

The Continuous Prisoner's Dilemma and the Evolution of Cooperation through Reciprocal Altruism with Variable Investment

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ABSTRACT: Understanding the evolutionary origin and persistence of cooperative behavior is a fundamental biological problem. The standard "prisoner's dilemma," which is the most widely adopted framework for studying the evolution of cooperation through reciprocal altruism between unrelated individuals, does not allow for varying degrees of cooperation. Here we study the continuous iterated prisoner's dilemma, in which cooperative investments can vary continuously in each round. This game has been previously considered for a class of reactive strategies in which current investments are based on the partner's previous investment. In the standard iterated prisoner's dilemma, such strategies are inferior to strategies that take into account both players' previous moves, as is exemplified by the evolutionary dominance of "Pavlov" over "tit for tat." Consequently, we extend the analysis of the continuous prisoner's dilemma to a class of strategies in which current investments depend on previous payoffs and, hence, on both players' previous investments. We show, both analytically and by simulation, that payoff-based strategies, which embody the intuitively appealing idea that individuals invest more in cooperative interactions when they profit from these interactions, provide a natural explanation for the gradual evolution of cooperation from an initially noncooperative state and for the maintenance of cooperation thereafter.

Keywords: evolution of cooperation, prisoner's dilemma, reciprocal altruism, adaptive dynamics, variable investment.

The origin and maintenance of cooperative or altruistic behavior is one of the most enduring and intractable the-

oretical problems in evolutionary biology (see, e.g., Hamilton 1963, 1964a, 1964b; Trivers 1971; Axelrod and Hamilton 1981; Axelrod 1984; Dugatkin 1997). Cooperative behavior, by which we mean behavior that while involving a cost to the individual or individuals performing it, benefits another individual or individuals, is extremely widespread in nature (see Dugatkin 1997 for a review of many types of cooperative behavior), and yet there is a fundamental difficulty in giving a satisfactory theoretical explanation of such behavior. The difficulty arises from the fact that selfish individuals can reap the benefits of cooperation without bearing the costs of cooperating themselves. Thus selfish individuals, who do not cooperate, will have a fitness advantage over cooperative individuals, and natural selection will lead to the cooperators being eliminated by the noncooperators.

Since increased levels of cooperation among the individuals in a group result in increased mean fitness for the group members, there would be no paradox surrounding the evolution of cooperation if natural selection acted effectively at the group level (Wynne Edwards 1962). However, although it is in principle possible for selection to act at such a level, it is generally the case that selection acts much more effectively at the individual level (Maynard Smith 1964, 1976; Williams 1966; Grafen 1984). Thus the paradox of cooperation remains: although a general increase in cooperation benefits all members of a group, individual selection will favor selfish individuals who benefit from the cooperation of others while not incurring the costs of cooperating themselves.

The evolution of cooperation among related individuals can typically be explained by kin selection (Hamilton 1963, 1964a, 1964b; see Frank 1998). Fundamentally different ideas are required to explain the emergence of cooperation among unrelated individuals. Proposed explanations include reciprocal altruism (Trivers 1971), trait-group selection (Wilson 1975, 1980; Cohen and Eshel 1976; Matessi and Jayakar 1976), spatial structure (Nowak and May

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1992; Killingback et al. 1999), and **indirect reciprocity** (Alexander 1986; Nowak and Sigmund 1998).

Kin selection, which is the standard theoretical framework for understanding cooperation between relatives, depends on the fact that genes determining altruistic traits can increase in frequency if the **interacting individuals are genetically related**. This idea, which was anticipated by Fischer (1930) and Haldane (1932) and which was expressed by Haldane in 1955 in his memorable comment that he was willing to lay down his life to **save two brothers or eight cousins**, was developed into a systematic theory by Hamilton (1964a, 1964b). The essence of kin selection lies in **Hamilton's famous formula**, which states that if an interaction occurs in which a "donor" sacrifices c offspring and a "recipient" gains an additional b offspring, then the gene causing the donor to act in this way will increase in frequency if $br > c$, where r is the degree of relatedness of the donor to the recipient. If the gene is rare, then this result is rather clear; however, what is much less clear, as was shown by Hamilton (1964a, 1964b), is that this result still holds good even if the gene is at high frequency. Kin selection is bound to operate wherever related individuals interact. It is now generally accepted to be an important factor in the evolution of altruistic behavior in the social insects (Wilson 1971; Hamilton 1972; West-Eberhard 1975; Bourke and Franks 1995; Crozier and Pamilo 1996). It is also relevant to the evolution of **cooperation in vertebrates** (Brown 1978, 1987; Emlen 1978, 1984, 1995, 1996; Pusey and Packer 1994) and perhaps even to the **origin of the integration of the components of eukaryotic cells** (Maynard Smith and Szathmari 1995).

Kin selection provides an elegant and powerful theoretical framework for studying the evolution of cooperation among relatives. Understanding the evolution of cooperation among nonrelatives, however, requires quite different ideas. Cooperative behavior among individuals who are either not related or who have a low degree of relatedness is common. From the large number of examples of such behavior (which are reviewed, e.g., in Dugatkin 1997), the following may be selected as illustrations: allogrooming in impala (Hart and Hart 1992; Mooring and Hart 1992), egg swapping in hermaphroditic fish (Fischer 1980, 1984, 1986, 1988) and hermaphroditic worms (Sella 1985, 1988, 1991), predator inspection in fish (Milinski 1987, 1990a, 1990b, 1992), and blood sharing in vampire bats (Wilkinson 1984).

