Axelrod 1984). The prisoner's dilemma is a symmetric two-person game that illustrates well the paradox surrounding the evolution of cooperation. Each player in the prisoner's dilemma has two possible strategies: cooperate (C) and defect (D), with the payoffs for the game given in figure 1. The temptation to cheat is T, R is the reward for mutual cooperation, P is the punishment for mutual defection, and S is the payoff one obtains when cooperating against an opponent who defects (i.e., S is the sucker's payoff). The prisoner's dilemma is defined by requiring that $T > R > P > S$ and $2R > T + S$. The dilemma inherent in this game is the following: since $T > R$ and $P > S$, player 1 should always play D, whatever player 2 does; however, since the game is symmetric, the same reasoning also applies to player 2. Thus both players play D and receive a payoff of P, but had they both played C they would have received the higher payoff of R. The prisoner's dilemma contains, in prototype form, the fundamental paradox of cooperation—that while there is an advantage to cheating over cooperating, mutual cooperation is more profitable than mutual defection. The significance of the prisoner's dilemma as a simple model for the evolution of cooperation seems to have been appreciated first by Hamilton and by Trivers (see comments in Trivers 1971). It follows directly from the structure of the game that if individuals are trapped in a prisoner's dilemma, with each pair of individuals playing the game only once and with random interactions between the individuals, then natural selection will always favor defectors (Axelrod and Hamilton 1981; Axelrod 1984). Thus in a population of cooperators and defectors, evolution will always result in the cooperators being eliminated and the defectors going to fixation.

Although cooperation can never evolve for any entities trapped in a one-shot prisoner's dilemma, it is possible for cooperation to evolve if the game is played repeatedly between the same individuals. The simplest model embodying Trivers's (1971) concept of reciprocal altruism is the iterated prisoner's dilemma (Axelrod and Hamilton 1981; Axelrod 1984), which consists of a repeated sequence of prisoner's dilemma games played between the same two players, with the players' moves at each stage depending on the history of past moves by both players. The great merit of the iterated prisoner's dilemma is that it provides a simple, yet precise, model with which to study the evolution of cooperation via reciprocity. The iterated prisoner's dilemma is now the standard model for studying the evolution of cooperation by reciprocal altruism and has generated a vast amount of research (some of which is reviewed by Axelrod and Dion 1988).

Much of this research has focused on identifying strategies for the iterated prisoner's dilemma that allow the evolution of cooperation. In their original work on the iterated prisoner's dilemma, Axelrod and Hamilton (1981) and Axelrod (1984) considered the strategy "tit for tat" (which had been devised by Anatol Rapoport). Tit for tat is defined as follows: cooperate on the first round of the game and, on subsequent rounds, play the same move that your opponent played in the previous round. Axelrod and Hamilton (1981) and Axelrod (1984) found that tit for tat often did well in the iterated prisoner's dilemma and that this strategy could lead to the evolution of cooperative behavior. Subsequent work on the evolution of cooperation in the iterated prisoner's dilemma has found that there are other strategies that often perform even better than tit for tat. Nowak and Sigmund (1992) found that a more generous variant of tit for tat ("generous tit for tat") that does not always retaliate against a defection by one's opponent is often a good strategy. In further work, Nowak and Sigmund (1993) found that a new strategy, "Pavlov," which depends on both players' previous moves, usually outperforms tit for tat. The Pavlov strategy cooperates on the first move, and on subsequent moves, it repeats its own last move after receiving a payoff of R or T and plays the opposite of its own last move after receiving a payoff of P or S. Pavlov has two important advantages over tit for tat: first, it is able to correct mistakes, and unlike tit for tat, a single mistake does not lead to a permanent breakdown in cooperation; second, Pavlov is able to exploit unconditional cooperators and thereby prevent them from increasing in frequency to the point where they can lead to the growth of unconditional defectors.

	C	D
C	R	S
D	T	P

Figure 1: Payoff matrix for the prisoner's dilemma. The entries are the payoff to a player using a strategy from the left column when the opponent uses a strategy from the first row.

In studying the evolution of cooperative strategies in the iterated prisoner's dilemma, it is necessary to specify whether or not the two players make their moves simultaneously. If the two players' moves are not synchronized, then one obtains an iterated game consisting of an alternating sequence of prisoner's dilemma games (Frean 1994; Nowak and Sigmund 1994). Different strategies do well in these two variants of the iterated prisoner's dilemma. In the simultaneous case, Pavlov appears to be a very good strategy (Nowak and Sigmund 1993), while in the alter-

nating case, generous tit for tat seems to be the better strategy (Nowak and Sigmund 1994).

