



The Continuous Prisoner's Dilemma: I. Linear Reactive Strategies

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We present a general model for the Prisoner's Dilemma in which variable degrees of cooperation are possible, and payoffs are scaled accordingly. We describe a continuous strategy space, and divide this space into strategy families. We derive the payoff function for these families analytically, and study the evolutionary outcome when a wide range of strategies play against each other. Our results show that the initial degree of cooperation offered by a strategy is a decisive factor for evolutionary robustness: the most successful strategies in our model offer full cooperation as an initial move, but thereafter cooperate fully *only* if their opponent does the same. These strategies gradually raise the stakes when playing a strategy which is initially reticent to cooperate, but differ from the strategies predicted by other continuous models in that they are not only generous, but are also consistently optimistic and uncompromising.

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1. Introduction

In spite of the fierce competition inherent to natural selection, reciprocal altruism plays a fundamental role in both human and animal behaviour (Hamilton, 1963, 1964; Trivers, 1971; Packer, 1977; Wilkinson, 1984; Axelrod, 1984; Milinski, 1987; Milinski *et al.*, 1990; Bull & Rice, 1991; Krebs & Davies, 1991; Külling & Milinski, 1992; Frank, 1995; Dugatkin & Mesterton-Gibbons, 1996; Dugatkin, 1997). The evolution of stable patterns of mutually beneficial interaction, particularly among selfish, unrelated individuals, appears paradoxical because such behaviour is so clearly vulnerable to exploitation. The Prisoner's Dilemma (Rapoport & Chammah, 1965; Trivers, 1971; Smale, 1980; Axelrod & Hamilton, 1981) is the mathematical framework for the study of cooperation, and had led to a large number of theoretical investigations (Selten & Hammerstein, 1984; Molander, 1985; Peck & Feldman,

1985; May, 1987; Boyd & Lorberbaum, 1987; Axelrod & Dion, 1988; Kraines & Kraines, 1989; Lindgren, 1991; Mesterton-Gibbons & Dugatkin, 1992; Nowak & Sigmund, 1992, 1993; Crowley, 1996; Crowley *et al.*, 1996; but see Boyd, 1988; Dugatkin *et al.*, 1992). Cooperation can emerge because of repeated interactions between two individuals (direct reciprocity), indirect reciprocity (Alexander, 1987; Nowak & Sigmund, 1998) or spatial interactions (Nowak & May, 1992).

An implicit limitation of the traditional Prisoner's Dilemma is that interactions are discrete: each player can choose between only two options, cooperating or defecting. Recent papers have investigated the possibility of extending this classical game by allowing a variable degree of cooperation, with payoffs scaled accordingly (Verhoeff, 1993; Doebeli & Knowlton, 1998; Roberts & Sherratt, 1998; Killingback *et al.*, 1999; see also Smale, 1980; Freat, 1996). Modelling the Prisoner's Dilemma in the continuous spectrum has allowed these researchers to examine situations in which the current degree of

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cooperation depends either on previous payoffs (Doebeli & Knowlton, 1998), or on a partner's previous move (Verhoeff, 1993; Roberts & Sherratt, 1998; Killingback *et al.*, 1999).

These models have been applied to such topics as interspecific mutualisms (Doebeli & Knowlton, 1998) or escalating investments (Roberts & Sherratt, 1998), and the robustness of cooperation has been demonstrated in many contexts. The proposed models, however, differ significantly, as do the types of strategies that can be incorporated into each. We present here a general model for the Continuous Prisoner's Dilemma which describes a continuous three-dimensional strategy space, and divide this space into strategy families that behave in qualitatively identical ways. We derive the payoff function for these families analytically, and determine regions of Nash equilibria in the strategy space. We also study the evolutionary outcome when a wide range of strategies play against each other, using a new approach which we call stochastic adaptive dynamics. In these simulations, strategies evolve by small mutations from previously successful strategies, and a stochastic element is used to capture the effects of random drift in populations at equilibrium.

We are particularly interested in the initial degree of cooperation offered by "successful" strategies. Our results show an extremely strong correlation between mean payoff and this initial offer, for a wide range of strategies. We also find a set of essentially cooperative strategies which are Nash equilibria. These strategies gradually raise the stakes (Roberts & Sherratt, 1998) when playing a strategy which is initially reticent to cooperate, but differ in other ways from the most successful strategies predicted by other continuous models (Verhoeff, 1993; Roberts & Sherratt, 1998; Doebeli & Knowlton, 1998). The distinguishing feature of the successful strategies in this model is that they are not only generous, but also consistently optimistic and uncompromising, offering full cooperation as a first move but thereafter cooperating fully *only* if their opponent does the same.

2. The Continuous Prisoner's Dilemma

We propose a general model of the Iterated Prisoner's Dilemma, in which both the costs and

benefits of cooperation vary continuously. If player 1 moves x in a given round (where x is in the interval $[0, 1]$), the cost to player 1 is $-cx$, and the benefit to player 2 is bx , with $b > c$. One "round" is complete after player 2 responds to this event by moving y in turn, entailing cost $-cy$ to player 2 and benefit by to player 1. Thus, in our model, playing 1 corresponds to complete cooperation, while playing 0 corresponds to complete defection. Obviously, this model could also be used to describe the simultaneous game, with responses y depending on opponents' moves in the previous round, but we restrict the description below to the alternating game (Freen, 1994; Nowak & Sigmund, 1994). The model we describe is closely related to those proposed by Verhoeff (1993), Roberts and Sherratt (1998) and Killingback *et al.* (1999).

We are interested in the set of all strategies, $y = S(x)$, which define the response y to an opponent's move x . Thus, S is a function on $[0, 1]$ defined over the interval $[0, 1]$. When S is nonlinear, we find that chaotic sequences of moves could result; for example if $y = 4x(1 - x)$ (the logistic equation, May 1976) plays against itself. We also note an extension of this model, in which any number of previous moves by an opponent could be taken into account: $y = S(x_i, x_{i-1}, x_{i-2}, \dots)$.

For simplicity, we consider here only those strategies which vary linearly with x and with only one "layer" of x , the immediately previous move. Each strategy is then defined by a slope, k , an intercept, d , and a starting move x_0 . Where $kx + d > 1$ we set $y = 1$, and likewise where $kx + d < 0$, $y = 0$. This subset of all S can be pictured as the set of straight lines which have a non-empty intersection with the unit square. We use the notation S_{k,d,x_0} to describe a given strategy (abbreviated to $S_{k,d}$ to describe a class of strategies which differ only in x_0).

Clearly, the strategy $S_{0,1,1}$ or $y = 1$ corresponds to indiscriminate cooperation, while $S_{0,0,0}$ or $y = 0$ corresponds to indiscriminate defection, regardless of the opponent's previous move. For brevity, we denote these strategies *AllC* and *AllD*, respectively. The strategy $S_{1,0,1}$ or $y = x$ is analogous to Tit-for-Tat in the discrete case; this strategy lies on the line of identity and is denoted *I*.

We define a payoff function, $F(S, S')$ which corresponds to the mean payoff per round that strategy S receives when playing against S' . The payoff is clearly a function of the slopes, intercepts and starting moves of the two strategies, of the cost c and benefit b , and of the total number of rounds in the game. In this paper, we discuss two treatments of the number of rounds: the case when the total number of rounds, n , is fixed; and the case when \bar{n} denotes the average number of rounds per game, such that the probability of a further move after each round of the game is given by $(1 - 1/\bar{n})$.