A number of theoretical ideas have been suggested to explain the occurrence of cooperation among nonrelatives. Trivers (1971) laid the foundations of the theory of reciprocal altruism by pointing out that if there are opportunities for **repeated interactions between the same individuals**, then an individual who behaves altruistically only to those which reciprocate the altruistic act will be favored

by natural selection. In general, such reciprocal altruism can evolve only if the same individuals meet repeatedly, if they are capable of memory and recognition, and if the benefits to the individual who is helped exceed the costs to the helper.

There is strong evidence for reciprocal altruism in a number of animal systems. In fact, the examples of cooperation among nonrelatives given above are all cases where reciprocal altruism is believed to play an important role. There is very good evidence of reciprocal altruism in the context of **allogrooming in impala** from the work of Hart and Hart (1992) and Mooring and Hart (1992). In this species, pairs of individuals engage in reciprocal bouts of allogrooming, the apparent function of which is to reduce the tick load of the groomed individual. There is also strong evidence of reciprocal altruism in **predator inspection in fish** from the work of Milinski (1987, 1990a, 1990b, 1992) and others (see, e.g., Dugatkin 1988; Dugatkin and Alfieri 1991). During predator inspection, a small group of fish detach from a shoal to approach a potential predator (Pitcher et al. 1986) and subsequently convey (either actively or passively) the information that they have obtained to the noninspectors (Magurran and Higgam 1988). There is also good evidence for reciprocal altruism in **hermaphroditic fish** (Fischer 1980, 1984, 1986, 1988) and **worms** (Sella 1985, 1988, 1991), **in vampire bats** (Wilkinson 1984), and in a number of other systems (Packer 1977; Lombardo 1985). For a detailed review of those cases where reciprocal altruism is believed to play a role, see Dugatkin (1997).

Other theoretical ideas that have been proposed as possible explanations of cooperation among nonrelatives include the following: **trait-group selection** (Wilson 1975, 1980; Cohen and Eshel 1976; Matessi and Jayakar 1976), which depends on there being a synergistic fitness component, so that **it is not possible to represent the interactions between members of a group in terms of a simple loss of fitness by one of them and a corresponding gain by the others**, with the losses and gains combining additively); **spatially structured populations** (Nowak and May 1992; Killingback et al. 1999), which may, in particular, provide **a natural explanation of how cooperation can evolve among very simple organisms**; and **indirect reciprocity** (Alexander 1986; Nowak and Sigmund 1998), which may provide a **new type of explanation for cooperative behavior among humans and perhaps some higher animals such as primates**.

Cooperative behavior is both widespread in nature and fundamentally perplexing from an evolutionary perspective. It is most important, therefore, to have simple models of cooperation that allow detailed theoretical investigation of the evolution of altruism. The standard metaphor for the problem of cooperation is the "prisoner's dilemma" (Trivers 1971; Smale 1980; Axelrod and Hamilton 1981;

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

	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.

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.

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 1999a, 1999b). 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 (1999a, 1999b). 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 3A shows a linear benefit function and a

linear cost function, figure 3B shows a concave benefit function and a linear cost function, and figure 3C 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:

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

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 σ' : $I'_k = \sigma'(I_{k-1}, \dots, I_{k-l}, I'_{k-1}, \dots, I'_{k-l})$. 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

