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DILEMMAS OF PARTIAL COOPERATION

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Related to the often applied cooperation models of social dilemmas, we deal with scenarios in which defection dominates cooperation, but an intermediate fraction of cooperators, that is, "partial cooperation," would maximize the overall performance of a group of individuals. Of course, such a solution comes at the expense of cooperators that do not profit from the overall maximum. However, because there are mechanisms accounting for mutual benefits after repeated interactions or through evolutionary mechanisms, such situations can constitute "dilemmas" of partial cooperation. Among the 12 ordinally distinct, symmetrical 2 × 2 games, three (barely considered) variants are correspondents of such dilemmas. Whereas some previous studies investigated particular instances of such games, we here provide the unifying framework and concisely relate it to the broad literature on cooperation in social dilemmas. Complementing our argumentation, we study the evolution of partial cooperation by deriving the respective conditions under which coexistence of cooperators and defectors, that is, partial cooperation, can be a stable outcome of evolutionary dynamics in these scenarios. Finally, we discuss the relevance of such models for research on the large biodiversity and variation in cooperative efforts both in biological and social systems.

KEY WORDS: **Diversity, evolutionarily stable state, game theory, natural selection, social dilemmas.**

The emergence and maintenance of cooperative behavior in competitive environments is a withstanding question in biology, economics, and social sciences, but it also attracts much attention from mathematicians and physicists. Game theory (von Neumann and Morgenstern 1953) and particularly evolutionary game theory (Taylor and Jonker 1978; Maynard Smith 1982; Friedman 1991; Nowak and May 1992; Hofbauer and Sigmund 1998; Szabó and Fáth 2007), has proven to be a powerful tool for describing and investigating such real-life conflicts. Certainly, one of the most important solution concepts of such conflicts (represented in games) is that of the Nash equilibrium (Nash 1950), where no player has an incentive to unilaterally deviate from this state. If there is such an equilibrium solution that is not Pareto efficient, that is, another solution is better for at least one player of the game and not worse for any other player, one speaks of a "social dilemma" situation (Dawes 1980; Macy and Flache 2002; Hauert et al. 2006). Due to its interdisciplinary relevance, the field of evolutionary game theory has been applied to innumerous investigations regarding the "evolution of cooperation" in biology (Maynard Smith 1982; Nowak 2006; Ackermann et al. 2008), social sciences (Fehr and Fischbacher 2003; Henrich 2003), and economics (Kreps et al. 2001; Gintis 2005). The most simple, yet powerful way of analyzing cooperation dilemmas is through symmetrical 2×2 games, where two individuals can either cooperate (C) or defect (D). This can be best illustrated by a payoff matrix like the following ones:

$$\begin{array}{c} \\ C \\ D \end{array}\!\!\begin{array}{c} \begin{array}{cc} C & D \end{array} \\ \begin{pmatrix} b-c & -c \\ b & 0 \end{pmatrix} \end{array} \qquad \begin{array}{c} \\ C \\ D \end{array}\!\!\begin{array}{c} \begin{array}{cc} C & D \end{array} \\ \begin{pmatrix} R & S \\ T & P \end{pmatrix} \end{array}, \tag{1}$$

where, due to symmetry, payoffs are given only for the row-individual. A specific configuration of the Prisoner's Dilemma game is often used as standard cooperation model in evolutionary biology (left matrix in eq. 1). Compared are two genotypes or genetically encoded behaviors that are subject to evolutionary selection. A behavior is called cooperative if individuals endow a reproductive fitness benefit b (the evolutionary equivalent of payoff) to other individuals at a certain fitness cost c to themselves

($b > c > 0$). The noncooperative counter-part is called defective as individuals will receive b from cooperators, but do not act cooperatively.

In the present article, we consider a more general universe of situations by applying the right parameterization of equation (1). This implies that a general definition of the cooperative act is more difficult, because one and the same act might have opposing fitness consequences for the other individual. Mainly for illustrative reasons, the choice in this work (which will be further discussed below) is to impose $T > S$. However, it is important to notice that this is a naming convention for the binary choices in this article and not meant to semantically redefine the notion of cooperation. We use the different symmetrical 2×2 games as basis for repeated and evolutionary games. In our argumentation on a specific subclass of games, we show the existence of a cooperation dilemma both in "classical" game theory (with a fixed set of players) as well as in evolutionary game theory (population dynamics). The specific kind of dilemma discussed here has to be distinguished from the one of the Prisoner's Dilemma (and other well known social dilemmas). In particular, we focus on scenarios in which partial cooperation plays an important role. Partial cooperation means that, at a given time, only a part of the individuals apply the cooperative action, whereas the rest of the individuals do not, that is, the population of players partially consists of cooperators, and partially of defectors (1 cooperator and 1 defector in the two-person games).