Despite its widespread use as a model of cooperation, the prisoner's dilemma suffers from a fundamental limitation—each player has only two possible options: to cooperate or to defect. Behavior in real systems can hardly be expected to have this dramatically discrete nature. Indeed there is considerable evidence that cooperative behavior in nature should be viewed as a continuous rather than a discrete trait. For example, it has been found in the work on allogrooming in impala (Hart and Hart 1992; Mooring and Hart 1992) that the number of grooming bouts delivered varies substantially. It has also been shown in the context of predator inspection in fish that different degrees of "cooperation" often occur (see Dugatkin and Alfieri 1991). It seems likely that in most cases cooperative behavior can vary in degree, with complete defection being one extreme.

The importance of allowing variable degrees of cooperation in theoretical studies of the evolution of cooperation has been appreciated for some time (Smale 1980; May 1987; Frean 1996; Wilson and Dugatkin 1997). However, it is only recently that detailed models extending the standard prisoner's dilemma to situations with varying degrees of cooperation have been formulated (Doebeli and Knowlton 1998; Roberts and Sherratt 1998; Killingback et al. 1999; Wahl and Nowak 1999*a*, 1999*b*). This extension, which we shall refer to as the "continuous prisoner's dilemma," is described in detail in the next section. The continuous prisoner's dilemma provides a natural model for studying cooperation when the cooperative trait is continuous in nature.

An important consequence of the formulation of the continuous prisoner's dilemma is that it allows detailed study of the evolution of cooperation via reciprocal altruism for systems with continuous cooperative traits. This approach allows us to consider fundamental new aspects of the evolution of cooperation. The two most important questions are, Can reciprocal altruism with variable degrees of cooperation result in cooperative behavior evolving gradually from an initially selfish state? and Can cooperative behavior be maintained indefinitely, or does the continuous nature of the trait result in a cooperative state being gradually undermined? That is, in the continuous framework, we can investigate how cooperative behavior can arise in the first place and whether or not it is stable. It is worth noting that the problem of how cooperation initially evolves in a selfish world has proved to be hard to resolve satisfactorily within the standard framework of the discrete prisoner's dilemma (see, e.g., Axelrod and Hamilton 1981; Axelrod 1984). The approach introduced here, in which cooperation is a continuous trait, allows a new attack on this fundamental problem.

Understanding the evolution of cooperation by reciprocal altruism in this framework involves formulating the iterated version of the continuous game (that is, the iterated continuous prisoner's dilemma) and understanding how strategies for the iterated game can evolve to allow cooperation. This problem has been studied by Roberts and Sherratt (1998) and by Wahl and Nowak (1999*a*, 1999*b*). The authors of these two works study different strategies for the continuous prisoner's dilemma (which are described in more detail in "Discussion"), but in both cases, the strategies depend only on the opponent's previous move. In this respect, these strategies are analogous to reactive strategies, such as tit for tat, in the standard iterated prisoner's dilemma. However, in view of the success of strategies in the iterated prisoner's dilemma that depend on both players' previous moves, such as Pavlov (Nowak and Sigmund 1993), it is natural to ask whether there are successful strategies for the continuous prisoner's dilemma that depend on both players' moves. Here we introduce such a class of strategies, which depend on the players' payoff in the previous round (and which are related to those considered by Doebeli and Knowlton [1998] in the context of mutualism), and we show, both analytically and by simulation, that they give a simple and elegant explanation of the evolution of cooperation via reciprocal altruism when the degree of cooperation can vary. In particular, we show that this new class of strategies (which we call payoff-based strategies) provides a natural resolution of the fundamental problem of how cooperative behavior can evolve in an initially selfish world and how such behavior can be maintained thereafter.

The Continuous Prisoner's Dilemma and Payoff-Based Strategies

We introduce here the continuous prisoner's dilemma (following the general approach described in Killingback et al. 1999) and the class of strategies (payoff-based strategies) that we shall consider in the iterated game. Perhaps the simplest way to arrive at the continuous prisoner's dilemma is to start with the discrete prisoner's dilemma, expressed in its most biologically intuitive formulation. As above, we let C and D denote the strategies of cooperation and defection, respectively. We assume that cooperation involves a cost c to the "donor" (i.e., it results in the donor having c fewer offspring than it would otherwise have had) and brings a benefit b to the "recipient" (i.e., it results in the recipient having b extra offspring in addition to those that it would otherwise have had). Defection has zero cost to the donor and gives zero benefit to the recipient. It is clear now that, under these assumptions, the payoffs to two individuals adopting the strategies C and D are as shown in figure 2. In the context of the evolution of co-

