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Christoph Hauert, *et al.*
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# Via Freedom to Coercion: The Emergence of Costly Punishment

Christoph Hauert,[1] Arne Traulsen,[1] Hannelore Brandt,[2] Martin A. Nowak,[1] Karl Sigmund[3,4]*

In human societies, cooperative behavior in joint enterprises is often enforced through institutions that impose sanctions on defectors. Many experiments on so-called public goods games have shown that in the absence of such institutions, individuals are willing to punish defectors, even at a cost to themselves. Theoretical models confirm that social norms prescribing the punishment of uncooperative behavior are stable—once established, they prevent dissident minorities from spreading. But how can such costly punishing behavior gain a foothold in the population? A surprisingly simple model shows that if individuals have the option to stand aside and abstain from the joint endeavor, this paves the way for the emergence and establishment of cooperative behavior based on the punishment of defectors. Paradoxically, the freedom to withdraw from the common enterprise leads to enforcement of social norms. Joint enterprises that are compulsory rather than voluntary are less likely to lead to cooperation.

An impressive body of evidence shows that many humans are willing to pay a personal cost in order to punish wrongdoers (*1*–*8*). In particular, punishment is an effective mechanism to ensure cooperation in public goods interactions (*9*–*11*). All human populations seem willing to use costly punishment to varying degrees, and their willingness to punish correlates with the propensity for altruistic contributions (*12*). This raises an evolutionary problem: In joint enterprises, free-riding individuals who do not contribute, but who exploit the efforts of others, fare better than those who pay the cost of contributing. If successful behavior spreads, for instance through imitation, these defectors will eventually take over. Punishment reduces the defectors' payoff, and thus may solve the social dilemma. However, because punishment is costly, it also reduces the punishers' payoff. This raises a "second-order social dilemma": Costly punishment seems to be an altruistic act, given that individuals who contribute but do not punish are better off than the punishers. The emergence of costly punishing behavior is acknowledged to be a major puzzle in the evolution of cooperation. "We seem to have replaced the problem of explaining cooperation with that of explaining altruistic punishment" (*13*).

This puzzle can be solved in situations where individuals can decide whether to take part in the joint enterprise. We considered four strategies. The nonparticipants (individuals who, by default, do not join the public enterprise) rely on some activity whose payoff is independent of the other players' behavior. Those who participate include defectors, who do not contribute but exploit the contributions of the others; cooperators, who contribute but do not punish; and punishers, who not only contribute to the commonwealth but also punish the defectors. We showed that in such a model, punishers will invade and predominate. However, in the absence of the option to abstain from the joint enterprise, punishers are often unable to invade, and the population is dominated by defectors. This means that if participation in the joint enterprise is voluntary, cooperation-enforcing behavior emerges. If participation is obligatory, then the defectors are more likely to win.

This result was originally presented by Fowler (*14*), but he based his argument on a model that lacked an explicit microeconomical foundation. It assumes (i) that single cooperators can play the public goods game alone, which fails to recognize that contributing to a joint effort is a risky investment, the return of which depends on the behavior of other players, and (ii) that cooperators will be punished, even in the absence of defectors, which fails to recognize that the cooperators' unwillingness to punish cannot be observed in that case. Correcting for this leads to a dynamic that is structurally unstable for infinitely large populations and hence inconclusive (*15*). It is thus necessary to tackle the stochastic dynamics of finite populations.

We considered a well-mixed population of constant size $M$, the members of which live on a small but fixed income $\sigma$. In this situation, $N$ individuals are randomly selected and offered the option to participate instead in a risky, but potentially profitable, public goods game. Those who participate can decide whether or not to contribute an investment at a cost $c$ to themselves. All individual contributions are added up and multiplied with a factor $r > 1$. This amount is then divided equally among all participants of the public goods game. After this interaction, each contributor can impose a fine $\beta$ upon each defector, at a personal cost $\gamma$ for each fine. By $x$ we denote the total number of cooperators, by $y$ that of defectors, by $z$ that of the nonparticipants, and by $w$ the number of punishers. Thus, $M = x + y + z + w$.

Among the random sample of size $N$, there will be $N_x$ cooperators, $N_y$ defectors, $N_z$ nonparticipants, and $N_w$ punishers. These are random variables distributed according to a multivariate distribution which describes sampling without replacement. Each nonparticipant receives a constant payoff $\sigma$. The group of those willing to participate in the public goods game has size $S = N_x + N_y + N_w$. If $S > 1$, each participant of the public goods game obtains

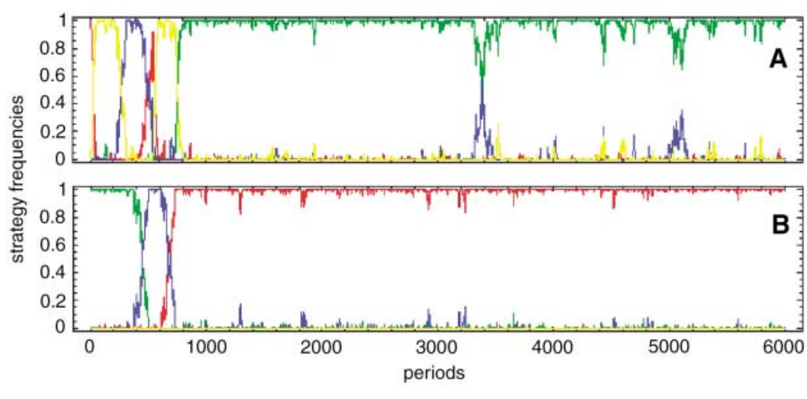


**Fig. 1.** Punishment and abstaining in joint-effort games. (**A**) Simulations of finite populations consisting of four types of players show that after some initial oscillations, punishers usually dominate the population. In longer runs, their regime can occasionally break down as a result of cooperators invading by neutral drift, but after another series of oscillations punishers will emerge again. The transient oscillations generally display a rock-paper-scissors–like succession of cooperators, defectors, and nonparticipants. When nonparticipants are frequent, groups are small, and punishing therefore is less costly, so that punishers have a chance to invade. (**B**) If participation is compulsory (no nonparticipants), defectors take over in the long run, even if the population consisted initially of punishers. Parameter values are $M = 100$, $N = 5$, $r = 3$, $\sigma = 1$, $\gamma = 0.3$, $\beta = 1$, $c = 1$, and $\mu = 0.001$.

[1]Program for Evolutionary Dynamics, Department of Organismic and Evolutionary Biology, Department of Mathematics, Harvard University, Cambridge, MA 02138, USA. [2]Vienna University of Economics and Business Administration, A-1090 Vienna, Austria. [3]Faculty of Mathematics, University of Vienna, A-1090 Vienna, Austria. [4]International Institute for Applied Systems Analysis, A-2361 Laxenburg, Austria.

*To whom correspondence should be addressed. E-mail: karl.sigmund@univie.ac.at

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an income $r(N_x + N_w)c/S$. The payoff for the contributors (i.e., the cooperators and the punishers) is reduced by $c$. The payoff for the defectors is reduced by $\beta N_w$, and the payoff for punishers by $\gamma N_y$. The social enterprise is risky in the sense that if all defect, the payoff is below that of the nonparticipants; it is promising in the sense that if all cooperate, the payoff is larger than that of the nonparticipants. This means that $0 < \sigma < (r - 1)c$. This assumption offers players a nontrivial choice: to stick with a safe, self-sufficient income or to speculate on a joint effort whose outcome is uncertain because it depends on the decisions of others. (If $S = 1$, then the public goods game does not take place. In this case, a single player who volunteers for the joint effort receives the default payoff σ.)