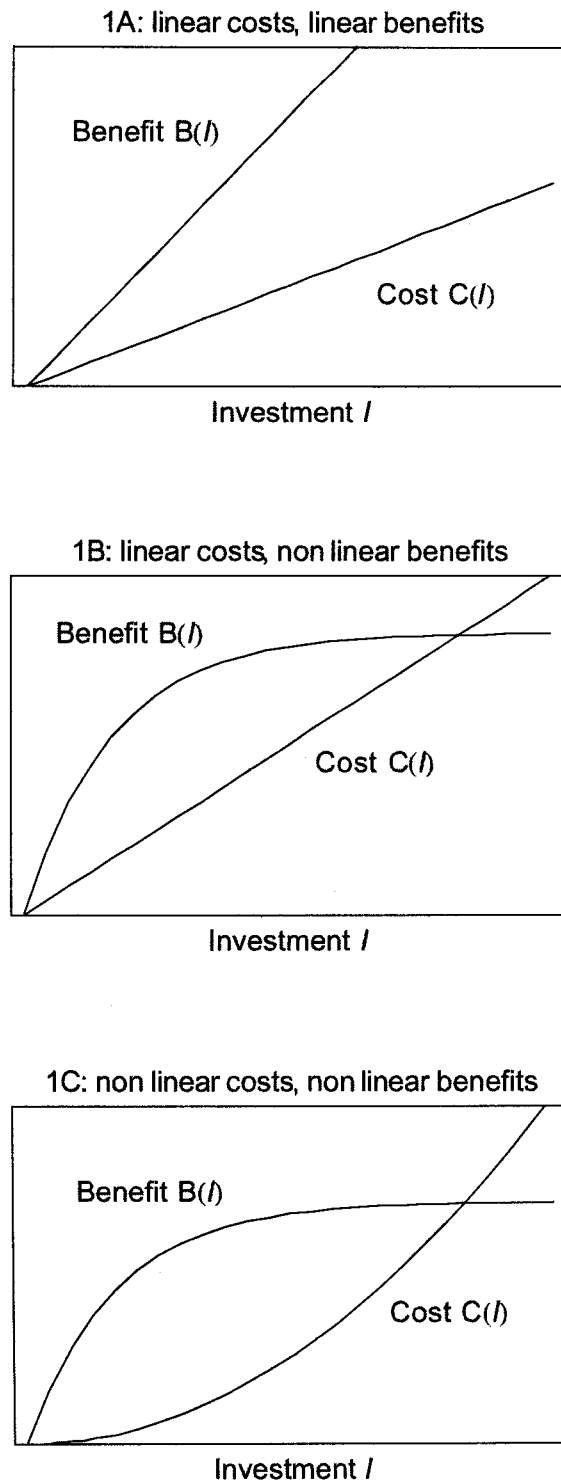


Figure 3: Possible cost and benefit functions in the continuous prisoner's dilemma. A, Linear cost function, $C(I) = C_0 \cdot I$, and linear benefit function, $B(I) = B_0 \cdot I$. Such functions were used for the numerical simulations shown in figures 4A and 5A. B, Linear cost functions, $C(I) = C_0 \cdot I$, and nonlinear benefit functions, $B(I) = a(1 - \exp[-b \cdot I])$. With

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

$$I_{k+1} = \alpha + \beta P_k, \quad (2)$$

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

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

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 $(I_1, I'_1, I_2, I'_2, \dots)$, then the sequence of payoffs for the two players is

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

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

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

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

$a, b > 0$, this nonlinearity implies diminishing returns for increased investments I . Such functions were used for the numerical simulations shown in figures 4B and 5B. 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 4C and 5C.

and 2 invest $I_1 = \alpha$ and $I'_1 = \alpha'$, respectively, and in round $k + 1$, players 1 and 2 invest

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

$$I'_{k+1} = \alpha' + \beta'[B(I_{k+1}) - C(I'_k)], \quad (4b)$$

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

$$I'_{k+1} = \alpha' + \beta'[B(I_k) - C(I'_k)], \quad (5a)$$

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

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 dy-

namics 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 $\xi = (\xi_1, \dots, \xi_n)$, where the ξ_i , $i = 1, \dots, n$ 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

$$\dot{\xi}_i = \frac{\partial}{\partial \xi_i} E(\zeta, \xi) \Big|_{\zeta=\xi}. \quad (6)$$

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 $(\partial/\partial \xi_i)E(\zeta, \xi)|_{\zeta=\xi}$, $i = 1, \dots, n$ 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 $\dot{\xi}_i$, $i = 1, \dots, n$. 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 ξ_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 $(\partial/\partial \xi_i)E(\zeta, \xi)|_{\xi=\xi}$, so that (6) is, up to some positive constants of proportionality describing the rate and magnitude of mutations in each direction ξ , 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 $(\partial/\partial \xi_i)E(\zeta, \xi)|_{\xi=\xi}$ for small ξ , 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 $B_0 I$ and $C_0 I$, 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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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 $i = 1, \dots, n$, 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 $W_i = \sum_j p_j E_w(\sigma_i, \sigma_j)$ and the mean fitness of the population is $\bar{W} = \sum_i p_i W_i$. 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 $p'_i = p_i W_i / \bar{W}$. 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

strategies, although the number of distinct strategies present at any one time may be quite small (for more on this effect, in the context of the standard iterated prisoner's dilemma, see Nowak and Sigmund 1993, where a similar simulation scheme is used).

The evolutionary dynamics of typical simulations are shown in figures 4 and 5. Figures 4A, 4B, and 4C show the evolutionary dynamics of the simultaneous game for (A) linear costs and benefits, (B) linear costs and nonlinear benefits, and (C) nonlinear costs and benefits. The corresponding cases for the alternating game are shown in figures 5A, 5B, and 5C. We see in these simulations that, starting from a population with small values of α and β , with β exceeding the critical value $\beta_c = C'(0)/[B'(0)^2 - C'(0)^2]$, the population mean values of α and β evolve to higher values, where they remain. This corresponds to a population of uncooperative individuals evolving into a population of highly cooperative individuals. Our evolutionary simulations confirm the analytical results obtained above and show that these results continue to hold even if the populations involved are heterogeneous and the game is finitely iterated. Thus, evolutionary simulations corroborate the insights obtained from the analytic approach and show that payoff-based strategies are a general and robust means of obtaining cooperation in the iterated continuous prisoner's dilemma, in both the simultaneous and alternating cases.

Discussion

We have shown, both analytically and using evolutionary simulations, that payoff-based strategies for the iterated continuous prisoner's dilemma provide a natural framework for understanding the evolution of cooperation via reciprocal altruism when the degree of cooperation can vary. In particular, we have shown that such strategies allow a simple resolution of the fundamental problem of how cooperative behavior can evolve gradually from an initially selfish state. In this section, we shall discuss how our payoff-based strategies contrast with other strategies that have been proposed for the iterated continuous prisoner's dilemma. We shall also discuss here whether there is any sense in which the evolution of cooperation via reciprocal altruism is facilitated by cooperation being a continuous trait. Finally, we consider how we may distinguish empirically between payoff-based strategies and strategies that depend only on the opponent's previous move.

First, let us contrast and compare the payoff-based strategies we have introduced here with the other strategies that have been proposed for the iterated continuous prisoner's dilemma. These other strategies are the "raise-the-stakes" strategy (Roberts and Sherratt 1998) and the linear reactive strategies (Wahl and Nowak 1999a, 1999b). These

strategies are defined as follows: Raise the stakes (RTS) is, in general, characterized by two parameters (a, b). On the first move, RTS invests a ; subsequently, if the opponent's move exceeds RTS's previous investment, then RTS raises its investment by $2b$, while, if the opponent matched RTS's previous move, then RTS raises its investment by b . If the opponent invests less than RTS's previous move, then RTS matches the opponent's last investment. The linear reactive strategies, which are characterized by three parameters (a, d, r), are defined as follows: On the first move, invest a ; on subsequent moves, invest $d + rI'$, where I' is the opponent's previous investment. It is also assumed in the definition of the linear reactive strategies that there is a fixed range of possible investments, with $I = 0$ being the minimum investment and $I = I_{\max}$ being the maximum investment (see Wahl and Nowak 1999a, 1999b). It is assumed for both these strategies that the game is played in alternating sequence (see Roberts and Sherratt 1998; Wahl and Nowak 1999a, 1999b).