	C	D
C	b-c	-c
D	B	0

Figure 2: Payoff matrix for the prisoner's dilemma in terms of costs c and benefits b. The entries are the payoff to a player using a strategy from the left column when the opponent uses a strategy from the first row.

operation, we require that the cost and benefit are positive (i.e., $b, c > 0$) and that the benefit exceeds the cost (i.e., $b > c$). If this latter condition is not satisfied, then it is intuitively clear that cooperation can never evolve for trivial reasons. When both these conditions hold, then the payoffs given in figure 2 define a prisoner's dilemma (i.e., if we set $T = b$, $R = b - c$, $P = 0$, and $S = -c$, then $T > R > P > S$ and $2R > T + S$). It is now straightforward to make the transition to the continuous prisoner's dilemma.

The degree of cooperation that an individual engages in is defined by an investment (or perhaps the term "donation" would be more appropriate) I. Making an investment I involves a cost (i.e., a decrease in fitness) $C(I)$ to the donor and brings a benefit (i.e., an increase in fitness) $B(I)$ to the individual who is the recipient, where both the cost and benefit depend on the level of investment I. Thus if two individuals, making investment I and I', respectively, play simultaneously, then the payoff to individual 1 is $S(I, I') = B(I') - C(I)$, while the payoff to individual 2 is $S'(I', I) = B(I) - C(I')$. Although, in principle, we could consider arbitrary functions for B and C, there are two cases for B and two cases for C that are particularly natural. The first is when B is a concave function of I. In this case, the benefit shows diminishing returns as the investment increases. It seems likely that in most natural system the benefit will exhibit diminishing returns for sufficiently large levels of investment (see Altmann 1979; Weigel 1981; Schulman and Rubenstein 1983). The second case is when the benefit is a linear function of the investment. Linear benefit functions arise as approximations to more general concave functions when the investment levels are low. The two most natural cases for C are those of a linear and a quadratic function. There is good evidence that in many situations the cost is well described by a quadratic function (Sibly and McFarland 1976). Linear cost functions are also interesting to consider because they arise as approximations to more general cost functions. Typical cost and benefit functions are shown in figure 3: figure 3*A* shows a linear benefit function and a linear cost function, figure 3*B* shows a concave benefit function and a linear cost function, and figure 3*C* shows a concave benefit function and a quadratic cost function. Once the cost and benefit functions have been defined, this system defines the continuous prisoner's dilemma (see Killingback et al. 1999). The analytical results we describe below hold for arbitrary cost and benefit functions. The simulation results we present below are for the cost and benefit functions shown in figure 3. However, similar simulation results are obtained for a wide variety of qualitatively similar cost and benefit functions—the specific form of the cost and benefit functions affects only the quantitative details of the results, not the qualitative behavior of the system.

In order to study reciprocal altruism, we wish to consider the iterated continuous prisoner's dilemma, which in turn requires that we have strategies that determine a player's move given the past history of moves by both players. A strategy σ of memory l for the iterated continuous prisoner's dilemma determines the players investment I_k in round k, in terms of the previous l moves made by both players:

$$I_k = \sigma(I_{k-1}, I_{k-2}, \ldots, I_{k-l}, I'_{k-1}, I'_{k-2}, \ldots, I'_{k-l}), \qquad (1)$$

where I_j and I'_j denote the investment in round j of the player and opponent, respectively. The opponent's investment in round k is similarly determined by a strategy $\sigma' : I'_k = \sigma'(I_{k-1}, \ldots, I_{k-l}, I'_{k-1}, \ldots, I'_{k-l})$. In each round, the payoffs are calculated as described above. Given two strategies σ and σ' and a probability w of a further move after each round of the game (which corresponds to a game with an average of $n = 1/[1 - w]$ rounds), we define the payoff $E_w(\sigma, \sigma')$ to be the expected mean payoff per round that σ obtains when playing against σ'. The limiting case $w = 1$ corresponds to an infinitely iterated game.