We next specify how strategies propagate within the population. We only need to assume that players can imitate each other and are more likely to imitate those with a higher payoff. This can be done in various ways (*16*, *17*). For simplicity, let us assume here that players can update their strategy from time to time by imitating a player chosen with a probability that is linearly increasing with that player's payoff. In addition, we shall assume that with a small probability μ, a player can switch to another strategy irrespective of its payoff (we refer to this as "mutation" without implying a genetic cause; it simply corresponds to blindly experimenting with the alternatives).

The analysis of the corresponding stochastic dynamics is greatly simplified in the limiting case $\mu \to 0$. The population consists almost always of one or two types at most. Indeed, for $\mu = 0$, the four monomorphic states are absorbing: If all individuals use the same strategy, imitation will not introduce any change. For sufficiently small μ, the fate of a mutant (i.e., its elimination or fixation) is settled before the next mutant appears (*18*). This allows us to calculate the probability that the population is in the vicinity of a pure state (i.e., composed almost exclusively of one type) (*17*). Computer simulations show that the approximation also holds for larger mutation rates (on the order of $1/M$).

The outcome is notable: In the limit of rare mutations, the system spends most of the time in the homogeneous state with punishers only, irrespective of the initial composition of the population. For large populations ($M = 1000$ can be considered large for most of our prehistory) and small mutation rates, the system spends most of the time in or near the punisher state (Figs. 1A and 2A; fig. S1). The outcome is robust with respect to changes in σ and $r$ (fig. S1).

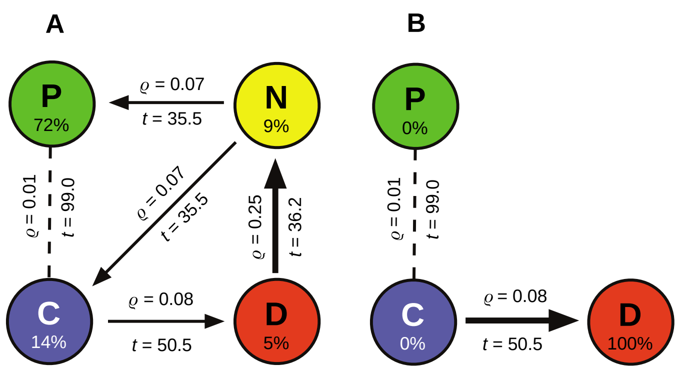


**Fig. 2.** Stationary probability distributions, transition probabilities, and fixation times can be computed analytically for sufficiently small mutation rates, if we assume that players update their strategies according to some specified rule. [In all figures, we use a Moran process with selection strength $s = 0.249$ (*17*) (SOM text).] The dynamics are reduced to transitions between homogeneous population states consisting entirely of cooperators (C), defectors (D), nonparticipants (N), or punishers (P). The transition probabilities ρ denote the probabilities that a single mutant takes over; the conditional fixation time $t$ indicates the average number of periods required for a single mutant to reach fixation, provided that the mutant takes over. (**A**) Voluntary participation in the joint-effort game with punishment. Parameter values are $N = 5$, $r = 3$, $\sigma = 1$, $\gamma = 0.3$, $\beta = 1$, $c = 1$, and $M = 100$. (**B**) Compulsory participation in a joint-effort game with punishment, for the same parameter values.

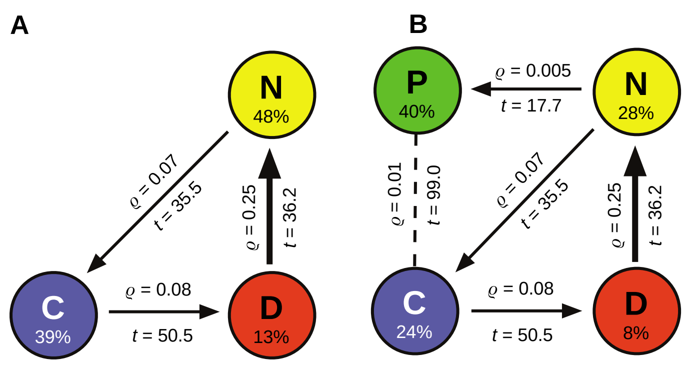


**Fig. 3.** Punishment is best directed at defectors only. (**A**) Same as in Fig. 2A, but without punishers. The three remaining strategies supersede each other in a rock-paper-scissors type of cycle. (**B**) Same as in Fig. 2A, but assuming that punishers equally punish the nonparticipants. This makes it more difficult for punishers to dominate.

The situation is very different in the traditional case of a public goods game where participation is compulsory. If only cooperators and defectors are present, defectors obviously win. Adding the punishers as a third strategy does not change the qualitative outcome: In the limit of rare mutations, the system spends most of the time in or near the state with defectors only. For the same parameter values as before, the state is time dominated by defectors, and there is hardly any economic benefit from the interaction (Figs. 1B and 2B; fig. S2).

Volunteering in the absence of punishment leads to a more cooperative outcome than for the obligatory game, but not to the fixation of the cooperative state (Fig. 3A). Instead, the system exhibits a strong tendency to cycle (from cooperation to defection to nonparticipation and back to cooperation), as a result of a rock-paper-scissors mechanism (*19*–*21*). If there are many defectors, it does not pay to participate in the joint enterprise, but if most players refuse to participate, then the typical group size can become sufficiently small such that the social dilemma disappears: Cooperators earn on average more than defectors (and nonparticipants). However, this is a fleeting state only; cooperators spread quickly, group size increases, the social dilemma returns and the cycle continues.

The gist of the analysis for small mutation rates is captured in Fig. 2. The effect of substantial mutation rates can only be handled by numerical simulations (*17*, *22*). In the absence of punishers, defectors do worst, whereas nonparticipants and cooperators perform comparably well. In the compulsory game, punishers do not prevail, except for large mutation rates, in which case mutational drift supplying defectors keeps the punishers active and prevents them from being undermined by cooperators. If all four types are admitted, punishers prevail.

This result remains unaffected if we assume that the punishers are also punishing the cooperators (who are not punishing defectors, and thus can be viewed as second-order defectors). It is well known that any norm that includes the rule to punish those who deviate is evolutionarily stable—once established, it cannot be displaced by an invading minority of dissidents (*9*). But how can such punishing behavior gain a foothold in the population? The trait has to be rare, initially, and thus will incur huge costs by ceaselessly punishing. To model this situation, it seems plausible to assume that for this second type of punishment, fines and costs are reduced

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by a factor α, with $0 \le \alpha \le 1$ (*14*). Thus the payoff for cooperators is reduced by $\alpha\beta N_w$, and that for punishers by $\alpha\gamma N_x$, provided that $N_y > 0$ (if there are no defectors in the group, nonpunishing behavior will go unnoticed). As it turns out, whether cooperators who fail to punish are punished plays a surprisingly small role. The parameter α has little influence on the dynamics (*17*). The reason is that for small μ, the three types of punishers, cooperators, and defectors rarely coexist. Hence, punishers cannot hold cooperators accountable for not punishing defectors. Interestingly, experimental evidence for the punishment of nonpunishers (i.e., for nonvanishing α) seems to be lacking (*23*).