Both raise-the-stakes and the linear reactive strategies depend only on the opponent's last move and, in this sense, are reminiscent of strategies such as tit for tat in the standard (noncontinuous) iterated prisoner's dilemma. In view of the success of strategies such as Pavlov for the standard game (in the simultaneous case), which depend on both players' previous moves, it is reasonable to anticipate that strategies for the iterated continuous prisoner's dilemma that depend on both players' moves will be of similar importance. In addition to simply depending on both players' previous moves, the payoff-based strategies introduced here have the attractive property that the amount individuals invest is dependent on how well the individual is doing at any given moment. That is, for given strategy parameters, if an individual's payoff is high, it will invest more, and if its payoff is low, it will invest less. This general property seems to agree with our biological intuition.

It is important to note that although payoff-based strategies are analogous to strategies such as Pavlov in the sense that they depend on the previous moves of both players, they do not behave in an identical way to Pavlov. In particular, after receiving the score T (i.e., Pavlov defects against a cooperator), Pavlov plays D again. By contrast, after receiving a high score (e.g., a payoff-based strategy makes a low investment against a high-investing opponent), a payoff-based strategy will increase its level of investment in the next round. Thus payoff-based strategies behave in a way that is rather like tit for tat. Moreover, in such a situation, the strategy that made the low investment will gradually increase its investment level back to a higher cooperative level. Therefore, with payoff-based strategies occasional mistakes do not lead to a permanent breakdown of cooperation. This property means that payoff-based strategies really behave more like generous tit

