

populations may decrease cooperation and lead to more frequent escalations of conflicts in situations in which cooperation persists in well-mixed populations. Thus, spatial structure may not be as universally beneficial for cooperation as previously thought. □

Methods

Spatial structure

In our spatially structured populations, individuals are confined to sites on regular 100×100 lattices with periodic boundary conditions, and interact with their neighbours. We used square lattices with $N = 4$ and $N = 8$ neighbours, hexagonal lattices ($N = 6$) and triangular lattices ($N = 3$). Whenever a site x is updated, a neighbour y is drawn at random among all N neighbours; the chosen neighbour takes over site x with probability $w_y = f(P_y - P_x)$, where the function f translates payoff differences into reproductive success, reflecting natural selection based on relative fitness. The site x remains unchanged, with probability $1 - w_y$. Lattice updating can be either synchronous or asynchronous. For synchronous updates, first all individuals interact in their respective neighbourhood and then all sites are updated simultaneously through competition with a randomly chosen neighbour. For asynchronous updates, only a single, randomly selected focal site is updated at each simulation step: first the payoffs of the focal individual and a random neighbour are determined, after which these two individuals compete to re-populate the focal site. See Supplementary Information for the case where competition involves all neighbours, rather than just a randomly chosen one.

Pure strategies

With pure strategies, each individual is either a cooperator or a defector. Lattices are initialized randomly with equal proportions of the two strategies. $f(z) = z_+/\alpha$ determines the transition probabilities, where z_+ is equal to z if $z > 0$ and 0 otherwise, and where $\alpha = T - P$ in the snowdrift game and $\alpha = T - S$ in the Prisoner's Dilemma, ensuring that $f(P_y - P_x) \leq 1$. In well-mixed populations this implements the replicator dynamics¹⁷. Equilibrium frequencies of cooperators and defectors are obtained by averaging over 1,000 generations after a relaxation time of 5,000 generations.

The individual-based spatial models are complemented by deterministic pair-approximation (ref. 28 and see Supplementary Information). This approach correctly predicts a decrease in the frequency of cooperators in spatially structured populations, but it underestimates the effects of local correlations: for larger r the fragility of cooperative clusters is underrated, as is the ability of cooperators to displace defectors for small r (Fig. 1). Near the extinction thresholds, interesting symmetrical dynamics occur: tiny patches of defectors (cooperators) meander in a sea of cooperators (defectors). Occasionally they divide into pairs or collide and vanish. This resembles a branching and annihilating random walk, which suggests that there are critical phase transitions and points to interesting relationships between game theory and condensed matter physics²⁹.

Mixed strategies

For mixed strategies in the hawk–dove game, an individual is characterized by the probability p to show dove-like behaviour. Exploration of this continuous strategy space requires mutations. Whenever an individual with strategy p reproduces, a mutation occurs with a small probability (0.01) that assigns the offspring the strategy $p + \xi$, where ξ denotes a gaussian-distributed random variable with a mean of 0 and an s.d. of 0.002. To speed up simulations, the lattice is initialized with random strategies drawn from a normal distribution with a mean corresponding to the equilibrium strategy in well-mixed populations and an s.d. of 0.02. The simulation results are insensitive to the initialization details.

An individual in x with strategy p interacting with a neighbour with strategy q gets an average payoff $P_x = pqR + p(1 - q)S + (1 - p)qT + (1 - p)(1 - q)P$. The small difference in the strategies of parents and mutant offspring leads to small payoff differences $P_y - P_x$ between neighbouring individuals. Thus, the update rule for pure strategies returns small probabilities for a strategy change, which slows down the simulations. We therefore used the nonlinear function $f(z) = [1 + \exp(-z/\kappa)]^{-1}$, in which κ is a noise term that reflects uncertainties in assessing the payoffs. This nonlinearity greatly speeds up the simulations and introduces an interesting and realistic form of error, whereby a worse performing player occasionally manages to reproduce. For $\kappa \rightarrow \infty$, errors in assessing the payoffs increase until no information is left and the players randomly adopt neighbouring strategies. We used $\kappa = 0.1$ in our simulations. The equilibrium levels of dove-like behaviour were determined by evolving the lattice over 10,000 generations and then averaging the mixed strategies over another 1,000 generations.

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Correspondence and requests for materials should be addressed to C.H. (hauert@zoology.ubc.ca).

Emergence of cooperation and evolutionary stability in finite populations

Martin A. Nowak^{1,2}, Akira Sasaki⁴, Christine Taylor^{1,5} & Drew Fudenberg³

¹Program for Evolutionary Dynamics, ²Department of Organismic and Evolutionary Biology and Department of Mathematics, ³Department of Economics, Harvard University, Cambridge, Massachusetts 02138, USA

⁴Department of Biology, Kyushu University, Fukuoka 812-8581, Japan

⁵Department of Mathematics, MIT, Cambridge, Massachusetts, 02139, USA

To explain the evolution of cooperation by natural selection has been a major goal of biologists since Darwin. Cooperators help others at a cost to themselves, while defectors receive the benefits of altruism without providing any help in return. The standard game dynamical formulation is the 'Prisoner's Dilemma'^{21–11}, in which two players have a choice between cooperation and defection. In the repeated game, cooperators using direct reciprocity cannot be exploited by defectors, but it is unclear how such cooperators can arise in the first place^{12–15}. In general, defectors are stable against invasion by cooperators. This understanding is based on traditional concepts of evolutionary stability and

dynamics in infinite populations^{16–20}. Here we study evolutionary game dynamics in finite populations^{21–25}. We show that a single cooperator using a strategy like ‘tit-for-tat’ can invade a population of defectors with a probability that corresponds to a net selective advantage. We specify the conditions required for natural selection to favour the emergence of cooperation and define evolutionary stability in finite populations.