We could also assume that punishers penalize nonparticipants, with a fine δβ and the cost to the punisher δγ (with $0 \le \delta \le 1$). Although this further stabilizes punishment once it is established, it also hinders the emergence of punishment (Fig. 3B) (*17*). It follows that resorting to stricter forms of social coercion may not be an efficient way to increase cooperation. Second-order punishment ($\alpha > 0$) barely affects the outcome, whereas punishing nonparticipants ($\delta > 0$) can even lead to contrary effects. The system responds to an increase in compulsion with a decrease in cooperation.

When punishers are common, individual-level selection against them is weak (because only little punishment occurs) and may be overcome by selection among groups (*11*). Several other models confirm that the punishment of defectors is stable provided that it is the prevalent norm. This happens, for example, if some degree of conformism in the population is assumed (*10*); individuals preferentially copy what is frequent. Similarly, cooperation in the public goods game can also be stabilized through additional rounds of pairwise interactions based on indirect reciprocity. In this case, players can reward contributors (*24*, *25*). Even so, in each case, the emergence of the prosocial norm remains an open problem (*26*, *27*).

Our model, in contrast, shows that even when initially rare, punishing behavior can be advantageous and is likely to become fixed. We consider the most challenging scenario, namely, a single well-mixed population whose members imitate preferentially the behavior that fares better, not the behavior that is more common. Once established, group selection, conformism, and reputation effects may maintain prosocial norms and promote their spreading. Eventually, institutions for punishing free-riders may arise, or genetic predispositions to punish dissidents.

Recent experiments show that if players can choose between joining a public goods game either with or without punishment, they prefer the former (*28*). The interpretation seems clear: Whoever freely accepts that defection may be punished is unlikely to be a defector. For contributors, it is thus less risky to join such a group. Players voluntarily commit themselves to sanctioning rules. This voluntary submission is not immediate, however. In the majority of cases, it requires a few preliminary rounds. Many players appear to have initial reservations against the possibility of sanctions and need a learning phase. In another series of experiments, it has been shown that a threat of punishment can decrease the level of cooperation in trust games (*29*). Experimental evidence for costly punishment can also be found in the ultimatum game (rejecting an unfair offer is costly to both players) (*2*) and in indirect reciprocity (by not helping defectors, players reduce their own chances of being helped) (*30*). If punishment is combined with rewarding through indirect reciprocity, punishment is focused on the worst offenders and is otherwise strongly reduced in favor of rewarding contributors (*31*). In all of these investigations, and in the experiments on voluntary public goods games without punishment (*21*), there is ample evidence that players can adapt their strategy from one round to the next, as a reaction to the current state of the population. Our model is based on this aptitude for social learning.

In our framework, the joint effort represents an innovation, a new type of interaction that improves the payoff of participants if it succeeds, but costs dearly if it fails. Abstaining from such a risky enterprise does not mean living a hermit's life. It means collecting mushrooms instead of participating in a collective hunt, remaining at home in lieu of joining a raiding party, dispersing in the woods rather than erecting a stronghold against an invader, and growing potatoes on one's plot of land instead of handing it over to a commons likely to be ruined by overgrazing.

Our model predicts that if the joint enterprise is optional, cooperation backed by punishment is more likely than if the joint enterprise is obligatory. Sometimes, there is no way to opt out of a public goods project—the preservation of our climate is one example (*32*). In that case, participation is obligatory, and defection widespread.

Reports from present-day hunter-gatherer societies often stress their egalitarian and "democratic" features: Individuals have a great deal of freedom (*33*). This creates favorable conditions for voluntary participation. On the other hand, ostracism was probably an early form of severe punishment. There seems to be a smooth transition between choosing not to take part in a joint enterprise and being excluded. Together, these two alternatives may explain the emergence of rule-enforcing institutions promoting prosocial behavior, following Hardin's recipe for overcoming the "tragedy of the commons": mutual coercion, mutually agreed upon (*34*).

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## Via Freedom to Coercion: The Emergence of Costly Punishment

Christoph Hauert, Arne Traulsen, Hannelore Brandt, Martin A. Nowak, Karl Sigmund*

*To whom correspondence should be addressed. E-mail: karl.sigmund@univie.ac.at

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# Supporting online material:
# Via freedom to coercion: the emergence of costly punishment

Christoph Hauert [1], Arne Traulsen [1], Hannelore Brandt [2], Martin A. Nowak [1] & Karl Sigmund [3,4,*]

[1] Program for Evolutionary Dynamics, Department of Organismic and Evolutionary Biology, Department of Mathematics, Harvard University, One Brattle Square, Cambridge, MA 02138, USA

[2] Vienna University of Economics and Business Administration, A-1090 Vienna, Austria

[3] Faculty of Mathematics, University of Vienna, A-1090 Vienna, Austria

[4] International Institute for Applied Systems Analysis, A-2361 Laxenburg, Austria

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## Analysis

In order to obtain analytic expressions, we chose, among the plethora of possible updating rules governing the transmission of strategies, a specific stochastic process. There are many candidates. For instance, with 'imitate the better', two players are chosen at random and the one with the lower payoff adopts the strategy of the player with the higher payoff. With the 'proportional imitation' rule, the player with the lower payoff adopts the strategy of the more successful player, with a probability proportional to the payoff difference. For our analysis, we adopt what is known as the frequency dependent Moran process (*1*, *2*): each individual updates by imitating a player who is selected with a probability proportional to its 'fitness'. We define each players' fitness as $1 - s + sP$, the convex combination of the 'baseline fitness', which is normalised to $1$ for all players, and the payoff $P$ from the optional public goods game with punishment. The relative importance of the two components is determined by $s$, which is usually called selection strength. We shall assume that occasionally, each player can change strategy by imitating a player chosen with a probability proportional to that player's fitness. This mimics a learning process similar to the Moran process describing natural selection: more successful players are more likely to be copied. In addition, we shall assume that with a small probability $\mu$, a player can switch to another strategy irrespective of its payoff (this 'mutation term' corresponds to blindly experimenting with anything different).

The analysis of the corresponding stochastic dynamics is greatly simplified in the limiting case $\mu \to 0$. The population consists almost always of one or two types at most. This holds because for $\mu = 0$ the four monomorphic states are absorbing, and for sufficiently small $\mu$ the fate of a mutant (i.e. its elimination or fixation) is settled before the next mutant appears. Thus the transitions between the four pure states - cooperators, defectors, non-participants and punishers - occur when a mutant appears and spreads to fixation (*3*).

