Sugden, R., 1986. *The Economics of Rights, Cooperation and Welfare*. Blackwell, Oxford.
- Taylor, M., 1987. *The Possibility of Cooperation*. Cambridge University Press, Cambridge.
- Tucker, A., 1950. A two-person dilemma. In: Rasmusen, E. (Ed.) (2001). *Readings in Games and Information*. Blackwell, Oxford, pp. 7–8.
- Turner, P.E., Chao, L., 2003. Escape from prisoner's dilemma in RNA phage $\Phi 6$. *American Naturalist* 161, 497–505.
- Velicer, G.J., Kroos, L., Lenski, R.E., 2000. Developmental cheating in the social bacterium *Myxococcus xanthus*. *Nature* 404, 598–601.
- Weesie, J., 1993. Asymmetry and timing in the volunteer's dilemma. *Journal of Conflict Resolution* 37, 569–590.
- Wright, J., Berg, E., De Kort, S.R., Khazin, V., Maklakov, A.A., 2001. Cooperative sentinel behaviour in the Arabian babbler. *Animal Behaviour* 62, 973–979.