In the Prisoner’s Dilemma, two players are offered a certain

payoff, R , for mutual cooperation and a lower payoff, P for mutual defection. If one player cooperates while the other defects, then the cooperator gets the lowest payoff, S , while the defector gains the highest payoff, T . Thus, we have $T > R > P > S$. In the non-repeated Prisoner’s Dilemma, defectors dominate cooperators, which means that in any mixed population, defectors have a higher fitness. In the repeated Prisoner’s Dilemma, the same two players meet more than once, and there are many conceivable strategies that allow cooperative behaviour which cannot be defeated by defectors. The most famous such strategy is tit-for-tat (TFT), in which the player cooperates in the first round and then does whatever the opponent did in the previous round. Another strategy is always to defect (AllD). If the number of rounds is sufficiently large, then AllD and TFT resist invasion attempts by the other strategy. Thus, TFT can maintain cooperation, but how it can become established is unclear.

In the standard evolutionary model of the finitely repeated Prisoner’s Dilemma, TFT cannot invade AllD, because if everyone in an infinitely large population uses AllD, then a small fraction of TFT players have a lower payoff. Every invasion attempt by TFT is therefore eliminated by natural selection. Past work has proposed several modifications to this model that allow TFT to invade successfully: (1) a mass of TFT players arises simultaneously to overcome an invasion barrier¹²; (2) TFT players form spatial clusters^{13,14}; or (3) aggregate payoffs are stochastic¹⁵. Here we show that none of these modifications are necessary to explain the emergence of cooperation in finite populations.

Consider a game between two strategies, A and B, with payoff matrix:

$$\begin{matrix} & \begin{matrix} A & B \end{matrix} \\ \begin{matrix} A \\ B \end{matrix} & \begin{pmatrix} a & b \\ c & d \end{pmatrix} \end{matrix} \quad (1)$$

If A and B denote, respectively, TFT and AllD, then we have $a > c > d > b$ provided the number of rounds is finite and greater than $(T - P)/(R - P)$. In this case, both TFT and AllD are strict Nash equilibria and evolutionarily stable strategies (ESS).

Box 1

Game dynamics in finite populations

The fitness of strategies A and B with payoff matrix (1) is, respectively, given by:

$$\begin{aligned} f_i &= 1 - w + w[a(i - 1) + b(N - i)]/[N - 1] \\ g_i &= 1 - w + w[c + d(N - i - 1)]/[N - 1] \end{aligned} \quad (4)$$

Here i denotes the number of individuals using strategy A, and $w \in [0, 1]$ specifies the contribution of the game to fitness. Selection dynamics can be formulated as a Moran process with frequency-dependent fitness. At each time step, an individual is chosen for reproduction proportional to its fitness. One identical offspring is being produced that replaces another randomly chosen individual. Thus N is strictly constant. The probability of adding an A-offspring is $f_i/[f_i + (N - i)g_i]$. At each time step, the number of A individuals can either increase by one, stay the same, or fall by one. Therefore, the transition matrix of the Markov process is tri-diagonal and defines a birth–death process given by:

$$\begin{aligned} P_{i,j+1} &= \frac{f_i}{f_i + (N - i)g_i} \frac{N - i}{N} \\ P_{i,j-1} &= \frac{(N - i)g_i}{f_i + (N - i)g_i} \frac{i}{N} \end{aligned} \quad (5)$$

We have $P_{i,i} = 1 - P_{i,j+1} - P_{i,j-1}$. All other entries of the transition matrix are 0.

The process has two absorbing states, $i = 0$ and $i = N$: if the population has reached either one of those states, then it will stay there forever. We denote by x_i the probability of ending up in state $i = N$ when starting in state i . We have:

$$x_i = P_{i,j+1}x_{i+1} + P_{i,j}x_i + P_{i,j-1}x_{i-1} \quad (6)$$

with boundary conditions $x_0 = 0$ and $x_N = 1$.

Let us calculate the probability, $\rho_A (= x_1)$, that a single individual A can invade and take over a population of B players. Solving equation (6), we obtain²⁷:

$$\rho_A = 1 / \left(1 + \sum_{k=1}^{N-1} \prod_{i=1}^k \frac{g_i}{f_i} \right) \quad (7)$$

If $\rho_A > 1/N$, then selection favours A replacing B.

The rate of evolution from all-B to all-A is given by $r = N\rho_A u$, where u is the mutation rate. We can rescale the rate of evolution in units of u . Thus, we set $u = 1$. The rate of evolution, r , can be an increasing or decreasing function of w . There can also be a maximum or minimum value of r for some intermediate $w \in (0, 1)$. It is possible that $r > 1$ for small w , but $r < 1$ for large w , or vice versa. For $w = 0$, we have $r = 1$.

In the limit of weak selection, $w \ll 1$, we find that:

$$N\rho_A \approx 1/[1 - (\alpha N - \beta)(w/6)] \quad (8)$$

with $\alpha = a + 2b - c - 2d$ and $\beta = 2a + b + c - 4d$. From this equation, we see that $N\rho_A > 1$ if $\alpha N > \beta$, which leads to equation (2). If $\alpha > 0$ then there is a minimum N for which $N\rho_A > 1$. It is given by $N_{\min} = \beta/\alpha$.

We define a strategy to be an ESS_N if selection opposes the invasion and fixation of any other strategy for any $w > 0$. Thus a necessary condition for ESS_N is that $N\rho_A$, as given by equation (8), is less than one. If instead we want to know whether a strategy is evolutionarily stable for a given N and a given w , then we cannot necessarily use the simplified equation (8), which only holds in the limit of small w . Instead, we have to check that the exact expression $N\rho_A$, as given by equation (7), is less than one.