In finite populations, the groups engaging in a public goods game are given by multivariate hypergeometric sampling. For transitions between two pure states, this reduces to sampling (without replacement) from a hypergeometric distribution. In a population of size $M$ with $m_i$ individuals of type $i$ and $m_j = M - m_i$ of type $j$, the probability to select $k$ individuals of type $i$ and $N - k$ individuals of type $j$ in $N$ trials is

$$H(k, N, m_i, M) = \frac{\binom{m_i}{k}\binom{M-m_i}{N-k}}{\binom{M}{N}}. \tag{1}$$

Thus, in a population of $x$ cooperators and $y = M - x$ defectors, the average payoffs to cooperators $P_{xy}$ and defectors $P_{yx}$ are

$$P_{xy} = \sum_{k=0}^{N-1} H(k, N-1, x-1, M-1)\left(\frac{k+1}{N}r - 1\right) = \frac{r}{N}\left(1 + (x-1)\frac{N-1}{M-1}\right) - 1$$

$$P_{yx} = \sum_{k=0}^{N-1} H(k, N-1, x, M-1)\left(\frac{k}{N}r\right) = \frac{r(N-1)}{N(M-1)}x.$$

Similarly, the payoffs $P_{ij}$ of strategy type $i$ competing against type $j$ for the other possible pairings are

$$
\begin{aligned}
P_{zx} &= P_{zy} = \sigma \\
P_{xz} &= P_{wz} = r - 1 - \frac{\binom{z}{N-1}}{\binom{M-1}{N-1}}(r - 1 - \sigma) \\
P_{yz} &= \frac{\binom{z}{N-1}}{\binom{M-1}{N-1}}\sigma \\
P_{xw} &= P_{wx} = r - 1 \\
P_{yw} &= \frac{(N-1)(r - N\beta)}{N(M-1)}w \\
P_{wy} &= \frac{r}{N} - 1 - \gamma(N-1) + \frac{(N-1)(r + N\gamma)}{N(M-1)}(w-1) \\
P_{zw} &= \sigma - \frac{N-1}{M-1}\delta\beta w \\
P_{wz} &= r - 1 - \frac{\binom{z}{N-1}}{\binom{M-1}{N-1}}(r - 1 - \sigma) - \frac{N-1}{M-1}\delta\gamma z
\end{aligned}
$$

The fitness of an individual of type $i$ in a mixed population of types $i$ and $j$ is then given by $1 - s + sP_{ij}$. Since the fitness has to be positive, there is an upper limit on the intensity of selection $s$ given by $s_{\text{max}} = 1/(1 - \min P_{ij})$ for all strategic types $i, j$ under consideration. The above payoffs together with $s$ determine the probability to change the number of individuals $m_i$ of type $i$ by $\pm 1$, $T_{ij}^{\pm}$ :

$$
T_{ij}^{+} = \frac{m_i(1 - s + sP_{ij})}{M(1-s) + s(m_i P_{ij} + (M - m_i)P_{ji})}\frac{M - m_i}{M} \tag{2a}
$$

$$
T_{ij}^{-} = \frac{(M - m_i)(1 - s + sP_{ji})}{M(1-s) + s(m_i P_{ij} + (M - m_i)P_{ji})}\frac{m_i}{M} \tag{2b}
$$

From these transition probabilities, the fixation probability $\rho_{ij}$ of a single mutant strategy of type $i$ in a resident population of type $j$ can be derived (*2*, *4*):

$$
\rho_{ij} = \frac{1}{\sum_{k=0}^{M-1}\prod_{m_i=1}^{k}\frac{T_{ij}^{-}}{T_{ij}^{+}}} = \frac{1}{\sum_{k=0}^{M-1}\prod_{m_i=1}^{k}\frac{1 - s + sP_{ji}}{1 - s + sP_{ij}}} \tag{3}
$$

Finally, the fixation probabilities $\rho_{ij}$ define the transition probabilities of a Markov process between the four different homogeneous states of the population. The transition matrix $\mathbf{A}$ is given by:

$$
\mathbf{A} = \begin{pmatrix} 1-\rho_{yx}-\rho_{zx}-\rho_{wx} & \rho_{xy} & \rho_{xz} & \rho_{xw} \\ \rho_{yx} & 1-\rho_{xy}-\rho_{zy}-\rho_{wy} & \rho_{yz} & \rho_{yw} \\ \rho_{zx} & \rho_{zy} & 1-\rho_{xz}-\rho_{yz}-\rho_{wz} & \rho_{zw} \\ \rho_{wx} & \rho_{wy} & \rho_{wz} & 1-\rho_{xw}-\rho_{yw}-\rho_{zw} \end{pmatrix} \tag{4}
$$

The normalized right eigenvector to the largest eigenvalue (which is $1$ for the matrix $\mathbf{A}$) determines the stationary distribution, i.e. indicates the probability to find the system in one of the four homogeneous states. It is given by

$$
\phi = \frac{1}{\mathcal{N}} \begin{bmatrix} \begin{pmatrix} \rho_{wy}\rho_{wz}\rho_{xw} + \rho_{wz}\rho_{xy}\rho_{xw} + \rho_{wy}\rho_{xz}\rho_{xw} + \rho_{xy}\rho_{xz}\rho_{xw} + \rho_{wy}\rho_{yz}\rho_{xw} + \rho_{xy}\rho_{yz}\rho_{xw} \\ +\rho_{wz}\rho_{zy}\rho_{xw} + \rho_{xz}\rho_{zy}\rho_{xw} + \rho_{wz}\rho_{xy}\rho_{yw} + \rho_{xy}\rho_{xz}\rho_{yw} + \rho_{xy}\rho_{yw}\rho_{yz} \\ +\rho_{wy}\rho_{xz}\rho_{zw} + \rho_{xy}\rho_{xz}\rho_{zw} + \rho_{xy}\rho_{yz}\rho_{zw} + \rho_{xz}\rho_{yw}\rho_{zy} + \rho_{xz}\rho_{zw}\rho_{zy} \end{pmatrix} \\ \begin{pmatrix} \rho_{wx}\rho_{wz}\rho_{yw} + \rho_{wx}\rho_{xz}\rho_{yw} + \rho_{wz}\rho_{yx}\rho_{yw} + \rho_{xz}\rho_{yx}\rho_{yw} + \rho_{wx}\rho_{yz}\rho_{yw} + \rho_{yx}\rho_{yz}\rho_{yw} \\ +\rho_{wz}\rho_{zx}\rho_{yw} + \rho_{yz}\rho_{zx}\rho_{yw} + \rho_{wz}\rho_{xw}\rho_{yx} + \rho_{xw}\rho_{xz}\rho_{yx} + \rho_{xw}\rho_{yx}\rho_{yz} \\ +\rho_{xz}\rho_{yx}\rho_{zw} + \rho_{wx}\rho_{yz}\rho_{zw} + \rho_{yx}\rho_{yz}\rho_{zw} + \rho_{xw}\rho_{yz}\rho_{zx} + \rho_{yz}\rho_{zw}\rho_{zx} \end{pmatrix} \\ \begin{pmatrix} \rho_{wx}\rho_{wy}\rho_{zw} + \rho_{wx}\rho_{xy}\rho_{zw} + \rho_{wy}\rho_{yx}\rho_{zw} + \rho_{wy}\rho_{zx}\rho_{zw} + \rho_{xy}\rho_{zx}\rho_{zw} + \rho_{wx}\rho_{zy}\rho_{zw} \\ +\rho_{yx}\rho_{zy}\rho_{zw} + \rho_{zx}\rho_{zy}\rho_{zw} + \rho_{wy}\rho_{xw}\rho_{zx} + \rho_{xw}\rho_{xy}\rho_{zx} + \rho_{xy}\rho_{yw}\rho_{zx} \\ +\rho_{wx}\rho_{yw}\rho_{zy} + \rho_{xw}\rho_{yx}\rho_{zy} + \rho_{yw}\rho_{yx}\rho_{zy} + \rho_{xw}\rho_{zx}\rho_{zy} + \rho_{yw}\rho_{zx}\rho_{zy} \end{pmatrix} \\ \begin{pmatrix} \rho_{wx}\rho_{wy}\rho_{wz} + \rho_{wx}\rho_{xy}\rho_{wz} + \rho_{wy}\rho_{yx}\rho_{wz} + \rho_{wy}\rho_{zx}\rho_{wz} + \rho_{xy}\rho_{zx}\rho_{wz} + \rho_{wx}\rho_{zy}\rho_{wz} \\ +\rho_{yx}\rho_{zy}\rho_{wz} + \rho_{zx}\rho_{zy}\rho_{wz} + \rho_{wx}\rho_{wy}\rho_{xz} + \rho_{wx}\rho_{xy}\rho_{xz} + \rho_{wy}\rho_{xz}\rho_{yx} \\ +\rho_{wx}\rho_{wy}\rho_{yz} + \rho_{wx}\rho_{xy}\rho_{yz} + \rho_{wy}\rho_{yx}\rho_{yz} + \rho_{wy}\rho_{yz}\rho_{zx} + \rho_{wx}\rho_{xz}\rho_{zy} \end{pmatrix} \end{bmatrix} \tag{5}
$$

where the normalisation factor $\mathcal{N}$ has to be chosen such that the elements of $\phi$ sum up to one. S 1 and S 2 display the stationary distribution as a function of the selection strength $s$.