In principle, a memory l strategy for the iterated continuous prisoner's dilemma can be an arbitrary function of the last l investments made by both players. Here we will consider a simple class of strategies obtained by restricting these general strategies in three ways. First, we will consider strategies of memory 1. Although it would be very interesting to include strategies of memory $l > 1$, the restriction to $l = 1$ is not unrealistic, since, even for humans, it has been shown that working memory limitations result in mostly memory 1 or 2 strategies being used in the iterated prisoner's dilemma (Milinski and Wedekind 1998). Second, we will assume that a player's strategy depends on the payoff the player obtained in the previous round. Third, we assume that the function σ specifying the strategy is a linear function of the payoff. Linear payoff-based strategies of this type can be defined

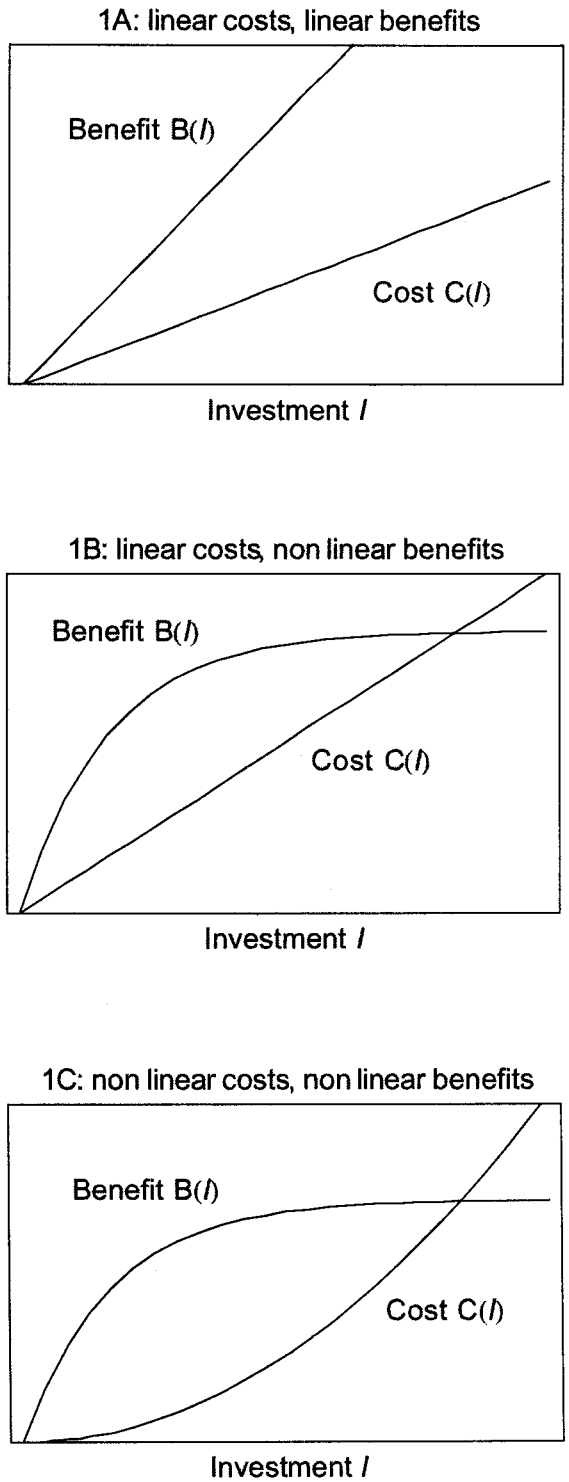

Figure 3: Possible cost and benefit functions in the continuous prisoner's dilemma. *A*, Linear cost function, $C(I) = C_0 \cdot I$, and linear benefit function, $B(I) = B_0 \cdot I$. Such functions were used for the numerical simulations shown in figures 4*A* and 5*A*. *B*, Linear cost functions, $C(I) = C_0 \cdot I$, and nonlinear benefit functions, $B(I) = a(1 - \exp[-b \cdot I])$. With $a, b > 0$, this nonlinearity implies diminishing returns for increased investments *I*. Such functions were used for the numerical simulations shown in figures 4*B* and 5*B*. *C*, Nonlinear cost function, $C(I) = C_0 \cdot I^2$, implying accelerated costs for increased investments, and nonlinear benefit function, $B(I) = a(1 - \exp[-b \cdot I])$. Such functions were used for the numerical simulations shown in figures 4*C* and 5*C*.

formally as follows: In the first round, invest $I_1 = \alpha$; in round $k + 1$, invest

$$I_{k+1} = \alpha + \beta P_k, \tag{2}$$

where $P_k = B(I'_k) - C(I_k)$ is the player's payoff in round k and α and β are real parameters. To exclude negative investments, we set $I_{k+1} = 0$ if $P_k < -\alpha/\beta$. Similarly, the opponent's strategy is defined by investing $I'_1 = \alpha'$ in the first round and, in round $k + 1$, by investing

$$I'_{k+1} = \alpha' + \beta' P'_k, \tag{3}$$

where $P'_k = B(I_k) - C(I'_k)$ is the opponent's payoff in round k and α' and β' are real parameters. Again we set $I'_{k+1} = 0$ if $P'_k < -\alpha'/\beta'$. We will denote the strategy with parameter α, β by $\sigma_{\alpha,\beta}$. The space of all strategies of the form $\sigma_{\alpha,\beta}$ will be denoted by Σ. The basic problem that we will address below concerns the question of how gradual evolutionary change occurs in the strategy space Σ.