Box 2

Invading AllD

Let strategies A and B denote, respectively, TFT and AllD in a Prisoner’s Dilemma which is repeated for n rounds on average. The payoff matrix is $a = Rn$, $b = S + P(n - 1)$, $c = T + P(n - 1)$ and $d = Pn$. If the average number of rounds, n , exceeds $(T - P)/(R - P)$ then we have $a > c > d > b$. In this case, there is an unstable equilibrium between TFT and AllD, and neither strategy can invade the other in the context of deterministic dynamics of infinitely large populations.

Condition (2) implies $n(R - P)(N - 2) > T(N + 1) - S(2N - 1) + P(N - 2)$. This inequality determines the minimum number of rounds required for (weak) selection to favour TFT replacing AllD for a given N . We need at least $N = 3$. For large N , the number of rounds must fulfill $n > (T + P - 2S)/(R - P)$. Let $R = 3$, $T = 5$, $P = 1$, $S = 0$. For $N = 3$ we have $n > 10.5$. For $N = 4$ we have $n > 6.75$. For large N we have $n > 3$.

Among all strategies of the repeated Prisoner’s Dilemma, TFT maximizes the probability of invading AllD in any finite population. More precisely, TFT belongs to a set of strategies that maximize this probability. All strategies of this set have the following property: (1) when playing themselves they cooperate all the time; (2) when playing AllD they cooperate on the first move and then never again. ‘Win-stay, lose-shift’ and ‘generous tit-for-tat’ have lower invasion probabilities because they attempt to cooperate with AllD too often. They work best once cooperation has been established^{12,30}.

Deterministic replicator dynamics of infinite populations admit an unstable equilibrium at a frequency of TFT given by $x^* = (d - b)/(a - b - c + d)$. If the initial frequency of TFT is less than this value, then it will be eliminated by natural selection. TFT can only replace ALLD if its initial frequency exceeds this invasion barrier. The same evolutionary dynamics hold for ALLD competing with other cooperative strategies such as ‘generous tit-for-tat’, ‘contrite tit-for-tat’ or ‘win-stay, lose-shift’.

We now study evolutionary game dynamics in finite populations. In this case, there is always a non-zero probability that a mutant strategy can invade and take over the population even though it is opposed by selection. TFT invading ALLD has a lower fitness if its frequency is less than x^* but has a higher fitness if its frequency is greater than this threshold. What is the probability that a single TFT player will take over a population of ALLD players?

Consider a stochastic process describing a finite population of size N . At each time step, one individual is chosen for reproduction proportional to its fitness, and its offspring replaces a randomly chosen individual²⁶. The population size is constant. The fitness of each player depends on the number of TFT or ALLD players. In addition, we introduce a parameter, w , which determines the contribution of the game’s payoff to fitness. This parameter, quantifying the intensity of selection, cancels itself out in deterministic replicator dynamics of infinite populations, but plays a crucial role in the stochastic process that we study here.

We calculate the probability, ρ_A , that a single individual using strategy A will invade and take over a population of B players²⁷ (Box 1). For a neutral mutant²⁸ this fixation probability is $\rho_A = 1/N$. If $\rho_A > 1/N$ then selection favours A replacing B. In Fig. 1, we show that in the case of TFT and ALLD, $N\rho_A$ is a one-humped function of N . For a wide choice of parameter values a, b, c, d and w there is an intermediate range of population sizes which ensure $N\rho_A > 1$. Thus, the invasion and replacement of ALLD by TFT, starting from a single individual of TFT, can be favoured by natural selection. Interestingly, there are critical minimum and maximum population sizes that allow positive selection of TFT. In very small populations, there is a strong effect of spite: helping another individual leads to a significant disadvantage. For example, in a population of only two players, TFT always has a lower fitness than ALLD. In a very large population it is extremely unlikely to reach the invasion barrier when starting with a single TFT player. Thus, neither small nor large but intermediate population sizes are optimum for initiating cooperation.

Can we derive the underlying principle that determines whether a particular payoff matrix (1) allows selection for TFT replacing

ALLD? The exact expression for ρ_A is complicated. The condition $\rho_A > 1/N$ requires the solution of N th-order polynomials, and a diffusion approximation yields transcendental equations. Nevertheless, the following surprisingly simple theorem holds. For a given N and sufficiently weak selection (small w), selection favours TFT replacing ALLD if:

$$a(N - 2) + b(2N - 1) > c(N + 1) + d(2N - 4) \quad (2)$$

For the smallest possible population size, $N = 2$ (it takes two to play), inequality (2) yields $b > c$ (which is not possible for the game between TFT and ALLD). For the limit of large N , we obtain $a + 2b > c + 2d$. The latter condition is equivalent to $x^* < 1/3$. Therefore, if the invasion barrier of TFT is less than 1/3, there can be positive selection for TFT to replace ALLD in a finite population (Box 2).

In general, for any two strategies which are the best replies to themselves, we find that selection can favour A replacing B for some N and w , if $b > c$ or $x^* < 1/3$ (Fig. 2).

Our results have immediate consequences for the concept of evolutionary stability. The well-known definition of an ESS is motivated by selection dynamics in infinite populations^{16–20}. Strategy B is an ESS if either (1) $d > b$ or (2) $d = b$ and $a < c$. These conditions imply that selection opposes the spread of infinitesimally small fractions of A in infinitely large populations of B.