Because the payoff will also depend on whether S or S' moves first, we define the payoff function as the average payoff between these two cases. As a limiting case, we sometimes consider the payoff of an infinitely iterated game (payoff averaged over n rounds as $n \rightarrow \infty$). For example, in the infinite game $F(AllC, AllC) = (b - c)$, and likewise $F(AllD, AllD) = 0$. We also find that $F(I, I) = (b - c)$, because the starting move for I is defined to be 1. For other strategies which lie on the identity line, the payoff when $S_{1,0,x_0}$ plays $S_{1,0,x'_0}$ will be equal to $1/2(b - c)(x_0 + x'_0)$.

2.1. STRATEGY FAMILIES

We define “cooperative” strategies as those which lie entirely on or above the line of identity, i.e. those strategies for which $S(x) \geq x$ for all x . When two such strategies play against each other, each successive move is greater than the opponent's previous move, and after some finite number of moves both players will cooperate fully. The mean payoff over an infinite game between cooperative players is thus $(b - c)$. For cooperators, $k \geq 0$; the slope of the line is positive, and repeated rounds move the play closer to one.

The space of all possible strategies is a three-dimensional polyhedron in k , d and x_0 . We can subdivide this space based on the qualitative features of the strategies; in particular, we find that the most important factors are whether k is greater than zero, and which sides of the unit square the strategy intersects. This classification on the plane of k and d is shown in Fig. 1. Here, strategy families denoted P or N have positive or negative slopes, respectively. Repeated rounds of

a game between two members of this strategy family move the play towards the value given by the superscript. For example, P^1 is the set of all cooperators, as described above. In a game between any two players in the family P^{01} , the play will move towards either zero or one, depending on the starting move. For N^{01} , the play will move towards a repeated sequence of alternating zero and one. In the central region of the plane, denoted M , are those strategies which move the play towards some intermediate value between zero and one. Thus, if two strategies $M_{k,d}$ and $M_{k',d'}$ play against each other, the moves played by strategy $M_{k,d}$ will approach $x = kx' + d$, while the moves played by $M_{k',d'}$ approach $x' = k'x + d'$. Solving, we find $x = (kd' + d)/(1 - kk')$ and $x' = k'(kd' + d)/(1 - kk') + d'$ (We will return to this interesting result in Section 3.2.).

In analogy with the cooperators, we define “defective” strategies as those strategies which lie completely below the identity line, for which $S(x) < x$ for all x . We see that after some finite number of moves both players will play zero consistently, and that the mean payoff when two such strategies play each other will approach zero as $n \rightarrow \infty$. The set of defectors is the family P^0 in Fig. 1. Indiscriminate cooperators, and indiscriminate defectors, lie along the boundaries of the regions above and below the unit square, respectively.

Figure 2 shows the payoff function for each of these strategy families. We show here the payoff received in the limit when a strategy plays an infinite game against itself, determined analytically. For those regions of the plane in which the payoff in the infinite game depends on x_0 , we plot the mean payoff for a mix of strategies with x_0 uniformly distributed on $[0, 1]$. We have not been able to determine an analytical expression for the payoff between two *arbitrary* linear reactive strategies in either the finitely or infinitely iterated game.

2.2. THE ROBUSTNESS OF COOPERATION

We are interested in which cooperative strategies, P_{k,d,x_0}^1 , can resist invasion by $AllD$, that is, under what conditions is

$$F(AllD, P_{k,d,x_0}^1) < F(P_{k,d,x_0}^1, P_{k,d,x_0}^1). \quad (1)$$

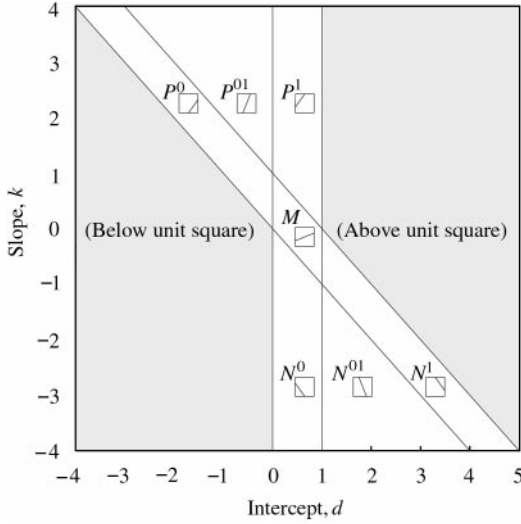


FIG. 1. Strategy families on the d - k plane. All possible linear reactive strategies, defined in the text as S_{k,d,x_0} , can be classified according to which sides of the unit square they intersect. Labels indicate the notation used in the text to describe each strategy family; the insets show an example of each type. Gray regions in the figure mark areas where the line $y = kx + d$ lies entirely above or below the unit square. The strategy families clearly extend beyond the region depicted in this figure, towards the upper left and lower right of the page.

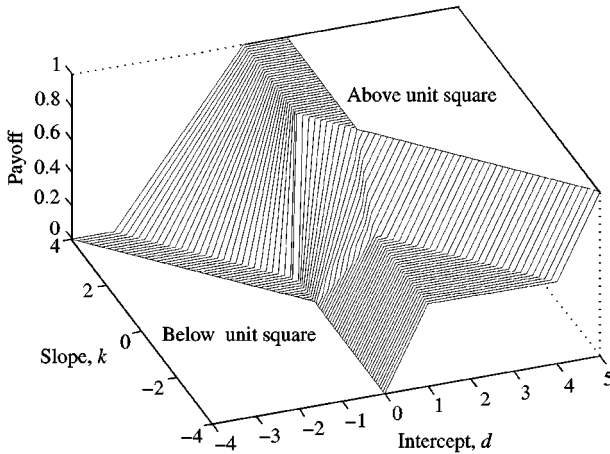


FIG. 2. Payoff against self in the infinite game. The payoff, $F(S, S)$ is shown for the limiting case of an infinite game, for $b = 2$ and $c = 1$. In those regions of the plane in which the payoff in the infinite game depends on x_0 , the mean payoff for a mix of strategies with x_0 uniformly distributed on $[0, 1]$ is shown. Note that the maximum payoff is achieved by the family of cooperators, P^1 .

For cooperative strategies, the response to an opponent's defection, $y = S(0)$, is given by the intercept, d , and thus the payoff received by *AllD* when playing a given cooperator will depend on

d , as well as on x_0 and the number of rounds in the game.

For the infinitely iterated game we find that $F(\text{AllD}, P_{k,d,x_0}^1) = bd$. Condition (1) above can therefore be written $b - c > bd$, or

$$d < 1 - \frac{c}{b}. \quad (2)$$

Thus in the limiting case of an infinite game, cooperative strategies must have intercepts less than $1 - c/b$ in order to resist invasion by *AllD*.