So far we have considered the continuous prisoner's dilemma in the case where both players move simultaneously. However, it is also possible to consider a variant in which the players move in alternating sequence (see Frean 1994; Nowak and Sigmund 1994). In the alternating game, if player 1, say, moves by investing *I*, then player 2 responds by investing I'. The move of player 1 and the response by player 2 constitute one round of the alternating game. The payoffs in this alternating game are as follows: Given an alternating sequence of moves, in which player 1 moves first $(I_1, I'_1, I_2, I'_2, \ldots)$, then the sequence of payoffs for the two players is

$$(B(I'_1) - C(I_1), B(I_2) - C(I'_1), B(I'_2) - C(I_2), B(I_3) - C(I'_2), \ldots).$$

If player 2 moves first, yielding the sequence of moves $(I'_1, I_1, I'_2, I_2, \ldots)$, then the sequence of payoffs is

$$(B(I_1) - C(I'_1), B(I'_2) - C(I_1), B(I_2) - C(I'_2), B(I'_3) - C(I_2), \ldots).$$

The payoff-based strategy for the alternating game is defined in exact analogy with the simultaneous case (cf. eqq. [1], [2]). In the case when player 1 moves first, the strategy is defined as follows: In the first round, players 1

and 2 invest $I_1 = \alpha$ and $I_1' = \alpha'$, respectively, and in round $k + 1$, players 1 and 2 invest

$$I_{k+1} = \alpha + \beta[B(I_k') - C(I_k)], \tag{4a}$$

$$I_{k+1}' = \alpha' + \beta'[B(I_{k+1}) - C(I_k')], \tag{4b}$$

respectively. If player 2 moves first, then in the first round, players 2 and 1 invest $I_1' = \alpha'$ and $I_1 = \alpha$, respectively, and in round $k + 1$, they invest

$$I_{k+1}' = \alpha' + \beta'[B(I_k) - C(I_k')], \tag{5a}$$

$$I_{k+1} = \alpha + \beta[B(I_{k+1}') - C(I_k)], \tag{5b}$$

respectively. In either of these cases, we again set the investments in round $k + 1$ to 0 if the right-hand sides in equations (4) and (5) are <0. As for the simultaneous game, the payoff from a given iteration of the alternating game is defined to be the expected mean payoff per round. As this payoff will depend on which player moves first, we define the final payoff in the alternating game to be the mean payoff obtained from these two cases. In this article, we study the evolution of cooperation via payoff-based strategies for both the simultaneous and alternating iterated continuous prisoner's dilemma.

Analytic Results and Evolutionary Simulations

In this section, we consider the fundamentally important question of whether strategies of the form $\sigma_{\alpha,\beta}$ can lead to the evolution of cooperation in the iterated continuous prisoner's dilemma. Since a strategy $\sigma_{\alpha,\beta}$ is characterized by the two parameters α and β, the phenotype space in which evolution takes place is two-dimensional. In this two-dimensional phenotype space, the point $(0, 0)$ corresponds to a totally noncooperative strategy that never makes any investments. Cooperative strategies are characterized by points (α, β) in the positive quadrant of phenotypes space that are far enough away from the origin to induce nonzero investments and, hence, positive payoffs. Thus, the principal question is whether selection in a population consisting of noncooperative strategies characterized by very small α and β drives these parameters to higher values inducing cooperation. We will study these issues both analytically, using ideas of adaptive dynamics, and through numerical simulations.

Adaptive Dynamics

Adaptive dynamics (Hofbauer and Sigmund 1990; Nowak and Sigmund 1990; Metz et al. 1996; Geritz et al. 1998; Hofbauer and Sigmund 1998) provide a convenient analytic framework for investigating the evolutionary dynamics of the iterated continuous prisoner's dilemma. In general, adaptive dynamics assumes that the population under consideration remains essentially homogeneous and evolves under a selection-mutation regime. It is assumed that mutations are small and occur only rarely, so that a mutant will either have vanished or taken over the population before the next mutation arises. Under these assumptions, it is possible to define a deterministic dynamics in phenotype space that follows the selection gradients obtained as derivatives of a mutant's payoff. These selection gradients specify the direction of the maximal increase of the mutant's fitness.