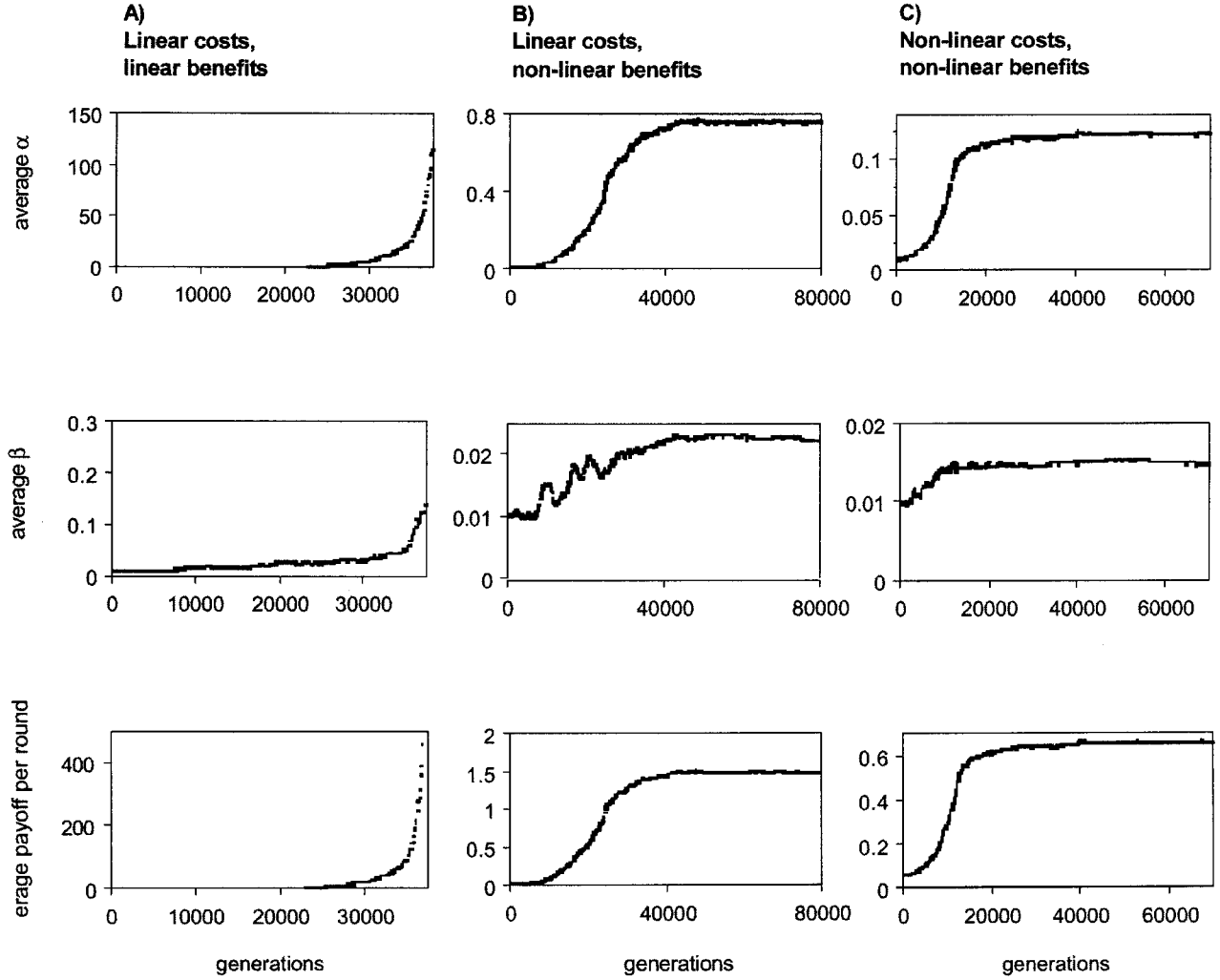


Figure 4: Numerical simulations of the evolution of cooperation in the continuous iterated prisoner's dilemma with simultaneous interactions. The simulations were run as described in the text, with 10 rounds per iterated game and with one new mutation every 20 generation on average. When a mutation occurred, one of the resident strategies was chosen at random from the population (taking into account the frequency of the strategies in the population at that time), and the new mutant was assigned a phenotype from a normal distribution with mean equal to the phenotype of the chosen resident and with variance equal to 5% of the mean. Runs were started with a population that is monomorphic for the strategy $\sigma_{\alpha, \beta}$, with $\alpha = \beta = 0.01$. A, Linear cost function, $C(I) = C_0 \cdot I$, and linear benefit function, $B(I) = B_0 \cdot I$, with $C_0 = 0.1$ and $B_0 = 5$. The top panel shows the evolutionary trajectory of the strategy parameter α , whose population mean was plotted every 100th generation. The middle panel shows the evolutionary trajectory of the strategy parameter β , whose population mean was plotted every 100th generation. The lower panel shows the population average of the mean payoff per round of the iterated game as a function of time. Every 100th generation, the payoffs from playing the continuous iterated prisoner's dilemma between each of the strategies present in the population were divided by the number of iterations (10) and then summed up with weights equal to the frequencies with which the various pairings of strategies occur at the given moment. The three quantities shown in the three panels increase without bounds due to the linearity of costs and benefits. B, Same as A, except for a nonlinear benefit function $B(I) = a(1 - \exp[-b \cdot I])$, with $a = 5$ and $b = 1$, so that $B'(0) = 5$ as in A. Again the parameter α evolves away from 0, but it levels off due to decreasing returns in the benefit function. The parameter β also evolves away from 0, although it levels off at smaller values compared with α . The reason for this is that higher β would, over the 10 iterations of investments made in each game, iteratively increase investments to values for which benefits are lower than costs due to the diminishing returns. The average payoff increases from very low levels and is maintained at high levels. In the run shown, which is a typical case of our numerical explorations of the evolutionary dynamics of the continuous iterated prisoner's dilemma, cooperation was maintained over 4,000,000 generations, after which the run was stopped. C, Same as B but with a quadratic cost function $C(I) = C_0 \cdot I^2$, with $C_0 = 1$. Note that $C'(0) = 0$, so that the conditions for the threshold theorem are always satisfied.