In evolutionary biology, partial cooperation is particularly relevant when genetic behavior is expressed through varying phenotypes, that is, when one and the same genetic basis can produce different behaviors. A good example are social insects, where a part of the population (workers) contributes to the welfare of the population, but cannot reproduce themselves. In more general, phenotypic plasticity (Via and Lande 1985) and phenotypic noise (Ozbudak et al. 2002; Ackermann et al. 2008) might lead to differences in the contributions to reproductive fitness, that, from a theoretical perspective, does not necessarily lead to an equilibrium state. Another, often cited example is single meerkats (but also other mammals) observing the environment and giving alarm calls in case of danger, whereas other individuals share food (Clutton-Brock et al. 1999).

Partial cooperation naturally arises in games in which the Nash equilibria are (C, D) and (D, C). However, in this article, we will focus on whether $\max(2R, 2P) > S + T$, or if this inequality is reversed. Verifying this inequality yields the system-optimal outcome in the sense of Schelling's collective total (Schelling 1978), that is, the solution of the game that yields the highest possible overall payoff. In a wide range of the literature, where game theory is applied to research on cooperation, the importance of this system optimum is neglected and mostly the cases in which $S + T$ is system optimal are excluded from the investigations. In our view, thereby, a specific subclass of symmetrical 2×2 games received too little scientific attention, although these games are shown to exhibit interesting strategical conflicts in repeated and evolutionary games. We explicitly derive this subclass of games and introduce it as "partial cooperation dilemmas" (PCDs). The three members of this class are the games "Route Choice," "Deadlock," and "Prisoner's Dilemma," but all three games are exclusively with the specification $S + T > \max(2R, 2P)$. In repeated setups of these games, a suitable, Pareto-efficient solution is turn-taking (Duncan 1972; Neill 2003; Browning and Colman 2004; Helbing et al. 2005; Tanimoto and Sagara 2007), that is, an anticoordination of the players (where one player takes the opposite decision of the other) and a permanent flipping between decision alternatives of both players. Despite its efficiency, this alternating behavior is not an equilibrium state in finitely repeated games, that is, players are permanently tempted to leave this solution. Hence, we find a cooperation dilemma in repeated games. In evolutionary terms, the most successful population of individuals would consist of cooperators (that provide help to others) and defectors (that only receive help), but such a coexistence is not a fixed point of the evolutionary dynamics. This constitutes the evolutionary dilemma of cooperation.

Note that we are not the first to deal with the particular games. However, the games Deadlock and Route Choice are, with rare exceptions (Helbing et al. 2005; Kaplan and Ruffle 2007; Stark et al. 2008), almost completely neglected in literature so far. One reason might be the choice of payoff values and the respective conclusion of Rapoport (1967) that was, for example, applied to investigations regarding the evolution of turn-taking behavior only in the archetype games (Browning and Colman 2004), but not to one of the PCDs. Most surprisingly, even the third member of this class, the prominent Prisoner's Dilemma with the specification $S + T > 2R$, is, despite some exceptions (e.g., Schüßler 1986; Kreps et al. 2001; Neill 2003), often explicitly excluded from the scientific investigations, although it is recognized as equivalent cooperation problem (see also May 1987). We conjecture that PCDs are able to serve as distinct and relevant models in the different scientific fields applying (evolutionary) game theory.

Symmetrical 2×2 games

A game is defined by the number of players, their set of strategies, the sequence of decisions to be taken by the players, and the payoffs for all players and for every possible strategy-combination. The class of games described here is one of the simplest: two players decide between two alternative strategies. The strategical situation is identical for both players, that is, the one for the row-player in the matrices of equation (1). After they decided simultaneously, they receive a payoff depending on their own strategy and the strategy of the other player.

Because we elaborate on different symmetrical 2×2 games, it is important to define which strategy is regarded "cooperative" and which "defective" in a general way. For the sake of convenient readability, we use the following simplification throughout this article:

Let us only consider an encounter of different strategies leading to the payoffs S and T ("partial cooperation"). In such a situation, the strategy which yields the lower payoff is regarded the cooperative strategy (C), and the other one the defective strategy (D).

In the games in which it makes sense to speak of cooperative behavior, this simplification yields the correct naming of strategies. For the other games, it is maybe the most useful way to name the strategies likewise. In all the cases, cooperation means to risk losing against the other player and defecting means holding the chance to end up with a higher payoff than the other. Therefore, this approach puts more weight on a player's relative payoff with respect to the coplayer's payoff. With these specifications in mind, we use the same variables commonly used for the Prisoner's Dilemma game for any symmetrical 2×2 game.

We assume that the absolute payoff values are not decisive for the strategical situation, but only the ranking of them (we will qualify this point later on). Because we defined $T > S$, which eliminates equivalent rankings, one can discern 12 ordinally distinct games. Figure 1 conveniently visualizes the phase space of symmetrical 2×2 games in a coordinate system and includes exemplary payoff matrices.