In general, let us consider a continuous n-dimensional phenotypic trait $\xi = (\xi_1, \ldots, \xi_n)$, where the $\xi_i, i = 1, \ldots, n$ are the various components that determine the phenotype of an individual. For example, in the case at hand, we have $n = 2$, $\xi_1 = \alpha$, and $\xi_2 = \beta$. To derive the adaptive dynamics, we assume that the population is essentially homogeneous with all individuals using the same strategy ξ except for an occasional mutant that uses a strategy ζ that is close to ξ. The payoff for such a mutant is $E(\zeta, \xi)$. The adaptive dynamics (Hofbauer and Sigmund 1990, 1998; Nowak and Sigmund 1990; Metz et al. 1996; Geritz et al. 1998) are then defined by

$$\dot{\xi}_i = \frac{\partial}{\partial \zeta_i} E(\zeta, \xi)\bigg|_{\zeta=\xi}. \tag{6}$$

This defines a vector field on the space of strategies that, for any ξ, points in the direction of the maximal increase of the mutant fitness advantage relative to the resident population.

In the quantitative genetics framework of Lande (1982) as well as in the adaptive dynamics framework of Metz et al. (1996), Dieckmann and Law (1996), and Geritz et al. (1998), the vector of fitness gradients $(\partial/\partial\zeta_i)E(\zeta, \xi)|_{\zeta=\xi}$, $i = 1, \ldots, n$ appearing on the right-hand side of (6) must be multiplied by a $n \times n$-matrix describing the mutational process in order to obtain the vector of phenotypic changes $\dot{\xi}_i$, $i = 1, \ldots, n$. This mutational matrix describes how the direction of change in phenotype space is influenced by the mutational variance-covariance structure among the n phenotypic components $\dot{\xi}_i$. Here we make the simplifying assumption that the covariance between mutations in the two components $\xi_1 = \alpha$ and $\xi_2 = \beta$ is 0. In other words, we assume that mutations in α occur completely independently from mutations in β. This implies that there are no constraining relations (e.g., trade-offs) between these traits. As a consequence, the matrix describing the mutational process is diagonal, and hence the change in each phenotypic direction ξ_i is pro-

portional to the fitness gradient $(\partial/\partial\zeta_i)E(\zeta, \xi)|_{\zeta=\xi}$, so that (6) is, up to some positive constants of proportionality describing the rate and magnitude of mutations in each direction ξ_i, an accurate description of the evolutionary dynamics. Finally, since we are only interested in whether phenotypes evolve away from the origin, that is, only in the sign of the fitness gradients $(\partial/\partial\zeta_i)E(\zeta, \xi)|_{\zeta=\xi}$ for small ξ_i, neglecting these constants of proportionality is appropriate for our purposes, so that (6) is a correct description of the adaptive process.

We will now apply these ideas to study the evolutionary dynamics of the iterated continuous prisoner's dilemma. The fundamental question of interest is whether the strategies $\sigma_{\alpha,\beta}$ allow cooperation to develop. This question will be answered in the affirmative if it can be shown that starting from any initial strategy $\sigma_{\alpha,\beta}$ with small values of α and β the evolutionary dynamics on the space Σ is such that it yields strategies with larger values of α and β. If this is true, then it follows that no strategy $\sigma_{\alpha,\beta}$ will evolve into the unconditional defector $\sigma_{0,0}$.

The continuous prisoner's dilemma, as we have defined it in the previous section, depends on, in general, the nonlinear benefit and cost functions B and C. However, in the problem under consideration here, we are concerned with the evolution of strategies $\sigma_{\alpha,\beta}$, where α and β are small. For small values of α and β, the investment determined by $\sigma_{\alpha,\beta}$ will also be small. Hence, for our purposes, we need only consider the functions $B(I)$ and $C(I)$ for small I. We are free, therefore, to approximate $B(I)$ and $C(I)$ by their linearizations B_0I and C_0I, respectively, where $B_0 = B'(0)$ and $C_0 = C'(0)$ are the derivative of the functions at $I = 0$. This replacement of nonlinear functions by linear ones results in an important simplification.

In order to give an analytical treatment of the evolutionary dynamics of the iterated continuous prisoner's dilemma, it is convenient to introduce one further simplification: namely, to consider the limiting case of an infinitely iterated game. The analytical results that we obtain for the infinitely iterated case will also hold for any finitely iterated game of sufficient length.