For the finite game with exactly n moves, the payoff *AllD* receives when playing cooperator P_{k,d,x_0}^1 is given by $(bx_0 + (n-1)bd + nbd)/2n$ (when the cooperator moves first, *AllD* gets bx_0 followed by $n-1$ rounds of bd ; but when *AllD* moves first the payoff to *AllD* is n rounds of bd). The payoff a cooperator receives when playing itself is the sum of a number of weighted costs and benefits as successive moves approach 1, followed by a number of terms in which the payoff is $b - c$ (both players are cooperating fully), all divided by the total number of moves n . We can see that the upper limit on $F(P_{k,d,x_0}^1, P_{k,d,x_0}^1)$ is $b - c$, and so *AllD* is able to invade P_{k,d,x_0}^1 if

$$b \frac{x_0 + (2n-1)d}{2n} > b - c. \quad (3)$$

This can be rewritten as a condition on x_0 :

$$x_0 > 2n \left(1 - \frac{c}{b} \right) - (2n-1)d. \quad (4)$$

Since x_0 must be greater than zero, this condition is always true when $2n(1 - c/b) - (2n-1)d < 0$, or when

$$d > \frac{2n}{2n-1} \left(1 - \frac{c}{b} \right). \quad (5)$$

Thus, for the finite game with n moves, a cooperator P_{k,d,x_0}^1 can be invaded by *AllD* if d is larger than $(1 - c/b)$ by a sufficient margin, and may be invaded by *AllD* if d is less than the same value but x_0 is above the threshold given in eqn (4).

2.3. ESTABLISHING COOPERATION

We are similarly interested in which cooperative strategies, P_{k,d,x_0}^1 , are able to invade a highly uncooperative population. In the infinitely iterated game, $F(AllD, AllD) = 0$ and $F(P_{k,d,x_0}^1, AllD) = -cd$, therefore a single cooperative player can never invade a population of defectors. If, however, the frequency of cooperators in the total population is h , and the population is mixed between complete defectors and cooperators, then the growth rate of the cooperative strategies will exceed the growth of *AllD* when

$$h(b - c) - (1 - h)cd > hbd, \quad (6)$$

which reduces to

$$h > \frac{cd}{(1 - d)(b - c)}. \quad (7)$$

We note that h can only be greater than this threshold if the right-hand side of inequality (7) is less than 1, which reduces to condition (2). This implies that cooperators can invade a population of defectors only if condition (2) is met *and* the starting frequency of the cooperators exceeds the threshold given by inequality (7).

3. Adaptive Dynamics

3.1. THE EVOLUTION OF x_0

We are interested in which starting move, or initial investment, is “best” for a given strategy. To determine this, we held k and d fixed and allowed x_0 to evolve (Maynard Smith, 1982), i.e. we start with an initial strategy S_{k,d,x_0} and consider a small perturbation in the starting move, $x'_0 = x_0 + \delta x$. If $F(S_{k,d,x'_0}, S_{k,d,x_0}) > F(S_{k,d,x_0}, S_{k,d,x_0})$ and $F(S_{k,d,x'_0}, S_{k,d,x'_0}) > F(S_{k,d,x_0}, S_{k,d,x'_0})$, it is clear that S_{k,d,x'_0} will invade and takeover a population of S_{k,d,x_0} : we let x'_0 replace x_0 and continue.

The results of these simulations are shown in Fig. 3. These surfaces plot the steady-state values of x_0 (\hat{x}_0) when x_0 is originally set to be 0 or 1 in the simulation. We note that $\hat{x}_0 = 1$ is robust for a significant fraction of the strategy space, and in particular we find a region of strategy space in which x_0 evolves towards one, regardless of its

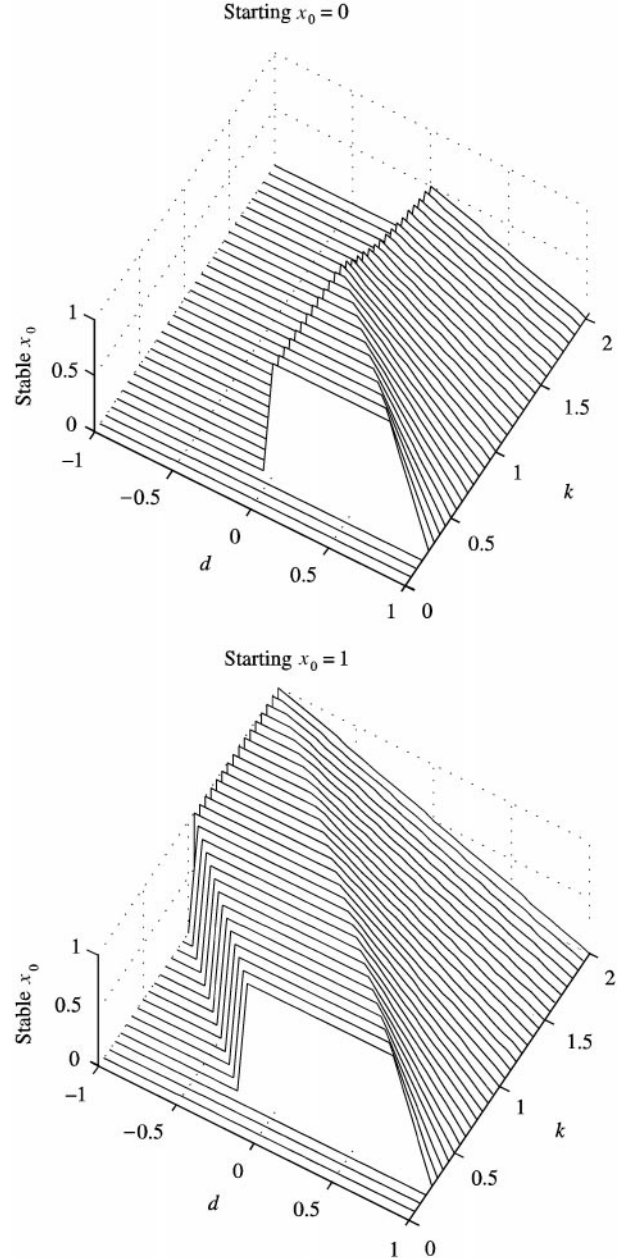


FIG. 3. Steady-state values of x_0 . The surfaces show the steady-state values of x_0 (\hat{x}_0) when both k and d are fixed. In these simulations, strategy S_{k,d,x_0} played a single game against S_{k,d,x'_0} where $x'_0 = x_0 + \delta x$, and $b = 5$, $c = 1$. We set δx to 0.02 or -0.02 when x_0 was initially set to 0 or 1, respectively. Games which were 20 rounds long on average ($\bar{n} = 20$) were modelled by simulating 100 rounds and weighting the payoff in round i by the probability that a game would last to round i , $(1 - 1/\bar{n})^{i-1}$. We note that $\hat{x}_0 = 1$ is robust for a significant fraction of the strategy space, and in particular we find a region of strategy space in which x_0 evolves towards one, regardless of its

initial value. This region appears in the upper corner (k is high) of strategy family M . The steady-state values of x_0 for strategy families

N^0, N^{01} and N^1 were zero, regardless of the starting value.

We are particularly interested in the steady-state x_0 value for the cooperative strategies, family P^1 . We have found (refer to Appendix A) that for most strategies in this family, the surface shown in Fig. 3 is described by the equation $\hat{x}_0 = (1 - d)/k$, that is, x_0 evolves from any initial value to the lowest x_0 which elicits full cooperation in a single move ($S(\hat{x}_0) = 1$ for $\hat{x}_0 = (1 - d)/k$). The best starting move for cooperators is not full cooperation but just enough to move the play to full cooperation in the next (and consequently every subsequent) move. Among cooperators, full cooperation is the best initial move ($\hat{x}_0 = 1$) only for those strategies along the boundary of P^1 and M (these strategies intersect the unit square at $[1, 1]$).