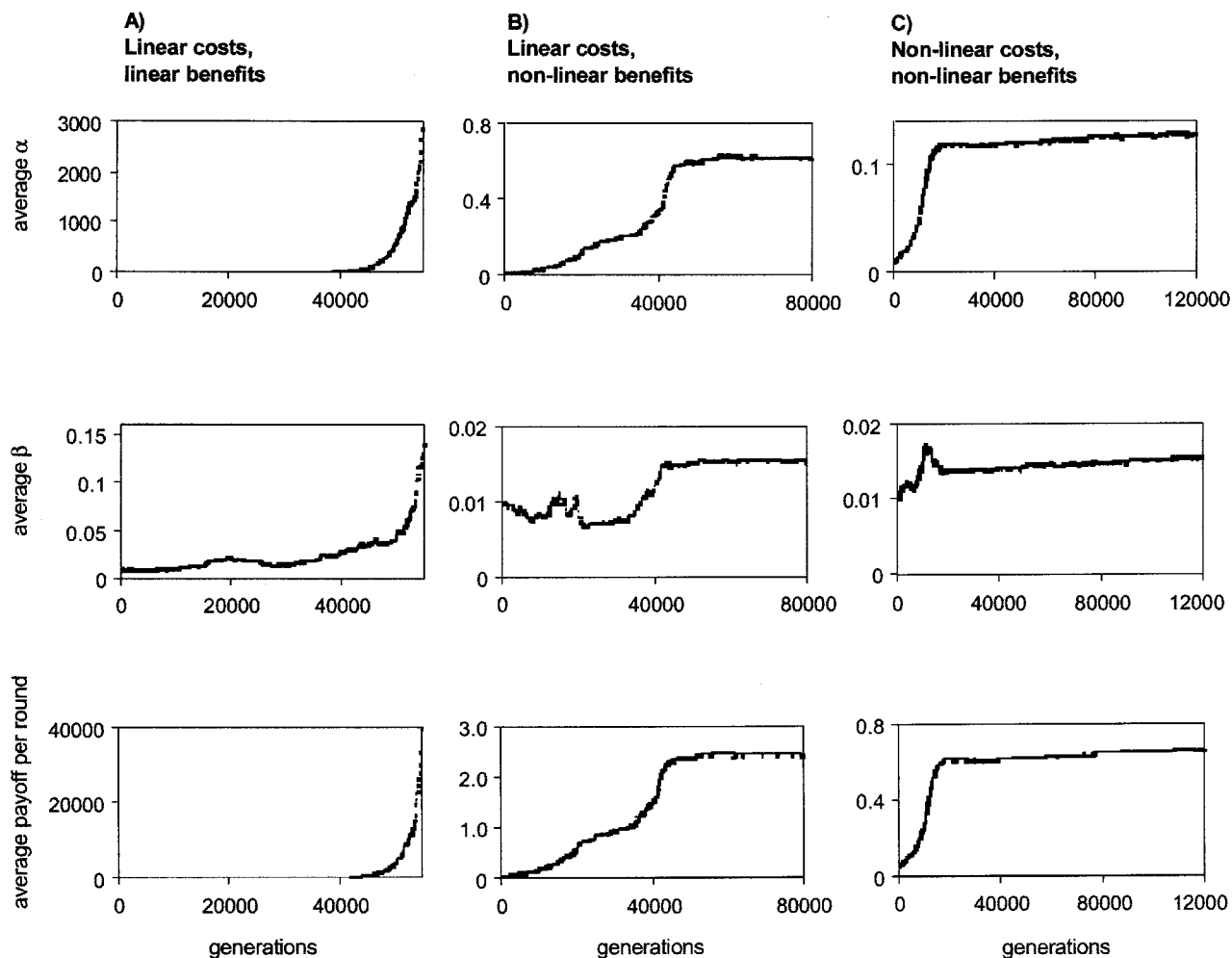


Figure 5: Numerical simulations of the evolution of cooperation in the continuous iterated prisoner's dilemma with alternating interactions. Everything else is the same as in figure 4. No systematic differences between the simultaneous and the alternating case were observed in our numerical simulations, which conforms with the fact that the threshold theorem holds true in both cases.

for tat than tit for tat. Payoff-based strategies, therefore, have elements in common with two of the most successful strategies for the standard iterated prisoner's dilemma: while they depend on both players' moves, like Pavlov, their general behavior is more like generous tit for tat.

This combination of features may explain the success of payoff-based strategies in both the simultaneous and alternating versions of the iterated continuous prisoner's dilemma. For the iterated discrete prisoner's dilemma, Pavlov appears to be the superior strategy in the simultaneous case (Nowak and Sigmund 1993), while generous tit for tat seems to be the better strategy in the alternating case (Nowak and Sigmund 1994). It should be noted, however, that generous tit for tat is also a good strategy even for the simultaneous game (Nowak and Sigmund 1992). It is also important to

note that although we have shown that payoff-based strategies lead efficiently to the evolution of cooperation in both the simultaneous and alternating cases, this does not preclude the possibility that there are other strategies, as yet undiscovered, which may perform even better in either the simultaneous or alternating games.

In addition to these general features, payoff-based strategies have certain important advantages over raise-the-stakes and linear reactive strategies in those situations where the benefit or cost is nonlinear. As it is likely that in most systems the benefit will increase faster for smaller investments than for larger ones and that the cost will increase more rapidly for larger investments than for smaller ones, this case is probably typical of most realistic situations.

The problem that occurs in such situations with strategies that depend only on the opponents move can be seen most clearly in the case of raise the stakes (Roberts and Sherratt 1998). Consider what happens when a strategy such as that considered by Roberts and Sherratt (1998), $(a, b) = (1, 1)$, plays against itself. The sequence of investment made by the two players is $(1, 1, 2, 3, 4, 5, \dots)$. Thus the players continue to raise one another's investments and consequently make larger and larger investments. One obtains the same result when a general RTS strategy (a, b) plays against itself, with the investment being $(a, a, a + b, a + 2b, a + 3b, a + 4b, \dots)$. However, if the benefit exhibits diminishing returns and the cost increases linearly or nonlinearly with investment, there exists an investment above which the benefit decreases relative to the cost, and eventually, for high enough investments, the cost will exceed the benefit. A key deficiency of RTS is that it is completely insensitive to this problem: two players using the same RTS strategy will continue to make higher and higher investments even though, in a sufficiently long game, they will eventually receive a negative payoff on each move. In view of the fact that successful strategies will increase in frequency and will often be playing against themselves, this defect of RTS means that it is most unlikely that RTS can lead to the evolution of cooperation in the presence of nonlinear costs or benefits. This problem did not arise in the simulations of Roberts and Sherratt (1998) because they assumed that the cost and benefit increase linearly with the investment. However, it should also be noted that in addition to this deficiency, which occurs when the costs or benefits are nonlinear, it also appears that even with linear cost and benefit functions RTS is not evolutionarily robust in the sense that if the adaptive dynamics in the space of strategies given by the two parameters (a, b) is considered, then RTS evolves into an unconditional defector (Killingback and Doebeli 1999).

Linear reactive strategies (Wahl and Nowak 1999a, 1999b) can also suffer from the problem of large investments yielding negative payoffs. When the benefits or costs are nonlinear, the evolutionary fate of this class of strategies depends on the value of the maximum investment I_{\max} . If I_{\max} is greater than the investment value I_0 for which the cost exceeds the benefit then, in a sufficiently long game, we will encounter the same problem as we did for RTS. When a cooperative strategy plays against itself, as it will often do if it is successful, each successive move will be greater than the opponents previous move and, hence, after some finite number of moves, both players will be investing I_{\max} . If $I_{\max} > I_0$, then, for a sufficiently long game, the players will receive a negative payoff. However, if $I_{\max} < I_0$ this problem will not arise. We see, therefore, that the success of linear reactive strategies in allowing the evolution of cooperation depends on the subtle issue of what the value of I_{\max} should

be. We note that this question does not arise in the framework employed by Wahl and Nowak (1999a, 1999b), where it is assumed that the benefits and costs are linear functions of the investment.