For finite N , we propose that B is an ESS, denoted ESS_N , if two conditions hold: (1) selection opposes A invading B, which means that a single mutant A in a population of B has a lower fitness; and (2) selection opposes A replacing B, which means $\rho_A < 1/N$, for any $w > 0$. The first condition is equivalent to $b(N - 1) < c + d(N - 2)$. The second condition, for small w , is equivalent to $a(N - 2) + b(2N - 1) < c(N + 1) + d(2N - 4)$. For $N = 2$, both conditions reduce to $b < c$. For large populations, the two conditions lead to $b < d$ and $x^* > 1/3$, respectively. Hence, for small populations, the traditional ESS concept is neither necessary nor sufficient; for large populations, it is necessary but not sufficient (Fig. 3). If we consider a game with many different strategies, then the two conditions must hold in pairwise comparison with every other strategy.

The motivation of the ESS_N concept is as follows. If a strategy is an ESS_N , then a single mutant of any other strategy must have a lower fitness. Therefore, selection opposes the initial spread of any other strategy. As we have seen in the case of ALLD and TFT, however, in a finite population it is possible that the fixation of a strategy is favoured by selection even though its initial increase is opposed by selection. Thus, the second condition states that a strategy can only be an ESS_N if the fixation probability of all other strategies is less

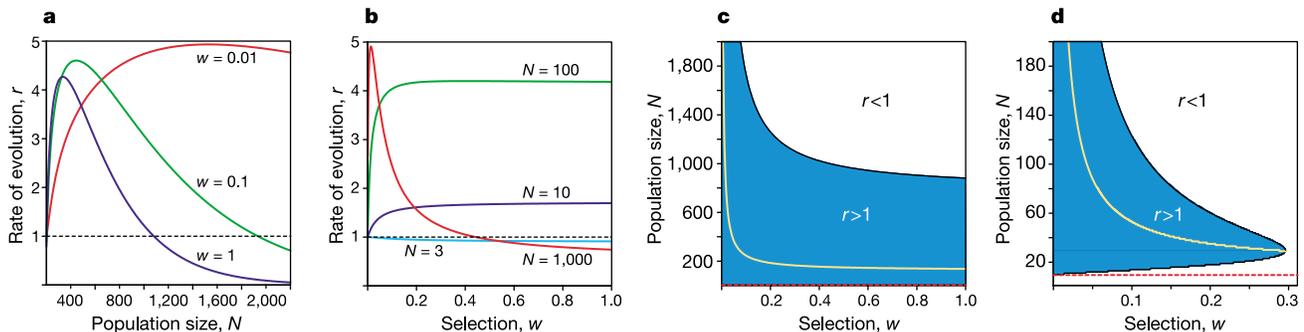


Figure 1 Selection can favour the replacement of ALLD by TFT in finite populations. **a**, The rate of evolution, $r = N\rho_A$, is a one-humped function of N . There is an intermediate range of N which leads to positive selection of TFT, $N\rho_A > 1$. **b**, $N\rho_A$ is shown as function of w . For small N , we have $N\rho_A < 1$ for all w . For larger N we have $N\rho_A > 1$ for all w . For even larger N we have $N\rho_A > 1$ as long as w is below a certain threshold. **c, d**, The blue-

shaded region indicates the parameter region where $N\rho_A > 1$. The yellow lines show the optimum value N for a given w maximizing $N\rho_A$. The broken red line indicates $N_{\min} = (2a + b + c - 4d)/(a + 2b - c - 2d)$, which is the predicted minimum population size required for positive selection of TFT in the limit of weak selection. Parameter choices are: $R = 3, T = 5, P = 1, S = 0$; and $n = 10$ rounds for **a–c** and $n = 4$ rounds for **d**.

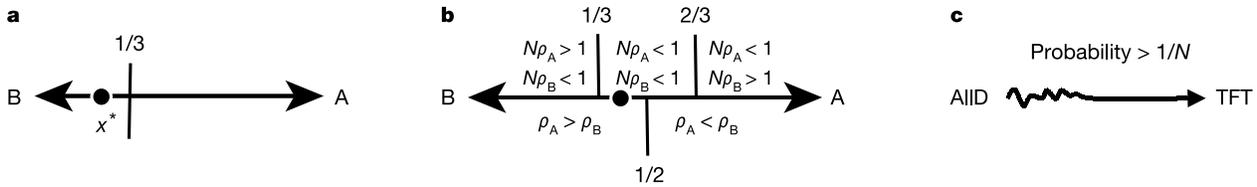


Figure 2 The 1/3-law of frequency-dependent evolution. **a**, Suppose A and B are the best replies to themselves, meaning $a > c$ and $d > b$ in payoff matrix (1). In this case all-A and all-B are stable equilibria of the replicator dynamics for infinite population size. The unstable equilibrium is located at a frequency of A given by $x^* = (d - b)/(a - b - c + d)$. If $x^* < 1/3$ then selection favours A replacing B for a sufficiently large population and weak selection. The minimum population size is given by $N_{\min} = (2a + b + c - 4d)/(a + 2b - c - 2d)$. **b**, The relationship between the 1/3-law and risk dominance. If $x^* < 1/3$ then $\rho_A > 1/N > \rho_B$. If $1/3 < x^* < 1/2$ then $1/N > \rho_A > \rho_B$. If

$1/2 < x^* < 2/3$ then $1/N > \rho_B > \rho_A$. If $2/3 < x^*$ then $\rho_B > 1/N > \rho_A$. We note that if A is risk dominant, meaning $x^* < 1/2$, then $\rho_A > \rho_B$. These results hold in the limit of weak selection and large population size. The location of x^* as shown implies that $1/N > \rho_A > \rho_B$. **c**, AIID and TFT in the repeated Prisoner's Dilemma. Although AIID is evolutionarily stable against invasion by TFT for deterministic dynamics of infinite populations, in a finite population the probability that a single mutant of TFT takes over an AIID population can exceed $1/N$. Selection can favour TFT replacing AIID, if the unstable equilibrium occurs at a frequency of less than $1/3$ TFT.

than the neutral threshold, $1/N$. In summary, we simply ask that a homogeneous ESS_N population is protected by selection against invasion and replacement. These requirements represent a natural extension of the original ESS concept formulated by Maynard Smith for infinitely large populations and deterministic evolutionary dynamics¹⁸.