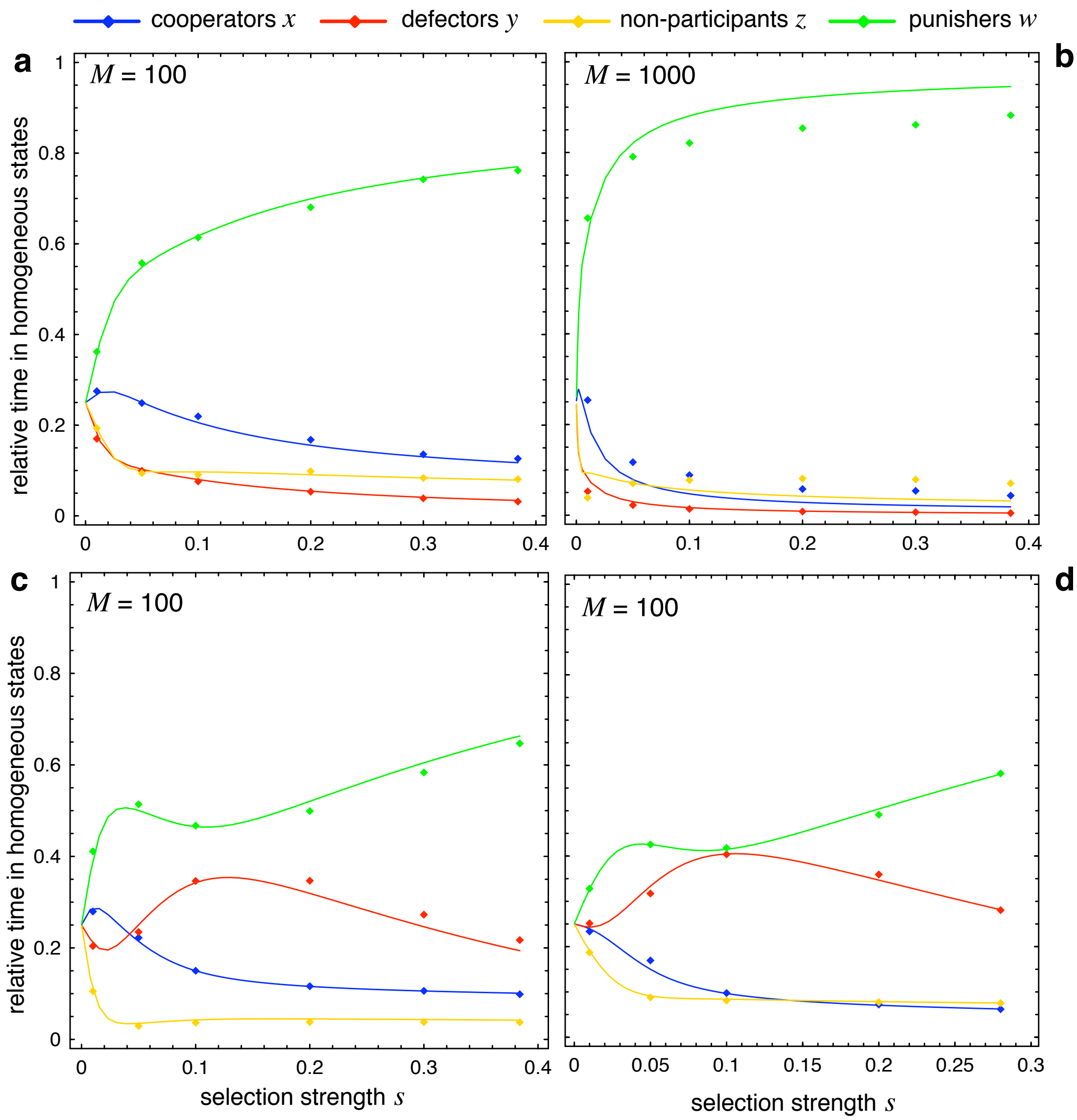


Figure 1: Punishment and abstaining in public goods games. For rare mutations, the dynamics is restricted to transitions between the four homogeneous states consisting entirely of cooperators (blue), defectors (red), non-participants (yellow) and punishers (green). All panels depict the probabilities of each state as a function of the selection strength $s < s_{\max} = 0.384$ for $N = 5, r = 3, \sigma = 1, \gamma = 0.3, \beta = 1$. In the limit of neutral evolution ($s = 0$), all states become equally likely. **a** Punishers are clearly dominant in voluntary joint enterprises with punishment. **b** The success of punishers is even more pronounced for larger population sizes. *(continued)*

Figure 1 *(continued)*: Individual-based simulation data confirms the analytical results for small mutation rates (colored dots, $\mu = 0.001$ **a** $M = 100$, sampling time $T = 10^7$, **b** $M = 1000, T = 10^6$). Whenever $> 90\%$ of the population opt for one strategy it is counted as being in the respective homogeneous state. The payoff determination, the mutation rate and the $90\%$ threshold are responsible for the systematic deviations but also illustrate the robustness of the model. **c** Lowering the payoff of non-participants to $\sigma = 0.1$ (one tenth of $\sigma$ in **a**,**b**) obviously reduces the risk of the public goods game, i.e. encourages participation and hence supports defectors. Nevertheless, punishers reign unchallenged. **d** Additionally, lowering the return of the joint effort to $r = 1.8$ impedes both cooperators and punishers but punishers win (somewhat surprisingly since in infinite populations, non-participants win and joint enterprises are abandoned for $r < 2$).