We first discuss the case of the simultaneous game. Consider an infinitely iterated game of the simultaneous continuous prisoner's dilemma played between a strategy $\sigma_{\alpha,\beta}$ and $\sigma'_{\alpha',\beta'}$. Denote the payoff of σ against σ' in round k of the game by P_k and similarly the payoff of σ' against σ in round k by P'_k. It follows from the definition of the strategies σ and σ' (see eqq. [2], [3]) that P_{k+1} and P'_{k+1} are given by the recursion relations

$$P_{k+1} = B_0 \cdot (\alpha' + \beta' P'_k) - C_0 \cdot (\alpha + \beta P_k), \tag{7a}$$

$$P'_{k+1} = B_0 \cdot (\alpha + \beta P_k) - C_0 \cdot (\alpha' + \beta' P'_k). \tag{7b}$$

In the limit $k \to \infty$, the payoffs $P = P_\infty$ and $P' = P'_\infty$ satisfy the fixed-point equations

$$P = B_0 \cdot (\alpha' + \beta' P') - C_0 \cdot (\alpha + \beta P), \tag{8a}$$

$$P' = B_0 \cdot (\alpha + \beta P) - C_0 \cdot (\alpha' + \beta' P'). \tag{8b}$$

From these fixed-point equations, we obtain the following expressions for P and P':

$$P = \frac{(B_0\beta')(B_0\alpha - C_0\alpha') + (B_0\alpha' - C_0\alpha)(C_0\beta' + 1)}{(C_0\beta + 1)(C_0\beta' + 1) - (B_0\beta)(B_0\beta')}, \tag{9a}$$

$$P' = \frac{(B_0\beta)(B_0\alpha' - C_0\alpha) + (B_0\alpha - C_0\alpha')(C_0\beta + 1)}{(C_0\beta + 1)(C_0\beta' + 1) - (B_0\beta)(B_0\beta')}. \tag{9b}$$

Analysis of the Jacobian matrix of the dynamical system defined by equations (7a) and (7b) at the fixed point (P, P') shows that the fixed point will be (globally) asymptotically stable if and only if $2 > 1 + \beta\beta'(C_0^2 - B_0^2) > (\beta + \beta')C_0$, which is satisfied for all sufficiently small β and β'. Thus for sufficiently small values of β and β' the payoffs $P = E_1(\sigma, \sigma')$ and $P' = E_1(\sigma', \sigma)$ in the infinitely iterated game are given by equations (9a) and (9b). We note that because we are interested in the question of whether payoff-based strategies of the form $\sigma_{\alpha,\beta}$ allow cooperation to develop, which is equivalent to the question of whether strategies with small values of α and β evolve into strategies with larger values of α and β, we are interested in the evolutionary dynamics of the system in precisely the range of small α and β values for which expressions (9a) and (9b) are valid.

In the problem under consideration, the general equations of adaptive dynamics defined by equation (6) take the form

$$\dot{\alpha} = \left.\frac{\partial E_1(\sigma', \sigma)}{\partial \alpha'}\right|_{(\alpha',\beta')=(\alpha,\beta)}, \tag{10a}$$

$$\dot{\beta} = \left.\frac{\partial E_1(\sigma', \sigma)}{\partial \beta'}\right|_{(\alpha',\beta')=(\alpha,\beta)}. \tag{10b}$$

Here we regard the strategy $\sigma = \sigma_{\alpha,\beta}$ as comprising the resident population and $\sigma' = \sigma_{\alpha',\beta'}$ as a mutant strategy. It follows from equations (9a) and (9b) that the equations of adaptive dynamics assume the explicit form

$$\dot{\alpha} = \frac{B_0(B_0\beta) - C_0(C_0\beta + 1)}{(C_0\beta + 1)^2 - (B_0\beta)^2}, \tag{11a}$$

$$\dot{\beta} = \frac{(B_0\beta + C_0\beta + 1)(B_0 - C_0)\alpha}{[(C_0\beta + 1)^2 - (B_0\beta)^2]^2} \times [B_0(B_0\beta) - C_0(C_0\beta + 1)]. \tag{11b}$$

For sufficiently small β, the denominators in (11a) and (11b) are positive. In addition, we must have $B_0 > C_0$ (otherwise costs would exceed benefits for any investment, and cooperation would not evolve for trivial reasons), and hence the expression $(B_0\beta + C_0\beta + 1)(B_0 - C_0)\alpha$ appearing in the nominator of (11b) is also positive. Therefore, growth of both α and β is determined by the sign of $B_0(B_0\beta) - C_0(C_0\beta + 1)$. Thus we obtain the "threshold theorem":