Schaffer²² has proposed that a strategy is evolutionarily stable in a finite population if a single mutant of any other strategy has lower fitness. This is the first of our two conditions. Schaffer²² also proposes a global stability condition, namely that the ESS strategy must have a greater fitness than the other strategy for any composition of the population. This very stringent condition is a finite- N extension of Hamilton's unbeatable strategy²⁹, which dominates every other strategy. We note that every unbeatable strategy is an ESS, but the reverse is not true. Unfortunately, unbeatable strategies are rare. Many biological games admit ESS, but not unbeatable strategies.

Sometimes it is of interest to ask whether strategy A is more likely to replace B than vice versa. Let ρ_A and ρ_B denote the respective fixation probabilities. In the case where both A and B are the best replies to themselves and in the limit of weak selection and large populations, we find that $\rho_A > \rho_B$ if A is risk-dominant, meaning that $a + b > c + d$. For general N and w , however, risk dominance does not determine the ordering of the fixation probabilities.

Here we have studied a frequency-dependent Moran process, which is a natural finite- N analogue to the replicator equation. One can envisage many different stochastic processes that describe game dynamics in finite populations. An interesting possibility is the following. Pick two players at random. One is chosen for reproduction, the other for elimination. Hence, only mixed pairs can change the population. Suppose that player A is chosen for reproduction with probability $f_i/(f_i + g_i)$ and player B with probability $g_i/(f_i + g_i)$. In this case, we obtain the same process as we have analysed here, up to rescaling time.

If, instead, the fitter player is always chosen for reproduction, then the resulting process is stochastic in speed, but deterministic in direction: it will always follow the gradient of selection. But if player A is chosen for reproduction with probability $1/(1 + \exp[-(f_i - g_i)/\tau])$, then parameter w cancels out. There is, however, a new parameter, τ , which has a similar role and is equivalent to temperature in statistical physics. If $\tau \rightarrow 0$ then the fitter player is always chosen; selection is strong. If $\tau \rightarrow \infty$ then selection is weak, and the process is dominated by random drift. In the limit of large τ , we obtain exactly the same results as are presented here.

Another possibility is studying a frequency-dependent Wright-Fischer process with discrete generations. Furthermore, in all of those models, stochasticity could arise in evaluating the payoffs of individual players. We expect that all these processes (as long as they are not deterministic in following selection) will have a similar behaviour to what we have described here.

To sum up, (1) in finite populations, natural selection can favour the invasion and replacement of the AIID strategy by a cooperative strategy, when starting from a single individual using that strategy. No specific mechanism of invasion is required. (2) For any two strategies A and B, natural selection can favour A replacing B in a finite population provided $b > c$ or $a - c > 2(d - b)$. If A and B are the best replies to themselves then the latter condition implies that the frequency of A at the unstable equilibrium, x^* , must be less than $1/3$. (3) Our analysis leads to natural conditions for evolutionary stability in finite populations. These conditions specify whether a given resident strategy is protected by selection against invasion and replacement of any mutant strategy. □

a		A	B	A is an ESS_N for $N > 12$
	A	20	0	B is an ESS_N for $N < 53$
	B	17	1	$\rho_A > \rho_B$ for $N > 19$
b		A	B	A is an ESS_N for $N < 22$
	A	1	28	B is an ESS_N for $N > 17$
	B	2	30	$\rho_A > \rho_B$ for $N < 20$

Figure 3 A strategy is ESS_N if it is protected by selection against invasion and replacement by another strategy for given N and any $w > 0$. **a**, Both A and B are classical ESS, but for $2 \leq N \leq 12$ only B is ESS_N ; for $12 < N < 53$ both A and B are ESS_N , for $N \geq 53$ only A is ESS_N . We note that strategy B is a classical ESS, but is not ESS_N for large N ; in large populations there is selection for A replacing B. **b**, B dominates A. Therefore only B is a classical ESS. For $2 \leq N \leq 17$, however, we obtain that only A is ESS_N . For $17 < N < 22$ both A and B are ESS_N . For $N \geq 22$ only B is ESS_N . Examples **a** and **b** illustrate that for small populations the traditional ESS concept is neither necessary nor sufficient to imply ESS_N , and for large populations it is necessary but not sufficient.

Methods

Remarks on ESS

If $d > b$ then B is both a strict Nash equilibrium and an ESS in comparison with A. A strict Nash equilibrium implies protection by selection against replacement in the following sense: for a given payoff matrix (a, b, c, d) with $d > b$ and for any given intensity of selection, $0 < w \leq 1$, we have $\rho_A \rightarrow 0$ as $N \rightarrow \infty$.

For every finite population size, N , however, we can calculate the maximum net selective advantage for a mutant replacing a strict Nash equilibrium. Given b, d with $d > b$, what is the maximum probability ρ_A of A replacing B? We are free to choose a and c .

To maximize ρ_A , we set $a \rightarrow \infty$ and $c = 0$. For large populations, we obtain $\rho_A = [1 - w(1 - b)]/[2 - w(2 - b - d)]$. For $w \rightarrow 0$ we have $\rho_A = 1/2$. For $w = 1$ we have $\rho_A = b/(b + d)$. This fixation probability of A corresponds to a constant relative fitness of $1 + (b/d)$ or a net selective advantage of b/d . Hence there can be enormous selection pressure for replacement of a strict Nash equilibrium in arbitrarily large, finite populations (when the other equilibrium is much more efficient).