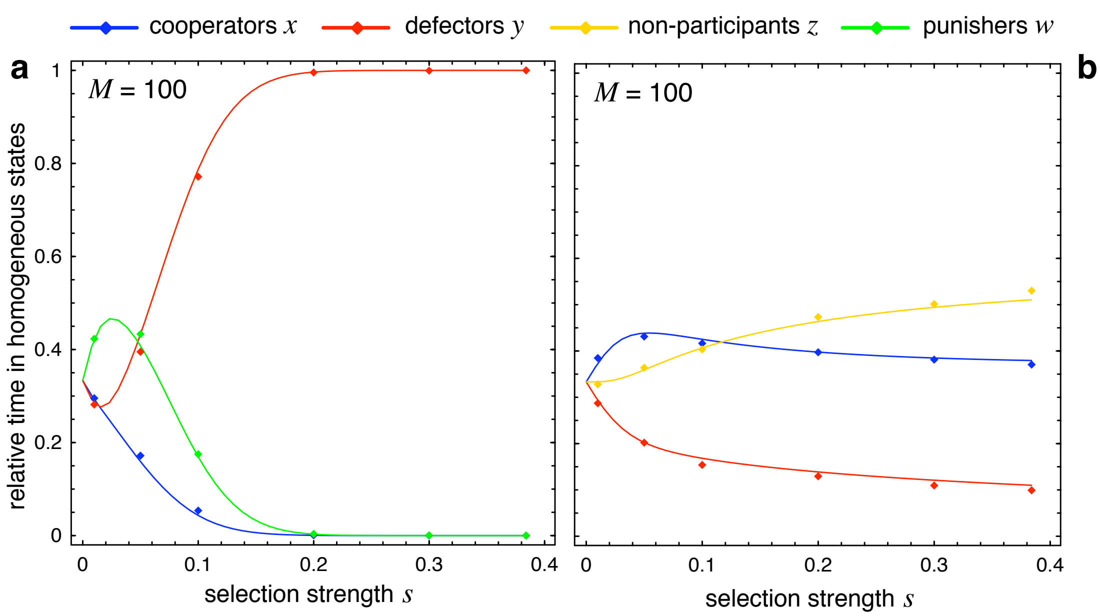


Figure 2: The role of non-participants and punishers in public goods games (all parameters are identical to S 1a). **a** Despite punishment, defectors reign in compulsory games except for very weak selection. **b** In the absence of punishers, no strategy clearly dominates due to the systems' tendency to cycle between cooperators, defectors and non-participants. However, the system spends significantly more time in the states with all cooperators or non-participants than in the defector state.

## Fixation time of punishers

In the limit of rare mutations, the average time to reach the punisher state for the first time can be derived analytically. This fixation time $\tau_i$ when starting in a pure state of $i$ (which can be $x$, $y$ or $z$ for cooperators, defectors, and non-participants, respectively) satisfies

$$\tau_i = 1 + \sum_{j=x,y,z} \tau_j \cdot R_{ji}, \tag{6}$$

where the time $\tau_i$ is measured in updating periods (which consist of $M$ individual update steps) and $R_{ji} = \delta_{ji} + \nu_j (A_{ji} - \delta_{ji})$ where $A_{ji}$ denotes the transition probability from pure state $i$ to pure state $j$ (see Eq. 4), $\delta_{ji}$ denotes the Kronecker symbol and $\nu_j$ denotes the rate at which mutants of type $j$ are produced. If all mutants are equally likely, this rate is simply $\nu_j = \mu M/3$ (on average there are $\mu M$ mutations per generation). Solving for $\tau_j$ leads to

$$\begin{pmatrix} \tau_x \\ \tau_y \\ \tau_z \end{pmatrix} = \frac{3}{\mu M} \begin{pmatrix} \rho_{yx} + \rho_{zx} + \rho_{wx} & -\rho_{yx} & -\rho_{zx} \\ -\rho_{xy} & \rho_{xy} + \rho_{zy} + \rho_{wy} & -\rho_{zy} \\ -\rho_{xz} & -\rho_{yz} & \rho_{xz} + \rho_{yz} + \rho_{wz} \end{pmatrix}^{-1} \begin{pmatrix} 1 \\ 1 \\ 1 \end{pmatrix}. \tag{7}$$

Thus, in the limit of rare mutations, the average waiting time to reach the punishment state scales inversely with the mutation rate $\mu$. According to numerical simulations, this relation still holds for larger $\mu$ as shown in S 3. However, for $\mu$ of the order $1/M$ or larger, pure states and their close vicinity may no longer be accessible.

Note, that the fixation times follow an exponential distribution. Hence the average fixation time equals its standard deviation and thus has limited predictive power for specific realizations. In the limit of neutral selection ($s = 0$) the fixation time of punishers reduces to $\tau_x = \tau_y = \tau_z = 3/\mu$.

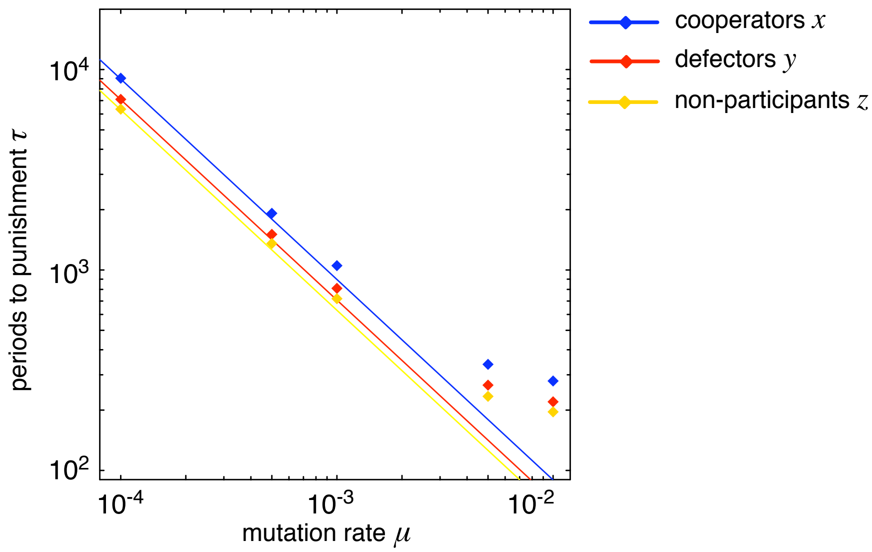


Figure 3: Average waiting time $\tau$ to reach the punisher state when starting with all cooperators (blue), defectors (red) or non-participants (yellow) as a function of the mutation rate $\mu$. The lines depict the analytical solution (see Eq. 10) for maximal selection strength. The symbols indicate simulation results for different mutation rates $\mu$. In order to determine whether the punisher state has been reached, a threshold of $90\%$ was used. Parameters: $N = 5, r = 3, \sigma = 1, \gamma = 0.3, \beta = 1, \alpha = 0, M = 100, s = 0.384$.

## Enforcing cooperation

Punishers can attempt to enforce cooperation through different means. In order to avoid second order free-riding, punishers can punish cooperators who have failed to punish defectors ($\alpha > 0$) or they can enforce participation in the joint effort game by punishing the non-participants ($\delta > 0$). The very small effects of second order punishment ($\alpha > 0$) are illustrated in S 4. Note that $\alpha$ does not enter the analytical approximation for the limit of vanishing $\mu$. For larger values of $\mu$, it barely affects the simulation results.

For $\delta > 0$ a new unstable equilibrium point appears along the non-participant–punisher edge. This results in bi-stability between the two states, just as between the defector and the punisher state. However, for small $\delta$ and/or weak selection, punishers can still relatively easily invade non-participant populations and reach the critical threshold through random drift. In this case the general conclusions of the main text remain unaffected (S 5).