We have also observed in some cases that when the initial value of x_0 is below some critical value, it may reach a stable equilibrium in region P^1 for intermediate values of x_0 ($0 < \hat{x}_0 < (1 - d)/k$). This occurs when full cooperation is elicited not in the partner's first but in a subsequent move of the game, when for example $S(S(\hat{x}_0)) = (1 - d)/k$. For instance, in the finite game with n moves with a starting x_0 of zero, the evolution of x_0 may halt when $S(S(\hat{x}_0)) = (1 - d)/k$ because the cost of a further increase in x_0 outweighs the benefit; we can show that this situation occurs when

the condition $k^2 - (b/c)k + 1 > 0$ is met (see Appendix A).

3.2. TRAJECTORIES THROUGH STRATEGY SPACE: THE EVOLUTION OF k, d AND x_0

We repeated these simulations, allowing k, d and x_0 to vary simultaneously. For each strategy S_{k,d,x_0} we considered strategies distributed in a sphere around that strategy, and accepted the parameter values of the strategy S' with the highest payoff against S_{k,d,x_0} , under the conditions that $F(S', S) > F(S, S)$ and $F(S', S') > F(S, S')$ (strategy S' invades and takes over a population of S).

Figure 4 illustrates two examples of such evolution through strategy space, where a given starting strategy has been followed for 1000 successful mutations. The circle on each graph shows the value of x_0 for the strategy illustrated. In the first example, the simulation was seeded with a fairly uncooperative strategy, for which $k = 0.51, d = 0.2$ and $x_0 = 0.35$. Despite the low values of x_0 and d , however, the strategy evolves towards a cooperative steady state [$S(x) > x, \forall x$], and x_0 evolves towards one. Note that in this example the steady-state strategy is along the boundary of strategy families M and P^1 , since the strategy intersects $[1, 1]$ on the unit square.

In contrast, when seeded with a highly cooperative strategy ($k = 0.3, d = 0.8$ and $x_0 = 1$) which

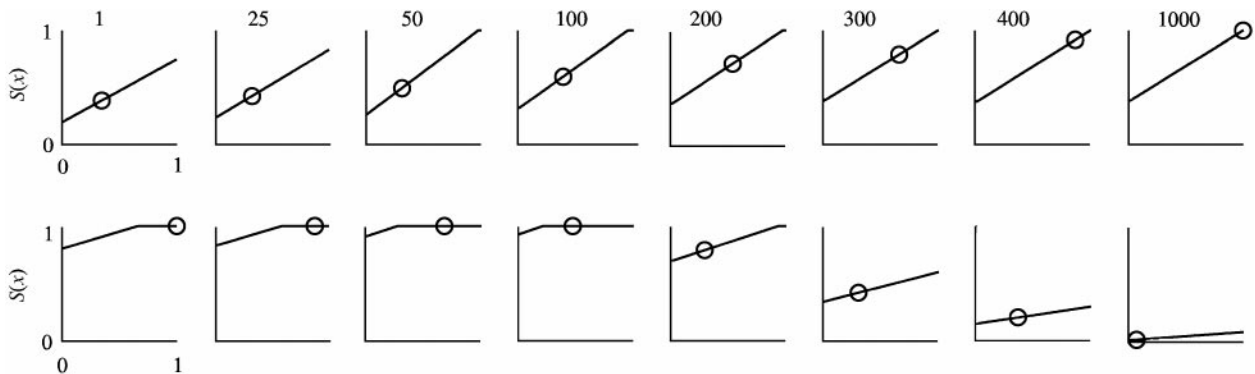


FIG. 4. Examples of strategy evolution. Two examples of the evolution of a given starting strategy are shown; all three parameters of the starting strategy were allowed to evolve. Each panel plots the value of $S(x)$ for $0 \leq x \leq 1$; the circle on each graph shows the value of x_0 for the strategy illustrated. Leftmost panels plot the starting strategies and subsequent panels show the strategy after 25 through 1000 successful mutations (indicated by the bold numbers above each column). We used $b = 2, c = 1$, and $\bar{n} = 20$ for these simulations. In the first example, the simulation was seeded with a $k = 0.51, d = 0.2$ and $x_0 = 0.35$. Despite the low values of x_0 and d , this strategy evolved towards a cooperative steady state [$S(x) > x, \forall x$], and x_0 evolves towards one. The second example was seeded with a highly cooperative strategy ($k = 0.3, d = 0.8$ and $x_0 = 1$), but evolved towards *AllD*.

offers full cooperation as an initial move, the strategy evolves initially to an even more cooperative state ($d \rightarrow 1$), but x_0 gradually decreases, and eventually x_0, k and d all evolve to zero; the steady state is *AllD*.

These examples are illustrative of two broad classes of steady-state strategies that we observed: (i) cooperative strategies that intersect $[1, 1]$ on the unit square and have fairly low intercepts; and (ii) indiscriminate defectors. To examine the evolutionary trajectories through strategy space more generally, we seeded strategies at uniform intervals in k, d and x_0 , and followed the evolution of each strategy for a small number of mutations. Figure 5 shows one plane through the results of this simulation, the d - k plane at the level $x_0 = 1$. Open circles show the initial positions of the strategies investigated.

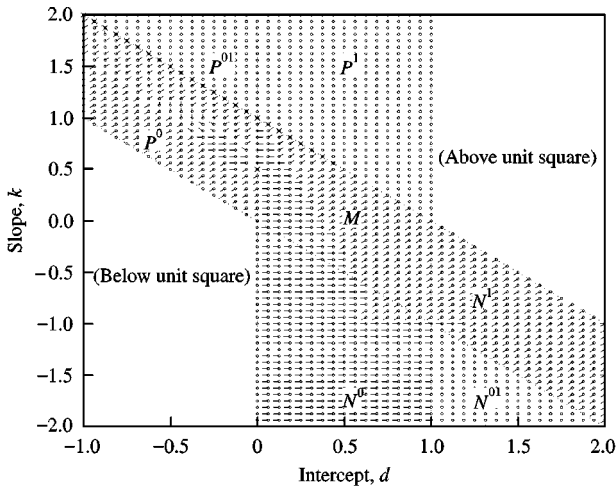


FIG. 5. Strategy trajectories, $x_0 = 1$. Strategies were seeded at uniform intervals in k, d and x_0 and were allowed to evolve through two successful mutations; all three parameters of the starting strategies were allowed to evolve. For this figure we used $b = 2, c = 1$ and $n = 20$, the results for $\bar{n} = 20$ were qualitatively identical. The figure illustrates the d - k plane at the level $x_0 = 1$. Open circles show the initial positions of the strategies investigated, and these are connected by solid lines to the final position of the strategy after two mutations. Crosses indicate strategies that are not invaded by their neighbors in strategy space. Where open circles appear without visible evolutionary trajectories in this plane, the trajectory is into the page; x_0 evolves towards smaller values in these regions. For the majority of strategies within P^0 and M , and for all strategies in N^1 and N^0 , strategies evolve towards the lower left boundary of the space, or towards indiscriminate defection. For sections of P^0 and M where k is sufficiently large, however, strategies evolve towards the upper left; they become more cooperative and move towards the line $k + d = 1$.

Lines indicate the direction of the evolution through strategy space. Where open circles appear without visible evolutionary trajectories in this plane, the trajectory is into the page; x_0 evolves towards smaller values in regions P^{01}, P^1 and N^{01} .