The calculation here uses the fact that from state $i = 1$ the system can go either to $i = 0$ or $i = 2$. Because $a \rightarrow \infty$ and $c = 0$, fixation of strategy A is certain from state $i = 2$. Hence, the fixation probability from $i = 1$ to $i = N$ is just the probability $P_{12}/(P_{12} + P_{10}) = (1 - w + wb)/(1 - w + wb + 1 - w + wd(N - 2)/(N - 1))$. This holds for all w . For large N , we obtain the above formula for ρ_A .

Risk dominance

Let ρ_A denote the probability that a single A player reaches fixation in a population of B. Let ρ_B denote the probability that a single B player reaches fixation in a population of A. We obtain:

$$\frac{\rho_A}{\rho_B} = \prod_{i=1}^{N-1} \frac{f_i}{g_i} \quad (3)$$

For weak selection (small w) we find $\rho_A/\rho_B = 1 + w[(N/2)(a + b - c - d) + d - a]$. It follows that $\rho_A > \rho_B$ is equivalent to $(N - 2)(a - d) > N(c - b)$. For large N this means $a - c > d - b$. Hence, if both A and B strategies are strict Nash equilibria then the risk-dominant equilibrium has a higher fixation probability when starting from a single player using that strategy. For general N and w , risk-dominance does not decide whether ρ_A is greater than ρ_B .

More general strategies

We have mostly studied the dynamics between ALLD and TFT. The repeated Prisoner's Dilemma, like other repeated games, admits a huge set of possible strategies, which makes it difficult to explicitly analyse the dynamics of evolution. In general, a strategy for playing the repeated Prisoner's Dilemma is a mapping from any history of the game between two players into the interval $[0, 1]$, denoting the probability of cooperation on the next move. However, we note that for the finitely repeated game, ALLD is a strict Nash equilibrium in comparison with all cooperative strategies, where we define a 'cooperative strategy' as a strategy which cooperates on the first move. Let us divide cooperative strategies into two subsets: (1) those that are dominated by ALLD and (2) those that are bistable with ALLD. In an infinitely large population, no cooperative strategy can ever invade ALLD. In a finite population of size N , strategies of the second subset can invade and replace ALLD provided inequality (2) holds and selection is sufficiently weak.

In an infinitely repeated Prisoner's Dilemma with time-average payoffs, it turns out that TFT dominates ALLD. In this case it can be shown that the 'win-stay, lose-shift'³⁰ strategy (also known as 'Pavlov' or 'perfect tit-for-tat') is the only simple strategy which cannot be invaded by any other strategy, and that it is the only strategy that is evolutionarily stable in an infinite population when actions are taken with a vanishingly small probability of error³¹. Moreover, this strategy is also the unique ESS in a model where strategies are encoded by finite-state automata, and the complexity of the automaton represents an evolutionary cost³¹.

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Correspondence and requests for materials should be addressed to M.A.N. (martin_nowak@harvard.edu).

Pre-social benefits of extended parental care

Jeremy Field & Selina Brace

Department of Biology, University College London, Wolfson House, 4 Stephenson Way, London NW1 2HE, UK

The evolution of helping, in which some individuals forfeit their own reproduction and help others to reproduce, is a central problem in evolutionary biology. Recently proposed insurance-based mechanisms rely on a pre-existing life history with a long period of offspring dependency relative to the short life expectancies of adult carers^{1–4}: a lone mother's offspring are doomed if she dies young, whereas after a helper dies, other group members can finish rearing the offspring^{5,6}. A critical question, however, is how this life history could evolve in ancestral non-social populations, as offspring survival would then depend on a single, short-lived carer. Here, we resolve this paradox by focusing on the extended parental care inherent in prolonged dependency. We show experimentally that in non-social wasps, extended care can significantly reduce the impact of interspecific parasites. Under extended care, offspring are less vulnerable by the time they are exposed to parasites, and costs of parasitism are reduced because mothers have the option to terminate investment in failing offspring. By experimentally simulating aspects of extended care in a species where it is lacking, we demonstrate that neither benefit requires specialized behaviour. Such benefits could therefore offset the disadvantage of prolonged dependency in non-social species, thereby facilitating the evolution of helping.

Immature nest-building wasps are helpless larvae that are entirely dependent on adult carers for food. The duration of parental care is minimized in 'mass provisioning' wasps, including most non-social taxa^{7,8}: before it even hatches from the egg, each offspring is sealed into a cell containing all of the food that it will require for maturation, so that it is nutritionally independent of its mother. In contrast, almost all eusocial and a few non-social wasps have extended parental care. These 'progressive provisioners' feed each developing larva gradually as it grows^{7,8}. Whereas a single mass provisioner can fully provision about 1 offspring per day, provisioning is extended over 5–70 days in progressive provisioners^{4,9,10}. Even if they provision multiple offspring simultaneously, non-social progressive provisioners will, on average, leave fewer independent offspring than mass provisioners, because mothers are more likely

could be released, the OMEGA results described by Bibring *et al.* exclude any possibility that the southern perennial cap could appreciably affect the atmospheric pressure.

The search for the existence of water on Mars, past and present, will continue. Future reports will often confirm less-direct evidence, as is the case with the information about the widespread existence of water ice at the martian south pole provided by OMEGA. But this does not lessen the importance of these discoveries.

Did Mars ever support life? Will Mars support human life in the future? The answers depend on understanding the past and present distribution of both water and CO₂. Life, as we know it, requires liquid water. Yet the long-term stability of liquid surface water requires a thicker atmosphere than Mars has at present. OMEGA's observations show that its past atmosphere, predominantly CO₂, is not locked up in the polar caps. We can hope that OMEGA and her sister instruments on Mars Express, Mars Global Surveyor and Mars Odyssey, along with reports from the

rovers Spirit and Opportunity, will deliver the necessary information to tell us where that ancient atmosphere went.