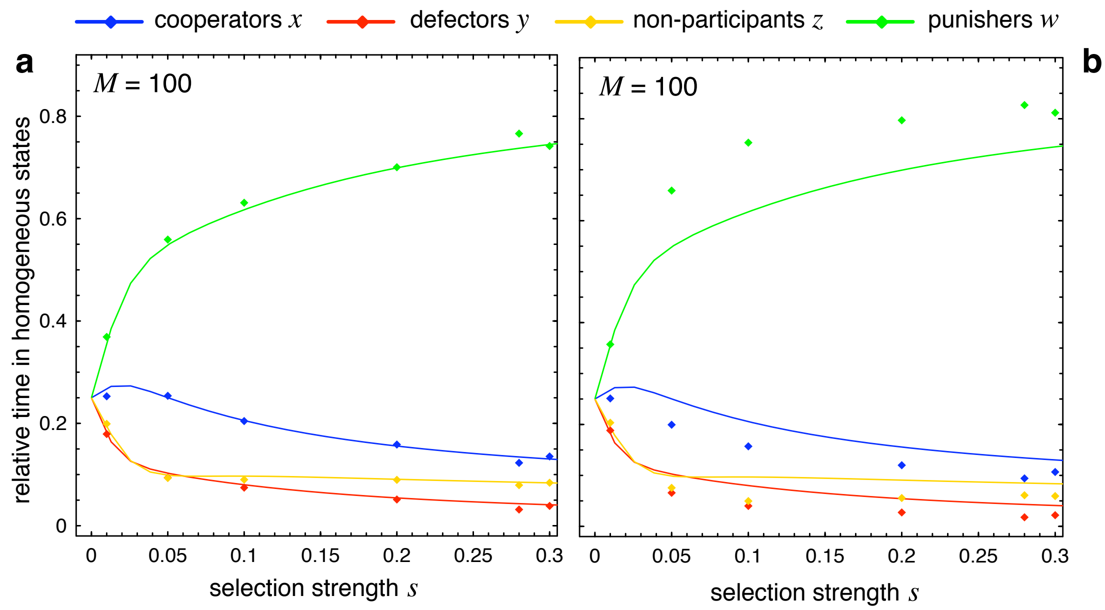


Figure 4: Effects of second order free-riding ($\alpha > 0$) in simulations as compared to the analytical results that are independent of $\alpha$. (**a**) For mild punishment of non-punishing cooperators, $\alpha = 0.1$, the result is essentially indistinguishable from the case $\alpha = 0$ (c.f. S 1a). (**b**) Equal punishment of cooperators and defectors, $\alpha = 1$, strengthens the position of punishers and the system spends even more time in the punisher state. However, punishers can invade less easily. Parameters: $N = 5, r = 3, \sigma = 1, \gamma = 0.3, \beta = 1, \delta = 0, M = 100, \mu = 0.01, s_{\text{max}} = 0.384$; **a** $\alpha = 0.1$; **b** $\alpha = 1$.

For small $\delta$ and strong selection, the systems generally spends $> 60\%$ in the punisher state and the defector state is suppressed to levels $< 10\%$ (S 5a). Similarly, punishers dominate for large $\delta$ and weak selection (S 5b). However, for large $\delta$ and strong selection the bi-stability essentially prevents transitions from the non-participant state to the punisher state or vice versa. Thus, punishment can only be established by invading cooperators through random drift. As a consequence, the system spends more time in the cooperator state and less in the punisher state. Quite intriguingly, punishment of non-participants does not diminish their success but, in fact, actually increases the time in the non-participant state. Nevertheless, even for large $\delta$ and strong selection punishers dominate with $40\%$ and the systems spends roughly equal times cooperator and non-participant state with around $25\%$ each, leaving merely $10\%$ for defectors. Interestingly, such strict social coercion maintains close to $60\%$ cooperation in total (cooperators

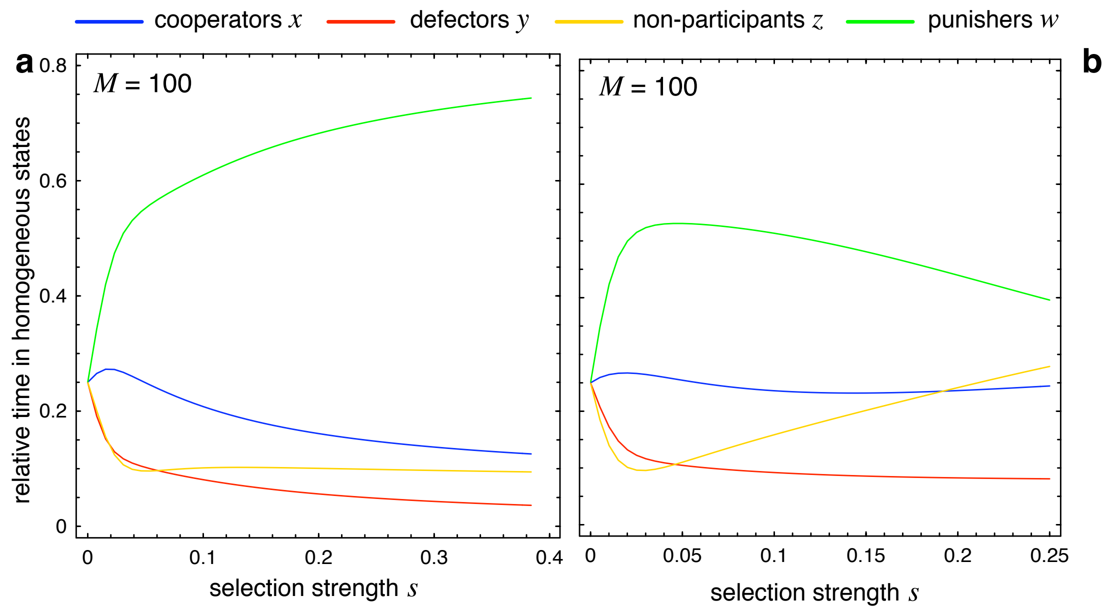


Figure 5: Effects of social coercion by punishing non-participants. (**a**) For mild measures against non-participants, the outcome is barely affected: punishers dominate (c.f. S 1a). (**b**) In contrast, heavy measures against non-participants tend to undermine the success of punishment and actually result in an increase of cooperators and non-participants while leaving the frequency of defectors largely unaffected. Parameters: $N = 5, r = 3, \sigma = 1, \gamma = 1, \beta = 2, \alpha = 0, M = 100$; **a** $\delta = 0.1, s_{\text{max}} = 0.151$; **b** $\delta = 1, s_{\text{max}} = 0.125$.

plus punishers), whereas the scenario with purely voluntary participation ($\delta = 0$) results in more than $80\%$ cooperation (c.f. S 1a). Hence the system responds to coercion by actually reducing the readiness to cooperate.

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specify a feedback coupling and determine the resulting interaction function; this has been done, for example, for coupled neural oscillators (*9*). In what amounts to turning the problem on its head, Kiss *et al.* proceed in the reverse direction: They specify the interaction function that they would like to have (that is, the interaction function that generates some specified behavior), and then follow an optimization procedure to determine the feedback that generates it.

The result is a systematic procedure for generating a wide variety of dynamical behaviors. One of the simplest is synchronization, where all oscillations are at the same frequency and the phase difference between each pair of oscillators is constant. By carefully choosing the target interaction function, however, the optimized feedback allows dynamics that switch between different synchronized states, each with a distinct set of phase differences. Still another choice for the target interaction function produces complete desynchronization when the feedback control is turned on. This is the goal in anti-pacemaker applications when one needs to destroy some pathological global resonance.

There is a voluminous literature on the mathematics of coupled oscillators. The approach of Kiss *et al.* is unique in that it does not merely involve theoretical models of coupled nonlinear oscillators, or a comparison between such theoretical models and experimental results. Rather, it shows that such models can be made sufficiently accurate to provide precise control of experimental systems.