This figure reveals a fairly complex set of trajectories on the $x_0 = 1$ plane. For the majority of strategies within P^0 and M , and for all strategies in N^1 and N^0 , strategies evolve towards the lower left boundary of the space, or towards indiscriminate defection. For sections of P^0 and M where k is sufficiently large, however, strategies evolve towards the upper left; they become more cooperative and move towards the line $k + d = 1$.

The crosses in this figure indicate strategies that are not invaded by their neighbors in strategy space. We are especially interested in the set of crosses which lies along the boundary between M and P^1 , since these represent *cooperative* strategies which are stable with respect to the adaptive dynamics. For this set of strategies $kx + d = 1$ when $x = 1$; as in the first example of Fig. 4, they intersect the unit square at $[1, 1]$.

Some insight into this set of strategies can be obtained analytically, particularly for the limiting case of an infinite game. Consider a set of strategies on the d - k plane (at $x_0 = 1$) with the property that $k + d = 1$. We denote one such strategy, S_{k,d,x_0} , and a near neighbor S_{k',d',x'_0} . If the neighbor is a member of M , then (as demonstrated previously) the play moves towards $x = (kd' + d)/(1 - kk')$ and $x' = k'(kd' + d)/(1 - kk') + d'$. In the limit of an infinitely repeated game, the mean payoff $F(S_{k',d',x'_0}, S_{k,d,x_0})$ is equal to $bx - cx'$. For S_{k,d,x_0} to be invaded by its neighbor, we find

$$F(S_{k,d,x_0}, S_{k,d,x_0}) \leq F(S_{k',d',x'_0}, S_{k,d,x_0}), \quad (8)$$

$$b - c \leq bx - cx' \quad (9)$$

which, substituting, reduces to

$$k \leq \frac{c}{b} \quad (10)$$

under the conditions that $k < 1$ and $k' + e' < 1$, which are true for members of M .

If the neighbor is a member of P^1 , then it is clear that $k'x + d' > 1$ and therefore the response of the neighbor to full cooperation will be full cooperation in return. Regardless of the initial moves, the play will move towards (1, 1); the two strategies are neutral with respect to each other.

Thus, we find analytically that none of the strategies on the boundary between M and P^1 can be invaded by near neighbors in the infinite game, as long as $k > c/b$ and $x_0 = 1$. The simulations illustrated in Fig. 5 indicate that this is also true for a finite game. Note that this group of strategies is not only cooperative, but also lies along a line where x_0 evolves towards 1. We also note that for this set of strategies in which $d = 1 - k$, the condition $k > c/b$ is equivalent to the condition under which a cooperative strategy is resistant to invasion by *AllD*, that is, $d < 1 - c/b$.

4. Nash Equilibria

Using simulations with $n = 20$ or $\bar{n} = 20$, we found strategies which cannot apparently be beaten by any other strategy in our strategy space, i.e. strategies for which $F(S, S) \geq F(S, S')$, $\forall S'$. (This condition defines Nash equilibria, NE.) In these simulations, each strategy was tested against approximately 5000 other strategies which varied in k, d and x_0 . The results are illustrated in Figure (6). In this figure, “x” represents NE with $x_0 = 0$, and “o” plots points which are NE with $x_0 = 1$. There was no difference in these NE regions for games with exactly 20 rounds or games with 20 rounds on average.

The star in Fig. 6 indicates a small region along the line segment $\{d = 0; 0 < k < 1\}$ in which strategies are NE over a range of x_0 values. This NE region was only observed when the number of rounds was fixed, i.e. when payoffs occurring earlier in the game were not weighted more highly than later gains. We can show that for a small region along the line $\{d = 0\}$ near $k = c/b$, strategies are stable against invasion by both *AllC* and *AllD* for any value of x_0 (Appendix B).

Thus, we find that three groups of strategies are Nash equilibria in the Continuous Prisoner's Dilemma. A small set of strategies for which the intercept, d is zero and the slope is close to c/b are NE for a range of x_0 values. *AllD* is a strategy

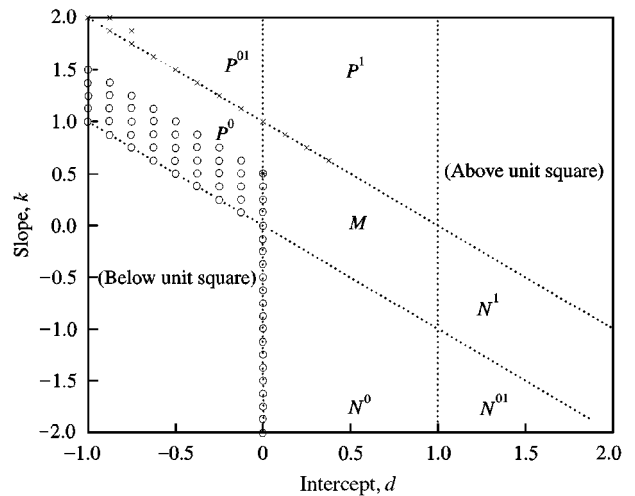


FIG. 6. Nash equilibria. Strategies were seeded at uniform intervals in k, d and x_0 and were tested against 4125 other strategies in which $-2 \leq k \leq 2$, $-1 \leq d \leq 2$ and $0 \leq x_0 \leq 1$, using $b = 2$ and $c = 1$. Strategies which were apparently Nash equilibria (NE, conditions described in the text) are shown: NE with $x_0 = 0$ (x); Points which are NE with $x_0 = 1$ (o). There was no difference in these NE regions for games with exactly 20 rounds or games with 20 rounds on average. The star indicates a small region along the line segment $\{d = 0; 0 < k < 1\}$ in which strategies are apparently NE for a range of x_0 values (⊙). This NE region only exists for the game with a fixed number of rounds.

at Nash equilibrium, as are strategies which are close to complete defection (in group P^0 with sufficiently low slope and $x_0 = 0$). We further find that strategies which intersect the unit square at $[1, 1]$, with $x_0 = 1$ and an intercept which is less than $1 - c/b$, appear to be stable not only against near neighbors (as shown analytically in Section 3.2) but against any other strategy in the space. This group of strategies is of particular interest in the region $c/b < k < 1$, where it defines a set of *cooperative* strategies which are Nash equilibria.

The three constellations of NE may be differentiated (as shown in Fig. 6) by the value of x_0 in each group. Thus, given a fixed value of x_0 , the most successful type of strategy in the system is determined. We find that for strategies which give nothing or very little as an initial move, all the NE are close to indiscriminate defection, and have very low mean payoffs (cf. Fig. 6 and Fig. 2). Conversely, for strategies which offer complete cooperation as an initial move, some cooperative NE exist and these receive the maximum possible payoff when playing against themselves.

We emphasize that all cooperative strategies which are NE share the feature that $x_0 = 1$.

5. Stochastic Adaptive Dynamics

Figure 5 suggests a fairly complex set of evolutionary trajectories through strategy space. To analyse the overall behavior of this system, we use a modification of adaptive dynamics, in which a stochastic element is introduced to capture the effects of random drift. We begin with a single strategy, S , and allow it to evolve by small random changes in k, d or x_0 to a new strategy S' . We let S' replace S if

$$F(S', S) > F(S, S) \quad (11)$$

and

$$F(S', S') > F(S, S') \quad (12)$$

This assumes that the frequency of advantageous mutations is low compared to the rate at which fixation occurs, and is the standard transition rule of adaptive dynamics (Nowak & Sigmund, 1990; Metz *et al.*, 1996; Hofbauer & Sigmund, 1998). To this standard rule we add the following three “stochastic” rules:

(1) Under the conditions

$$F(S', S) > F(S, S) \quad (13)$$

and

$$F(S', S') \leq F(S, S'), \quad (14)$$

we compute the equilibrium frequency of S , i.e. the frequency g such that

$$\begin{aligned} gF(S, S) + (1 - g)F(S, S') \\ = gF(S', S) + (1 - g)F(S', S'). \end{aligned} \quad (15)$$

We then draw a random number from a uniform distribution on $(0, 1)$ and accept S' if this number is greater than g . This step is equivalent to the assumption that stochastic fluctuations will eventually cause the chance extinction of one of the two strategies which are at equilibrium in the population.