Human exploration and ultimate colonization of Mars depend on accessibility of one resource — water. Martian water is necessary not only for human consumption, but is also the key to making breathable air and fuel for a return trip to Earth. For life on Mars, water is the elixir. ■

Timothy N. Titus is at the US Geological Survey, 2255 North Gemini Drive, Flagstaff, Arizona 86001, USA.

e-mail: ttitus@usgs.gov

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Behavioural evolution

Cooperate with thy neighbour?

Peter D. Taylor and Troy Day

What gives cooperation an evolutionary edge? Two features of a population — spatial structure and finite size — are factors in the success of any strategy, although more subtle than we thought.

In thinking about the evolution of cooperative behaviour¹, there is one main stumbling block: that cooperative individuals can be exploited by 'defectors', who benefit from cooperation while avoiding the costs that it entails. Solutions to this problem typically find ways for cooperative individuals to interact with one another more often than they would purely by chance. There are two basic ways in which this can happen. One involves the population having a spatial structure with local reproduction and dispersal, so that neighbours of a cooperative individual are themselves more likely to be cooperative^{2,3}. The other relies on some form of information transfer whereby players can assess the behaviour of a prospective partner and decide accordingly how, or even whether, to play. The assessment might be made on the basis of traits that are reliable indicators of likely behaviour^{4,5} or through a phase of negotiation^{6,7}.

Two papers in this issue^{8,9} add further insight. Hauert and Doebeli⁸ (page 643) propose that, under certain conditions, spatial structure might actually hinder cooperative behaviour. It has long been understood that population structure can be a mixed blessing for cooperation, because the gains that it provides through positive assortment are

countered by competition between like individuals^{2,10,11}. Hauert and Doebeli have uncovered yet another limitation of population structure, one that also gives a fascinating geometric distinction between games such as Hawk–Dove — in this case, in the guise of the snowdrift game — and the Prisoner's Dilemma, or blizzard game (Box 1, overleaf).

For a spatially structured population of players, with their choice of strategy displayed as a particular colour on a grid, Hauert and Doebeli see a shift in the geometry of clusters of cooperators at the point where the cost and benefit of the encounter are equal. In the Prisoner's Dilemma, when the cost is greater than the benefit, globular clusters form (Fig. 1a), which give cooperators enough protection to persist at a small frequency. But in playing the snowdrift game, when benefit outweighs cost, the clusters become more finger-like, or dendritic (Fig. 1b). Here the cooperators are vulnerable to exploitation and they die out. The transition is perplexing, but it is clear that spatial structure in a population might not always work in favour of cooperation.

In the second article, Nowak *et al.*⁹ (page 646) suggest that finite population size is also crucial in the evolution of cooperation. These authors focus on the Prisoner's Dilemma



100 YEARS AGO

A New Mineral from Ceylon. In the beginning of February I bought from Mr. Holland 5 cwt. of the mineral described by Prof. Dunstan in last week's NATURE (p. 510)... I had hoped to have positive and definite results to communicate before describing its constituents, but the publication by Prof. Dunstan of an analysis, and his statement that he is still engaged in its investigation, makes it necessary to write this letter...

Fractionation shows that the oxalate precipitate (the portion soluble in ammonium oxalate) gives equivalents between 25.0 (the most insoluble portion of the double sulphate) and 44.7 (the most soluble portion); by far the major part of the element has the last mentioned equivalent...

Assuming that the element is a tetrad, which is probable from its behaviour, it undoubtedly possesses an equivalent approaching the highest number (44.7), and for this there is a gap in the periodic table between cerium and thorium; one at least of the elements present (supposing that there is more than one present) will probably have an atomic weight of about 177, preceding tantalum (182.5) in the horizontal row of the periodic table...

Within the limits of this letter I am obliged to omit many more characteristics of this curious ore... I regret to have been obliged to tell an imperfect story.

William Ramsay

From *Nature* 7 April 1904.

50 YEARS AGO

The brain mechanisms which serve the sun navigation of the animals mentioned are presumably of a similar nature in all species and are probably based on the same principles as human sun orientation.

They can also be expected to share certain properties with other time-keeping mechanisms (internal clocks) which are of wide occurrence. They keep time fairly well on their own and they are set and kept in pace by light stimuli. Their metabolic nature has in certain cases been established. A third property of such systems is that they regulate motor activities. *Drosophila*, for example, normally emerge from their pupæ before dawn. If a bottle with larvæ and pupæ of *D. melanogaster* is artificially illuminated during three consecutive nights and kept in darkness during daytime, the flies which emerge during the following week will 'remember' the time of the artificial dawn and emerge in the evenings, even when now kept in perpetual darkness.

H. Kalmus

From *Nature* 10 April 1954.

to highlight dramatically the difference between evolutionary stability in a finite and an infinite population, and at the same time suggest a new factor that bears on the evolution of cooperation.

In the Prisoner's Dilemma, defectors always outcompete cooperative individuals when encounters are random. Axelrod and Hamilton demonstrated¹², however, that cooperative strategies can be enhanced if multiple encounters with the same partner are allowed and if current behaviour is based on past experience. Of all such conditional strategies, 'tit-for-tat' seems to be one of the best: a player cooperates initially but continues to cooperate only if its partner cooperated in the previous encounter. It turns out that if the number of encounters with the same partner is large enough, tit-for-tat can outperform a uniform all-defect strategy once its frequency is high enough. This means that there is an unstable mixed equilibrium at some particular frequency: above it, tit-for-tat dominates; below it, all-defect takes over. At least, this is true of an infinite population (in which changes in frequency are deterministic in evolutionary time). For example, with a benefit of 3, a cost of 4, and 10 encounters per partner, this unstable equilibrium is at a frequency of 1/8 tit-for-tat.