We have seen that both the RTS strategy and the linear reactive strategies suffer from problems when the benefits or costs are nonlinear, which raises questions as to whether the evolution of cooperation can be satisfactorily explained in this case by these strategies. In addition, RTS suffers from a general evolutionary instability (Killingback and Doebeli 1999) that would appear to eliminate it as a candidate for explaining cooperative behavior. In contrast, we have shown here that payoff-based strategies, which depend on both players' last move, are a natural class of strategies that allow cooperative behavior to evolve. In particular, it is important to note that payoff-based strategies do not suffer from any problems when the benefit and cost functions are nonlinear. This is because the investment made by such a strategy depends on the players' payoff in the previous round. Consequently, when a given cooperative payoff-based strategy is playing against itself, it automatically regulates the size of the investment it makes depending on how well it is doing in the game. This regulation mechanism means that a payoff-based strategy will never continue to increase its investment if this has the effect of decreasing the players' payoff. This feature is a crucial factor in allowing the evolution of cooperative behavior via payoff-based strategies when there are nonlinear costs and benefits.

We shall now discuss the issue of whether there is any sense in which the evolution of cooperation is facilitated by cooperation being a continuous trait. Interestingly, there appears to be at least one sense in which this is true for the payoff-based strategies considered here. Whether or not one obtains cooperative behavior in the discrete iterated prisoner's dilemma depends crucially on the (average) number of iterations that take place in the interaction (Axelrod and Hamilton 1981; Axelrod 1984), that is, on the "shadow of the future" w or, equivalently, the expected number of rounds $n = 1/(1 - w)$. Studies of the evolution of cooperation in the standard iterated prisoner's dilemma (Axelrod and Hamilton 1981; Axelrod 1984; Nowak and Sigmund 1992, 1993) have used very large numbers of iterations. In their simulations, Axelrod and Hamilton (1981) and Axelrod (1984) took n to be 200, while Nowak and Sigmund (1992, 1993) took n to be infinity (i.e., $w = 1$). It seems likely, however, that in most realistic situations the effective number of iterations will be significantly smaller than 200 and certainly much less than infinity. There is an important reason why the effective number of iterations will typically be reasonably small in many cases (see May 1981). Although the total number of interactions that a given individual has with another

individual may be quite large over its lifetime (e.g., as in the case of reciprocal allogrooming in impala), empirical studies show that animals have a strong tendency to discount future payoffs relative to immediate ones (Stephens et al. 1995). If the payoffs in the next iteration are discounted by a factor δ ($0 \leq \delta \leq 1$) relative to the payoffs in the current iteration and w is the probability of a further interaction, then the effective length of the game is determined by the product $\omega = w\delta$ (i.e., the effective number of iterations in the game is $\nu = 1/[1 - \omega]$). Since animals seem to have strong preferences for immediate gains (Stephens et al. 1995; i.e., δ may often be quite small), it is reasonable to anticipate that the effective number of iterations may often be rather small. In view of this, it is a reassuring feature of our payoff-based strategies that they lead to the evolution of cooperation even for small numbers of iterations. In the simulations presented here, cooperation evolved from an initially rather uncooperative state, for both the simultaneous and alternating games (with both linear and nonlinear costs and benefits), although there were only 10 iterations per game. It follows, therefore, that payoff-based strategies with continuous investment can lead to the evolution of cooperation even when the effective number of interactions is small. There is no evidence that the corresponding statement is true for the strategies that have been studied in the discrete iterated prisoner's dilemma.

The fact that cooperation can evolve via reciprocal altruism with payoff-based strategies even when there are only a small number of iterations has two potentially important implications. The first, and more obvious, is that payoff-based strategies may allow the evolution of cooperation among short-lived animals that are unable to have a large number of individual encounters as a result of their limited life span. For such animals, one would not expect the standard prisoner's dilemma model of reciprocal altruism to lead to the evolution of cooperation. The second, subtler implication is that since payoff-based strategies allow the evolution of cooperation with only a small number of individual encounters the following behavioral scenario becomes possible: An animal engages in a short sequence of cooperative interactions with only one other animal and then engages in another short sequence of cooperative interactions with another single animal and so on. During any given sequence of encounters it is only necessary for the animal to be able to remember how the one individual with which it is currently interacting behaved in the previous round. It seems likely that only rather modest cognitive abilities are required to perform such a task. In contrast, if cooperation can only be maintained with a large number of individual encounters, as is the case with the standard prisoner's dilemma model of reciprocal altruism, then it is likely that sequences of encounters with

different animals will overlap. In such a situation, an animal would have to discriminate between the behavior of several different individuals for reciprocal altruism to work. Such multiple discrimination would seem to require considerable cognitive abilities. Thus cooperation may be able to evolve in animals with only rather limited cognitive abilities via reciprocal altruism using payoff-based strategies—an outcome that would not be expected on the basis of the standard iterated prisoner's dilemma model. This feature of payoff-based strategies suggests that they are more likely to have general relevance than the strategies that have been studied in the standard iterated prisoner's dilemma.

It is interesting to note that reciprocal allogrooming in impala seems to follow exactly this scenario. Allogrooming in this species (see Hart and Hart 1992) consists of one animal delivering a bout of grooming episodes to another animal—where one episode is defined as one upward sweeping movement of the grooming animal's tongue and lower incisors against the head or neck of the partner. The recipient then typically reciprocates by delivering a bout of grooming episodes to the first animal. The number of episodes per bout varies from about four to about 16, and the number of bouts delivered in an encounter varies substantially, with most encounters consisting of less than about 20 bouts. During a single encounter, the two animals involved do not engage in allogrooming with any other animals. It is clear, therefore, from the work of Hart and Hart (1992) that allogrooming in impala conforms very closely to the scenario we described above—two individuals engage in a relatively short (in this case alternating) sequence of allogrooming bouts, the cooperative investment in each bout (i.e., the number of episodes per bout) can vary significantly, and during a given encounter, the two individuals do not take part in allogrooming with any other animals. Thus, in view of the theoretical results presented here, the cooperative allogrooming behavior observed in impala is very much in accord with our expectations.