(2) Under the conditions

$$F(S', S) < F(S, S) \quad (16)$$

and

$$F(S', S') > F(S, S'), \quad (17)$$

we likewise compute the frequency, h , of strategy S' that is necessary to overcome the invasion barrier. In this case we draw a random number, r , from $(0, 1)$ and accept S' in this case if $r < e^{-\lambda h}$. The exponent λ reflects how likely it is that random drift will cause a fluctuation of frequency h in the population, and in reality will be related to the total population size, spatial structures or assortative interactions.

(3) If S and S' are neutral with respect to each other, we assume that the chance that S disappears by chance extinction is inversely proportional to population size, N , and accept S' if $r < 1/N$.

Finally, we periodically introduce new mutants by choosing k, d and x_0 from random distributions, rather than constraining S' to be a near neighbor of S . These mutant strategies are then accepted or rejected according to the rules described above. Note that if S' does not invade S , we rewrite S in the sequence of successful strategies, and generate a new S' .

These transition rules allow us to “explore” the strategy space adaptively, by forming a discrete sequence of successful strategies. The introduction of randomly generated mutants gives this sequence the potential to span the entire strategy space, and from each new position in the space the natural adaptive trajectory is followed. In situations where this trajectory would reach a steady state according to standard adaptive dynamics, however, we allow the simulation to continue by invoking the stochastic rules (1)–(3) above. This allows the sequence to continue through regions of the space which are neutral with respect to each other, or to leave regions that are only subject to adaptive change after crossing an invasion barrier. We emphasize that these rules are called into play very infrequently in our simulations, accounting for only about 1–2% of all transitions. The weakest assumption of this method is that we do not allow equilibria to exist between different strategies; this avoids the modelling of complicated polymorphisms.

In the final adaptive sequence, the number of strategies which lie in each region of the space reflects how “successful” strategies in that region are, or how unlikely it is for strategies of this type to be invaded or to drift to zero frequency. This feature allows us to use the final sequence to build a probability distribution in strategy space, reflecting the success and overall robustness of every type of strategy.

Using this method, we simulated the long-term evolution of the system, starting with strategy I and producing 100 000 new strategies successively. Each strategy played a single 20 round game against each putative successor, with $b = 5$ and $c = 1$. We also simulated the case when $\bar{n} = 20$ by weighting the payoff in round i by the probability that a game would last to round i , $(1 - 1/\bar{n})^{i-1}$. We set $\lambda = 2$ in all of these simulations.

We found that along this trajectory of adaptive dynamics, only about 2% of newly generated strategies were accepted by overcoming an invasion barrier, about 1.5% by chance extinction of one of two strategies in equilibrium, and less than 0.1% by chance extinction of one of two neutral strategies. One in every ten new strategies was generated as a random, non-neighboring mutant, and such mutants successfully invaded about 3% of the time.

The results of this simulation are illustrated in Fig. 7. This figure shows the distribution, over the d - k plane, of 100 000 successive strategies, with $b = 5$, $c = 1$. The figure illustrates that strategies in this sequence are distributed throughout all strategy families, but that clusters of successful strategies occur predominantly in two regions of the d - k plane: we see a cluster of strategies near $[0,0]$ and along the boundary of the region corresponding to $AllD$ (for example along the line $d = 0$, $k < 0$); we also observe a cluster of cooperative strategies in the Nash equilibria region along the boundary of M and P^1 .

About 19% of these strategies were members of family P^1 , the cooperators, and fully 41% were close to full cooperation, in the sense that $F(S, S)$ was within 10% of the maximum payoff possible between identical strategies. Of the members of P^1 , 35% occurred at the region of NE on the boundary between P^1 and M (i.e. they met the

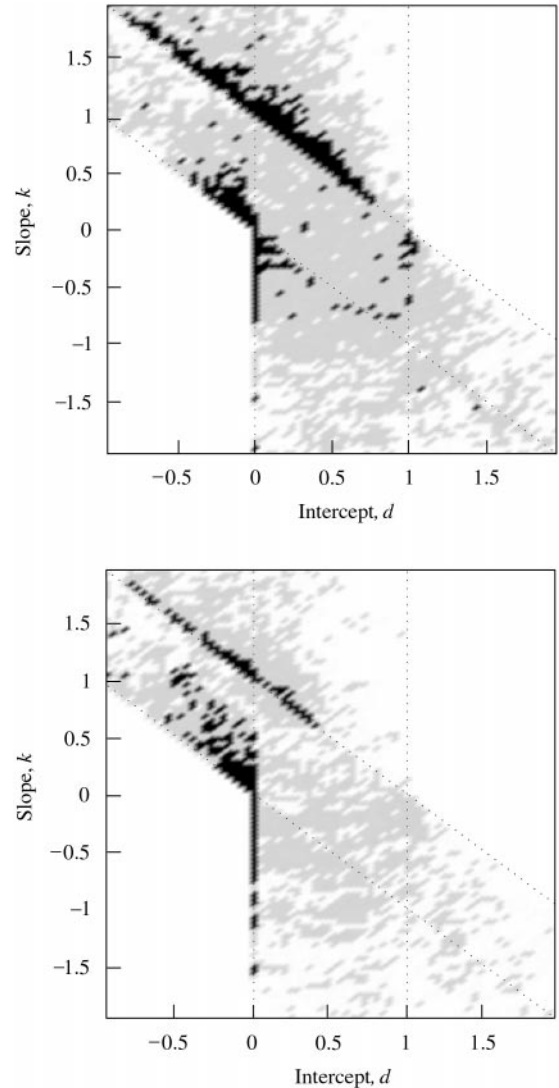


FIG. 7. Distribution of strategies determined by stochastic adaptive dynamics. A sequence of 100 000 successive strategies, with $b = 5$, $c = 1$ and an initial strategy I , was generated by stochastic adaptive dynamics. The distribution of these strategies is illustrated on the d - k plane (top panel). We show here the results for games of 20 rounds on average, but results for games with exactly 20 rounds were qualitatively and quantitatively similar. The plane was divided into pixels (width = height = 0.02), and the number of strategies in each pixel was determined from the sequence. The results were mapped to a three-level grey scale and then smoothed by Gouraud shading. The results illustrate two clusters of successful strategies; one around $d = 0$; $k = 0$ or $AllD$, and a second cluster of cooperative strategies in the NE region along the boundary of M and P^1 . The lower panel shows the same result but for $b = 2$. Here we note more defective strategies in the distribution.

conditions $k < -d + 1.1$ and $k > c/b$). About 18% of successful strategies were members of family P^0 , the defectors.