There are obvious limitations to the approach. The oscillators need to be sufficiently similar to one another, and the interactions must be independent of their spatial location—one cannot have specific arrangements in space, as for a school of fish or a flock of birds. In addition, there are cases of continuous spatiotemporal evolution, such as the Belusov-Zhabotinsky reaction, where one cannot identify specific agents and decompose the system into an array of discrete oscillators. But the method is worthy of further exploration. The ability to use a light touch is a strong plus, engineering change without altering the essential nature of the system. The possibility of doing so in the absence of detailed information about the elements of the system is another.

Ecological systems have a natural rhythm and, despite formidable obstacles, it may be tempting to look for applications in this area. The most promising applications, however, may arise in medical science and biological systems—not by creating order, but by destroying synchronization. Parkinson's disease and epilepsy are two compelling and challenging examples. The former is already being treated with some success using deep brain stimulation (*10*); it is hoped that further research into both the oscillations in the brain involved in such disorders and methods of the type introduced by Kiss *et al.* will, one day, lead to new, more effective ways of alleviating such conditions.

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BEHAVIOR

# A Narrow Road to Cooperation

A new model of collective action shows how socially beneficial punishment can arise and evolve.

**Robert Boyd and Sarah Mathew**

In every human society, from small-scale foraging bands to gigantic modern nation states, people cooperate with each other to solve collective-action problems. They share food to ensure against shortfalls, risk their lives in warfare to protect their group, work together in building canals and fortifications, and punish murderers and thieves to maintain social order. Because collective action benefits everyone in the group, whether or not they contribute, natural selection favors noncontributors. So, why do people contribute? Everyday experience suggests that people contribute to avoid being punished by others.

But this answer raises a second question: Why do people punish? From an evolutionary perspective, this question has two parts: First, how can contributors who punish avoid being replaced by "second-order" free-riders who contribute but do not incur the cost of punishing? There has been much work on this topic lately, and plausible solutions have emerged (*1*–*5*). However, these solutions are not much good unless we can solve the second problem: How can punishment become established within populations in the first place? On page 1905 of this issue, Hauert *et al.* provide the first cogent answer to this question (*6*). Surprisingly, they find that punishment can become established if there are individuals who neither produce collective benefits nor consume collective benefits produced by others.

In previous models of the evolution of collective action, individuals in a group can either contribute and benefit from the public good (i.e., cooperate), or not contribute and benefit (i.e., defect). In the absence of punishment, defection wins. However, if punishment is possible and punishers are common, it does not pay to defect. But punishment is costly to impose. A rare punisher in a group of defectors suffers an enormous disadvantage from having to punish everyone in the group. This means that in very large populations, punishment can sustain cooperation when punishment is common, but punishing strategies cannot increase in numbers when they are rare (i.e., invade a population of defectors). In a finite population, random chance affects the number of each type that reproduce, and the resulting stochastic fluctuations allow punishers to eventually invade a population of defectors, even though selection favors defectors. However, it can take a very long time for this to occur, and thus, most of the time there is no punishment and no cooperation.

Hauert *et al.* provide a way out of this dilemma. They introduce a strategy that simply opts out of collective action. These "nonparticipants" neither contribute to the collective good nor consume the benefits, but instead pursue some solitary activity. Surprisingly, this innovation allows punishment to increase when rare. To see why, consider a population of defectors. Hauert *et al.* assume that nonparticipants get a

The authors are in the Department of Anthropology, University of California, Los Angeles, CA 90095, USA. E-mail: rboyd@anthro.ucla.edu



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**In or out? (Top)** A group of Hadza men hunting cooperatively. Hadza hunter-gatherers living in Tanzania sometimes consume smaller kills in the bush, consistent with the Hauert *et al*. model. **(Center)** People from the village of Lamalera, Indonesia, hunt whales cooperatively. This form of cooperative hunting exhibits strong economies of scale not represented in the Hauert *et al*. model. **(Bottom)** Demonstrators in Kiev during the first anniversary of the Orange Revolution, November 2005. In the contemporary world people often participate in collective political action whose benefits are not excludable.

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higher payoff than defectors who attempt to free-ride when there are no cooperators in their group. Therefore, nonparticipants invade the defectors. Now, consider a population of all nonparticipants. Hauert *et al.* assume that two contributors working together can produce a higher payoff than a nonparticipant working alone. This means that rare contributors invade nonparticipants. Once contributors are common, defectors invade, and the cycle continues. The three strategies oscillate endlessly (*7*).

The key contribution of the current paper is to show that punishers readily invade this oscillating mixture of cooperators, defectors, and nonparticipants, and once they do they tend to persist. The reason is that defectors are absent during part of each cycle of the oscillation, and as a result punishers are not selected against during these periods. Consequently, stochastic fluctuations in a finite population cause punishers to invade rapidly. Once common, punishers do better than other types, and it takes a long time for cooperators and then defectors to drift back in. This means that the population spends most of the time in a happy state in which cooperation and punishment of defectors predominate.

Adding nonparticipants to the standard models required Hauert *et al.* to make a number of new assumptions. Three of these are crucial; punishment cannot invade without them. There are many examples of collective action that do not conform to these assumptions, and, as a consequence, the model explains the origin of punishment for some kinds of collective action but not others.

First, the collective good must be excludable. Otherwise, abstaining from the benefits once the good is created is not an option. In human societies, collective action produces many types of goods, and not all are excludable. For instance, if warriors steal cows on a cattle raid (*8*) and keep the cows that they steal, the booty doesn't benefit the entire group—the good is excludable (see the figure). On the other hand, when warriors successfully defend a village from an invading army, the benefits of deterrence from future attacks and protection of land, belongings, and lives flows to everyone in the victorious group—the good is not excludable.

Second, Hauert *et al.* assume that opting out is better than mutual defection. This assumption applies when defectors experience some opportunity cost that nonparticipants do not. For example, in some settings, hunters consume small kills before they return to camp (*9*). To share such kills, you need to leave your garden for the day and join a hunting party. But if the hunting party that you join consists of defectors who don't work hard enough to make a kill, you will be worse off than nonparticipants who stayed home and tended their gardens. However, in many small-scale societies, hunters bring their kills back to camp (*10*, *11*), where others have a chance to scrounge some meat. Here, defectors can tend their gardens just like nonparticipants, but then scrounge. In this case, defection has at least as high a payoff as opting out.

Third, Hauert *et al*. assume that there are no economies of scale. In their model, the per capita payoff from participating in collective action does not depend on the number of contributors, only on the ratio of contributors to defectors. This means that two contributors who work together can generate the same per capita payoff as a much larger group of contributors. This assumption applies to the payoff structure of recent public goods experiments (*12, 13*) and approximates some real-world situations like sharing food to reduce the risk of shortfall (*14*). However, many collective action problems are subject to strong economies of scale. These include warfare, hunting large game (*15*, *16*), and the construction and maintenance of capital facilities like forts, irrigation works, and roadways. These examples are important because it is the ability to mobilize sizable groups to solve such problems that distinguishes human cooperation from that of other mammals.

The model by Hauert *et al.* is an important contribution because it provides the first cogent mechanism that can jump-start the evolution of punishment. It can help us to understand the evolution of collective action in which benefits are excludable, opting out is preferable to mutual defection, and there are no economies of scale. The challenge is now to understand how punishment can arise in the remaining cases.

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