Finally, it is interesting to consider how we might be able to distinguish empirically between payoff-based strategies and strategies that depend only on the opponent's move. It is obviously important to have an empirical means of differentiating between these two classes of strategies if one is seeking to determine experimentally which, if either, of these two types of strategies is used in nature. Perhaps the clearest qualitative difference between payoff-based strategies and strategies that depend only on the opponent's move is that the former automatically regulate the size of their investment when the costs and benefits are nonlinear while the latter do not. This difference between the two types of strategies suggests a possible means of distinguishing them empirically. By studying a system in which individuals make cooperative investments that

vary in degree and in which the costs and benefits of those investment can be manipulated, we should be able to determine whether the individuals are using strategies that self-regulate the level of investment, depending on the costs and benefits, such as payoff-based strategies, or whether they are using strategies for which the level of investment is independent of the costs and benefits, such as raise-the-stakes and linear reactive strategies. If two individuals are using payoff-based strategies, then the levels of investment that they make will depend on the nonlinear cost and benefit functions and, consequently, will change as the costs and benefits are manipulated.

In order to use this general approach to attempt to distinguish empirically between payoff-based strategies and strategies that depend only on the opponent's move requires that we find an experimental system in which the following desiderata are satisfied. First, the individuals involved must display different degrees of cooperation (so that cooperation can be viewed as a continuous trait); second, the individuals involved should experience nonlinear costs and benefits; and third, by manipulating the experimental system, the costs and benefits can be varied. If these criteria are satisfied, then it should be possible to distinguish experimentally between payoff-based strategies and reactive strategies by observing whether, as the costs and benefits are varied, the degree of investment individuals make changes, as would be expected if payoff-based strategies are being used, or remains unchanged, as would be expected if reactive strategies are being employed. Predator inspection in fish (see Milinski 1987) seems to provide a convenient experimental system in which these criteria are satisfied. It is known that in predator inspection experiments fish display different degrees of cooperation (Dugatkin and Alfieri 1991), and thus cooperation in such systems can be regarded as a continuous trait. In addition, it is likely that the costs and benefits that fish experience in predator inspection are nonlinear. This is for the following reasons: First, regarding the benefit, the amount of information that an inspecting fish obtains about a predator probably obeys a law of diminishing returns as the fish approaches the predator more and more closely—so the benefit should be described by a concave function of the investment. Second, regarding the cost, in view of the risks inherent in predator inspection, it seems reasonable to expect that the cost experienced by an inspecting fish will increase more rapidly than linearly as it approaches a predator—thus the cost should also be nonlinear and perhaps described approximately by a quadratic function of the investment (see Sibly and McFarland 1976). Finally, it seems plausible that the cost and benefit can be varied in a suitable way by appropriate manipulations of the experimental system. For example, the cost an inspecting fish perceives can be manipulated by chang-

ing the state of the predator. Thus a fish should perceive a greater cost to be associated with inspecting a highly aggressive predator at a given distance than it would associate with inspecting a less aggressive fish at the same distance. In view of the highly tractable nature of the predator inspection system (as witnessed by the elegant experiments of Milinski 1987), it seems likely that the costs and benefits can be manipulated experimentally in a suitable way (e.g., by using mirrors, models, trained fish, etc.). Predator inspection therefore appears to provide a simple experimental system with which to investigate the types of continuous strategies that lead to cooperative behavior in nature.

Conclusions

Reaching a satisfactory understanding of the evolution of cooperative behavior is a fundamental theoretical problem in evolutionary biology. Reciprocal altruism is the most widely studied framework for attempting to explain cooperation among nonrelatives, and the iterated prisoner's dilemma is the most widely studied model of reciprocal altruism. Notwithstanding its widespread use, the prisoner's dilemma is an essentially unrealistic metaphor for cooperation, allowing as it does only two possible levels of cooperation. The continuous prisoner's dilemma is a much more realistic model of cooperation that allows variable degrees of cooperation. Consequently, the iterated continuous prisoner's dilemma provides a much more satisfactory model for reciprocal altruism than does the standard iterated prisoner's dilemma. The essential problem in attempting to elucidate the evolution of cooperation through reciprocal altruism in this framework lies in finding a suitable class of strategies for the iterated continuous prisoner's dilemma that naturally allow the development of cooperative behavior. Here we have introduced a new type of strategy for the iterated continuous prisoner's dilemma (analogous to those studied by Doebeli and Knowlton 1998 for mutualist interactions) that, rather than depending on the opponent's previous move (cf. Roberts and Sherratt 1998; Wahl and Nowak 1999a, 1999b), depends on the player's payoff in the previous round. These payoff-based strategies depend on the moves that both players made in the previous round and in this sense are in the same spirit as strategies for the standard iterated prisoner's dilemma such as Pavlov (Nowak and Sigmund 1993). Given the success of Pavlov in the standard iterated prisoner's dilemma, it is natural to consider strategies for the iterated continuous prisoner's dilemma that also depend on both players' moves. Here we have shown that payoff-based strategies allow cooperation to evolve from initially quite selfish strategies and subsequently allow cooperative behavior to be maintained indefinitely. Thus

payoff-based strategies, which embody the intuitively pleasing idea that individuals invest more when they are doing well, provide a natural explanation of the fundamental problem of how cooperation can evolve from an initially selfish state, and subsequently be maintained, through reciprocal altruism.

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