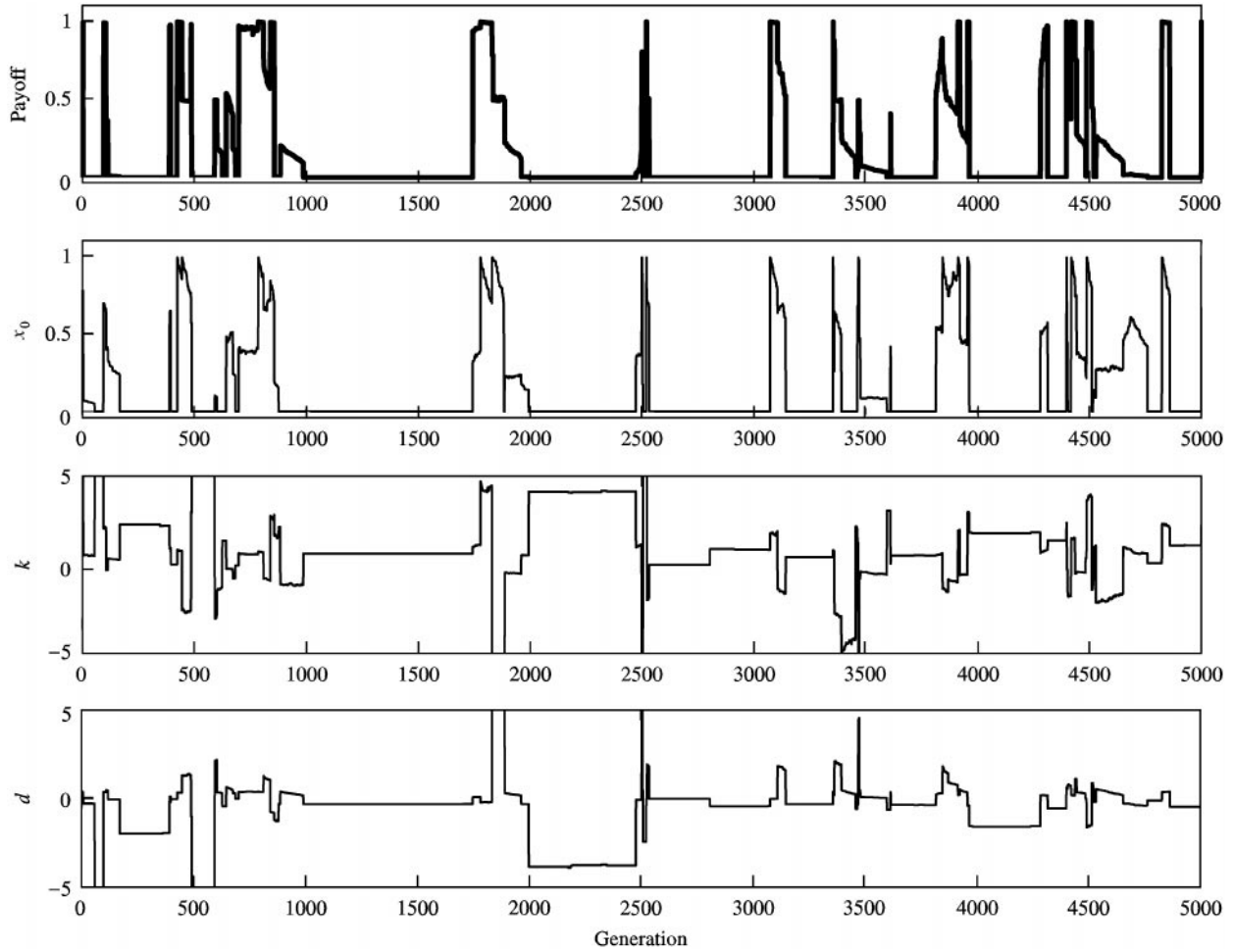


FIG. 8. Evolution of $F(S, S)$, x_0 , k and d for 2500 successive strategies. The value of the payoff function and the three parameters of the strategy are shown, for a typical segment of 2500 strategies from the stochastic adaptive sequence described for Fig. 7; for the sequence shown here $b = 2$. The payoff illustrated is the payoff received when the strategy plays itself, $F(S, S)$, and is highly correlated to x_0 .

We repeated this simulation with $b = 2$, and found only 7% cooperators, and 35% defectors [Fig. 7(b)]. This illustrates the sensitivity of this distribution in strategy space to the cost-to-benefit ratio.

Figure 8 shows the evolution of $F(S, S)$, x_0 , k and d over a subset of successive strategies, for the initial simulation with $b = 2$. Note the striking correlation between the payoff and x_0 . For 100 000 strategies, the correlation coefficient between $F(S, S)$ and x_0 was 0.86 (compared to -0.02 and 0.02 for k and d , respectively).

6. Discussion

By simulating the evolutionary dynamics of interspecific mutualisms, Doebeli and Knowlton

(1998) found that the initial offers of both host and symbiont evolve towards zero unless spatial effects are included in the model (but see Killingback *et al.*, 1999). We concur that many strategies in our strategy space evolve towards total defection, but have found some notable exceptions to this trend. In particular, strategies that respond sensitively to cooperation (k sufficiently high), but are not suckers (d sufficiently low), have the potential to evolve towards cooperative Nash equilibria.

These Nash equilibria are a set of cooperative strategies which receive the maximum payoff when playing against themselves, and yet are neither susceptible to invasion by defectors nor by more generous strategies. We note three defining characteristics of these

strategies:

1. Since $S(x) > x$, $\forall x$, these players consistently offer a little more than what was offered to them—they are *generous*. This feature is crucial because generosity can move the play continually towards greater cooperation. In particular, this generosity implies that these strategies give *something for nothing* [$S(0) > 0$]; they have intercepts which lie in the interval $[0, 1 - c/b]$. This result is counterintuitive because it appears that the most successful players are at a clear disadvantage when playing defectors. Giving something for nothing, however, prevents the play from getting “stuck” at $S(0) = 0$, and the limit $d < 1 - c/b$ ensures that the strategy is robust in the face of invasion by defectors.
2. We also find that all the cooperative NE strategies make the highest initial offer possible, $x_0 = 1$. When faced with a new opponent, these strategies offer complete cooperation—they are consistently *optimistic*. If the opponent defects, however, these strategies immediately respond with a very low second move [$S(0) = d < 1 - c/b$], and continue attempts to raise the stakes gradually. The initial optimism is important because it allows cooperative strategies to get on with cooperating, without the lengthy business of building up trust. All else being equal, these strategies assume the best of everyone.
3. Finally, we note that the most successful strategies in the continuous Prisoner’s Dilemma are *uncompromising*. By this we mean that these players offer full cooperation as a first move but thereafter do not cooperate fully unless their opponent does the same: $x_0 = 1$ and $S(1) = 1$, but $S(x) < 1$ for all $x < 1$. This feature is crucial because it ensures that these strategies cannot be exploited by players who consistently undercut full cooperation.

Roberts and Sherratt (1998) found that a low initial investment, followed by gradual increases, was a particularly effective strategy in their continuous model of the Prisoner’s Dilemma. A

direct comparison with our results is difficult, because the strategies used by Roberts and Sherratt are formulated differently. We note that the cooperative Nash equilibria in our model *do* attempt to raise the stakes when playing a strategy which is initially reticent to cooperate, since $S(x) > x$ for all x . Our NE strategies, however, offer full cooperation as an initial move. Cooperative strategies which offer anything less than complete cooperation as a starting move are not Nash equilibria in our model, but can be invaded by strategies with a higher initial offer; this appears to be the case in the formulation of Roberts and Sherratt as well.