Threshold Theorem. *Given any initial strategy $\sigma_{\alpha,\beta}$, where α and β are small, if β exceeds the threshold value $\beta_C = C'(0)/[B'(0)^2 - C'(0)^2]$, then the evolutionary dynamics will act to increase the values of α and β.*

It follows from the threshold theorem that any strategy $\sigma_{\alpha,\beta}$, with α, β small and $\beta > \beta_C$, will evolve into a strategy with larger α and β values. It is also a consequence of the threshold theorem that any strategy $\sigma_{\alpha,\beta}$, which satisfies the threshold condition $\beta > \beta_C$, will not evolve into the unconditional defector $\sigma_{0,0}$. The threshold theorem also implies that given any initial strategy $\sigma_{\alpha,\beta}$, with α, β small, and given a fixed cost per unit investment C_0, evolution will increase α and β if the benefit per unit investment B_0 is large enough (so that β_C is smaller than β). Thus, cooperation will gradually evolve from a noncooperative state if the benefits per unit investment are large enough compared with the costs.

It is important to note that for sufficiently large values of α and β the arguments leading to the threshold theorem will no longer remain valid. This is because, first, the assumption that we can linearize the cost and benefit functions will no longer be a good approximation and, second, the payoffs will no longer converge to the fixed point given by equations (9a) and (9b). However, in spite of this limitation, the threshold theorem guarantees that, under the standard assumptions of adaptive dynamics, any strategy $\sigma_{\alpha,\beta}$, with α, β small and $\beta > \beta_C$, will evolve into a strategy with larger α and β and, consequently, that any strategy that satisfies the threshold condition will never evolve into the unconditional defector. Thus, we can conclude from this analytical result that the class of payoff-based strategies $\sigma_{\alpha,\beta}$ allows more cooperative behavior to evolve from initial strategies that are rather uncooperative and allows cooperative behavior that has evolved to be maintained.

We have proved the threshold theorem here for the simultaneous form of the iterated continuous prisoner's dilemma. However, the theorem also holds for the alternating form of the game. This follows from the observation that in the infinitely iterated alternating game the asymptotic payoffs satisfy the same fixed-point equations as in the infinitely iterated simultaneous game (and the fixed point in the alternating case is also stable for sufficiently small values of β and β'). Thus, the argument used here to derive the threshold theorem for the infinitely iterated simultaneous game also applies to the infinitely iterated alternating game. Although we have only proved the threshold theorem for infinitely iterated games, the result will continue to hold for finitely iterated simultaneous and alternating games of sufficient length. We will comment further on the significance of this result, which should not be misconstrued as saying that payoff-based strategies necessarily perform equally well in both the simultaneous and alternating games, in "Discussion."

Evolutionary Simulations

We have seen above that the framework of adaptive dynamics allows an analytic discussion of the evolution of cooperation via payoff-based strategies. The analytic treatment was possible only under a number of assumptions: that the population remains essentially homogeneous, that the game is infinitely iterated, and that the analysis is restricted to strategies with small values of α and β. To obtain an insight into the evolutionary dynamics of payoff-based strategies without having to make such assumptions, we have to resort to simulations. We consider the finitely iterated continuous prisoner's dilemma, with a fixed probability $w < 1$ of a further move after any round and with defined benefit and cost functions B and C. To define the simulation scheme, we introduce a population of strategies σ_i for $i = 1, \ldots, n$, where σ_i denotes the strategy $\sigma_{\alpha_i,\beta_i}$. If p_i is the frequency of strategy i, then the fitness of σ_i is $W_i = \Sigma_j p_j E_w(\sigma_i, \sigma_j)$ and the mean fitness of the population is $\overline{W} = \Sigma_i p_i W_i$. The population is assumed to evolve according to the standard replicator dynamics (Maynard Smith 1982; Hofbauer and Sigmund 1998); that is, the frequency of strategy i in the next generation, p_i', is given by $p_i' = p_i W_i / \overline{W}$. To carry out the simulation, we start with an initial population of strategies σ_i^0 with initial frequencies p_i^0 and allow the population to evolve according to the replicator dynamics. Every N generations, on average, we introduce a randomly generated mutant strategy into the population and continue to follow the evolution of the system. If the frequency of any strategy falls below a threshold ε, then that strategy is removed from the population. Since the evolutionary dynamics are frequency dependent, it will typically maintain a heterogeneous population of