But what if the population is finite, say of size 80? Treated as an infinite population, we'd expect to need ten individuals playing tit-for-tat before this strategy could become more fit than all-defect; and by the standard definition, all-defect is evolutionarily stable (no rare mutant tit-for-tat-er can invade). In contrast, as a finite population, the stochastic nature of random sampling leads us to expect that, after many generations, all individuals will be descended from exactly one of the original members. With neutral strategies, each individual would have the same

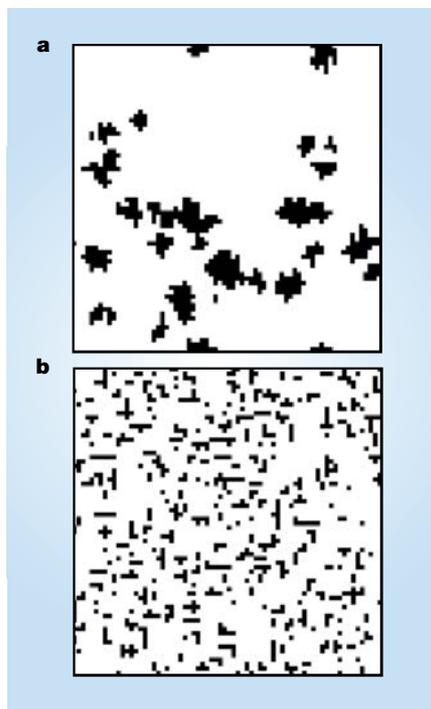


Figure 1 Cooperators versus defectors. With the spatial structure of a population represented by a grid, Hauert and Doebeli⁸ find different equilibrium configurations for two slightly different games that test the evolution of cooperation. Cooperators are shown in black, defectors in white. a, In the Prisoner's Dilemma game, clusters of cooperators develop and can offer protection to those in the interior of each cluster, increasing the fitness of cooperators. b, In the snowdrift game, however, the cooperative clusters develop into dendritic fingers that poke out into defector territory, exposing their members to exploitation. Cooperators can actually be worse off than if they had formed partnerships at random.

probability of being the founder, which suggests an alternative way of comparing the fitness of tit-for-tat versus all-defect — calculate the probability that an individual of each kind will be the founder¹³.

It turns out that, for the example of one lone tit-for-tat-er in a population of 79 all-defect players, the probability that the tit-for-tat individual is the founder is almost twice that of an all-defect individual (M. Nowak, personal communication). Should we still regard all-defect, then, as an evolutionarily stable strategy? In fact, Nowak *et al.*⁹ use this example to propose an extension of the standard definition of evolutionary stability for finite populations. The mutant strategy must be less fit in two ways: no rare mutant can invade (the traditional sense), and a rare mutant individual must have a lower than normal chance of being the founder of the ultimate population. Certainly, in a finite population such an extension is needed, but it's not at first so clear how to do this, nor exactly what role fixation probability should play. In a population subject to the forces of mutation and drift, what are the states that we might expect to observe? ■

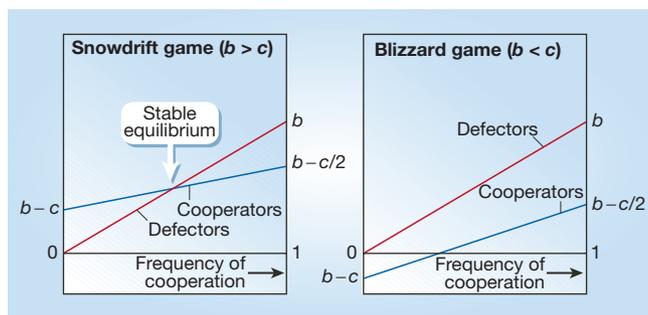
Peter D. Taylor and Troy Day are in the Department of Mathematics and Statistics, Queen's University, Kingston, Ontario K7L 3N6, Canada. e-mail: taylorp@post.queensu.ca

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Box 1 Snowdrifts and blizzards

Imagine two car drivers caught in a snowdrift. The total cost of shovelling out of the drift is c and the benefit to each of getting home is b . The drivers might follow either of two strategies — cooperate with the other, or defect. If both drivers cooperate, they split the cost of shovelling and both get home. If one cooperates and one defects, they will both get home, but the cooperator will bear the whole cost. Two defectors bear no cost but get no benefit.

It is reasonable to assume that $b > c/2$ — that getting home is worth more than the cost of half the shovelling (or the game is pointless). That leaves two interesting cases: $b > c$ and $b < c$. The first case is



known as the snowdrift game and (in the spirit of comparison) we call the second the blizzard game. In the latter, the shovelling is so hard that a driver who does it all suffers a net loss. The snowdrift game is a version of Hawk–Dove, and the blizzard

game is a version of the Prisoner's Dilemma, both of which are much studied in behavioural evolution.

In a biological population in which the payoff contributes to fitness, we are interested in comparing the average fitness

of a cooperator and a defector. Fitness is illustrated here as a function of frequency of cooperative encounters. There is a stable equilibrium where the lines intersect. For random encounters between drivers/players, the snowdrift game supports a stable mixture of cooperators and defectors (roughly half-and-half). The blizzard game does not: the only point of stable equilibrium is an all-defector population. But if there were some mechanism that increased the frequency of cooperative encounters, the lower portion of the cooperation line would rise, creating a point of stable equilibrium for the blizzard game as well. **P.D.T. & T.D.**