In summary we find that the initial offer, x_0 , is a decisive factor in the Continuous Prisoner’s Dilemma. The steady-state regions in this system can be distinguished by x_0 , the mean payoff a population of a given strategy receives is tightly coupled to x_0 , and x_0 evolves towards an offer which will elicit complete cooperation in a partner, whenever that is possible.

We have introduced an extension of standard adaptive dynamics which models the effects of random fluctuations in population frequencies. We use two ‘stochastic’ transition rules to model random drift in populations which are either at equilibrium or neutral with respect to each other, while a third rule models the possible fluctuation of population frequency past an invasion barrier. Although these stochastic transitions are actually very infrequent in our simulations, this approach (coupled with the introduction of randomly generated mutant strategies) allows adaptive change to continue through every region of the strategy space. We avoid modelling complicated polymorphisms by disallowing equilibrium states between different strategies; our results are therefore an approximation of population dynamics which may be more complex.

In the resulting sequence of successful strategies, the number of strategies in each region of the space reflects the overall success of strategies in that region. For example, the number of time steps for which a given strategy remains successful against putative invaders reflects the probability that this strategy will neither be invaded nor drift to zero frequency. The final sequence of strategies therefore represents a *probability distribution* in strategy space, allowing us to visualize

the overall success and robustness of every type of strategy. We find that this distribution is extremely sensitive to the cost-to-benefit ratio. When the benefits of cooperation are sufficiently high, cooperators will outnumber defectors.

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APPENDIX A

Intermediate Solutions of \hat{x}_0

We start with an initial cooperative strategy S_{k,d,x_0} and consider small perturbations in the starting move, $x'_0 = x_0 + \delta x$. We will denote the strategy S_{k,d,x'_0} as S' , and accept S' when the following two conditions are met:

$$F(S', S) > F(S, S) \quad (\text{A.1})$$

and

$$F(S', S') > F(S, S') \quad (\text{A.2})$$

First consider the case when x_0 is initially set to 1, and $x'_0 = 1 - \delta x$. As long as δx is small enough, $S(x'_0) = S(x_0) = 1$ (i.e. $kx'_0 + d > 1$). In this situation, strategy S' receives complete cooperation (full benefit) when playing strategy S , but pays a slightly smaller cost; condition (A.1) is clearly met. By similar arguments, it is clear that condition (A.2) will be met, and x_0 will evolve towards smaller values.

At some point in this downwards evolution, x_0 will cross a threshold \hat{x}_0 such that $S(\hat{x}_0) = k\hat{x}_0 + d = 1$ but $S(\hat{x}_0 - \delta x) = k\hat{x}_0 + d - k\delta x < 1$. We see that $\hat{x}_0 = (1 - d)/k$ and the sequence of moves, when player S' plays first, will be

Player S' : $\hat{x}_0 - \delta x$, Player S : $k\hat{x}_0 - k\delta x + d$

Player S' : 1 ..., Player S : 1 ...

Summing the costs and benefits over an iterated game with exactly n rounds, we find that

condition (A.1) is not met if

$$F(S, S) - F(S', S) = \frac{bk\delta x - c\delta x}{2n} > 0 \quad (\text{A.3})$$

This equation reduces to $k > c/b$. Thus, as long as the slope of the cooperative strategy is higher than the cost-to-benefit ratio, the downwards evolution of x_0 will stop at $\hat{x}_0 = (1 - d)/k$. The sequence of moves at this point is:

Player 1: $\hat{x}_0 = (1 - d)/k$, Player 2: 1,

Player 1: 1 ..., Player 2: 1 ...

We can show in an analogous way that for the cooperative strategies with $k > c/b$, x_0 will evolve from zero towards larger numbers.

Suppose, however, that x_0 has evolved upwards to \tilde{x}_0 , where \tilde{x}_0 is defined to be the point at which $S(S(\tilde{x}_0)) = (1 - d)/k$. Clearly $\tilde{x}_0 < \hat{x}_0$. The initial sequence of moves at this point will be

Player 1: \tilde{x}_0 , Player 2: $k\tilde{x}_0 + d$,

Player 1: $k^2\tilde{x}_0 + kd + d = (1 - d)/k$, Player 2: 1,

Player 1: 1 ..., Player 2: 1 ...

Consider the next possible step in the evolution of x_0 , $x'_0 = \tilde{x}_0 + \delta x$, with $\delta x > 0$. The sequence of moves would then be:

Player 1: $\tilde{x}_0 + \delta x$, Player 2: $k\tilde{x}_0 + k\delta x + d$,

Player 1: $k^2\tilde{x}_0 + k^2\delta x + kd + d$, Player 2: 1,

Player 1: 1 ..., Player 2: 1 ...

We will accept the new strategy, with $x_0 = \tilde{x}_0 + \delta x$, only if the benefit of this increase in x_0 outweighs the additional cost. Thus, for condition (A.1) to be met, we find that

$$bk\delta x > c(\delta x + k^2\delta x) \quad (\text{A.4})$$

which can be rewritten, for $\delta x \neq 0$, as

$$k^2 - \left(\frac{b}{c}\right)k + 1 < 0, \quad (\text{A.5})$$

This quadratic equation in k has two real roots for $b/c > 2$. When the benefit-to-cost ratio exceeds this limit, k must be between these roots in order for the benefit of increasing x_0 past \tilde{x}_0 to outweigh the additional cost involved. Thus, the upwards evolution of x_0 will stop at $\tilde{x}_0 < \hat{x}_0$ for cooperators with slopes outside this range.

We have therefore demonstrated that the steady-state value of x_0 is $\hat{x} = (1 - d)/k$ when x_0 is initially set to 1 and $k > c/b$, but that intermediate steady states are possible if x_0 is initially set to zero.

APPENDIX B

Stability of $S_{k,0,x_0}$

It is simple to show that for a game of exactly n moves, the payoff a strategy along the line segment $\{d = 0; 0 < k < 1\}$ receives against itself is given by

$$F(S_{k,0,x_0}, S_{k,0,x_0}) = (b - c) \frac{x_0 (1 - k^{2n})}{2n (1 - k)}. \quad (\text{B.1})$$

The payoff an indiscriminate defector receives when playing this strategy is clearly

$$F(AllD, S_{k,0,x_0}) = b \left(\frac{x_0}{2n} \right). \quad (\text{B.2})$$

Similarly, the payoff an indiscriminate cooperator receives against $S_{k,0,x_0}$ is

$$F(AllC, S_{k,0,x_0}) = b \left(\frac{x_0 + (2n - 1)k}{2n} \right) - c. \quad (\text{B.3})$$

Using these payoff values, we solve to determine the conditions under which strategy $S_{k,0,x_0}$ is stable against invasion by both *AllC* and *AllD*, and find that this is true for a small region defined approximately by

$$\frac{c}{b} \leq k \leq \frac{c}{b} \left(\frac{2n(1 - k) - x_0}{(2n - 1)(1 - k) - x_0} \right). \quad (\text{B.4})$$

AllC and *AllD* are representative of extremes in the spectrum of all strategies, and so we have some insight as to why strategies near $S_{c/b,0,x_0}$ appear to be stable against invasion by any strategy in the space. Also note that x_0 drops out of the equation, such that $S_{c/b,0,x_0}$ is stable for any value of x_0 , and further that $2n - 1 \rightarrow 2n$ as $n \rightarrow \infty$, so that $S_{k,0,x_0}$ only resists invasion when k is exactly equal to c/b for large values of n .