Each of the 12 rectangular or triangular parcels of the coordinate system (separated by full lines) host one ordinal payoff ranking. There, we find the prominent games such as the Prisoner's Dilemma and the Chicken game, which is also often called "Hawk-Dove" game or "Snowdrift" game. Complemented by Leader and Battle-of-the sexes, these are the four archetypes of Rapoport (1967) ("Martyr," "Exploiter," "Hero," and "Leader"). Harmony is also referred to as "By-Product Mutualism." The game of Route Choice reflects important characteristics of (vehicular- or data-) traffic systems and was named and experimentally investigated in (Helbing et al. 2005; Stark et al. 2008). The name Own Goal was chosen arbitrarily to not leave one parcel empty. The game is trivial as any deviation from the dominant strategy hurts the deviant most. The names of the other games are taken from the literature (see e.g., Skyrms 2004; Szabó and Fáth 2007).

PCD in Repeated Games

PARTIAL COOPERATION IN REPEATED GAMES

Taking turns, originally describing the sequential form of human conversation (Duncan 1972), has a considerable impact on

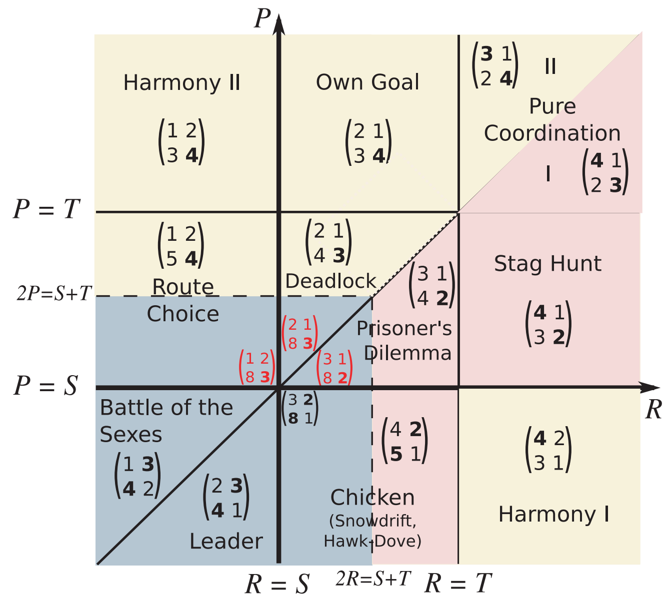

Figure 1. Classification of symmetrical 2×2 games according to payoff ranking and system-optimal solutions. Two-dimensionality is achieved by fixing $T > S$ and classifying ordinal differences only. Parcels separated by solid lines denote different rankings of the payoff values. The dashed lines divide the whole space in two regions according to whether partial cooperation is system optimal (dark-grey background) or not. Social dilemma games have a red background color. For each area a respective payoff matrix (in form of the left matrix in eq. (1), with $T > S$) is given. Red payoff matrices denote "partial cooperation dilemmas."

repeated games, too. Here, it means that players anticoordinate their actions over time such that both take different decisions, but switch their decisions in an alternating manner. This is also called "alternating cooperation" (Helbing et al. 2005; Stark et al. 2008), "alternating reciprocity" (Browning and Colman 2004), or "ST-reciprocity" (Tanimoto and Sagara 2007). The games in the dark-gray area of Figure 1 are the ones with the system-optimal solutions in partial cooperation, that is one of the players profits more than the other. We call this area turn-taking phase as, in repeated games, taking turns would strengthen the relevance of this solutions because of the fairness with respect to the equal average payoffs (see also Bornstein et al. 1997; Neill 2003; Browning and Colman 2004; Helbing et al. 2005; Stark et al. 2008). In games outside the dark-gray region or exactly on the dashed lines, an equal distribution of payoffs is provided by the system-optimal solution, that is, a unique strategy leads to equal and system-optimal payoffs both in one-shot and repeated games. Because there is a significant difference between games with the same payoff ranking depending on whether they are within or outside the turn-taking phase, it is important to address them precisely. For the Prisoner's Dilemma game with $S + T > 2R$, the name "Turn-Taking Dilemma" was already proposed

(Neill 2003). Accordingly, we will speak of the "TT-Chicken, TT-Route Choice, and the TT-Deadlock" for the respective games in the turn-taking phase.

Partial cooperation in repeated games can also mean to apply an interior mixed strategy. That means a player randomizes its decisions and applies a probability to cooperate. This allows for any individual level of cooperation, but does not bear the possibility to anticoordinate with other players over time. We will refer back to this form of partial cooperation in an example later on.

FROM SOCIAL DILEMMAS TO PCD

Following the arguments by Macy and Flache (2002), a social dilemma (Dawes 1980) is present if there exists a Nash-equilibrium, which is not Pareto-efficient. This is certainly true for the Prisoner's Dilemma and the Chicken game, where there are only Pareto-dominated equilibria. Additionally, this holds for Stag Hunt and Pure Coordination I, where the game dynamics might get stuck in an inefficient equilibrium. Social dilemmas are indicated by a red background color in Figure 1.

In this article, we investigate another type of dilemma that is there only in repeated games, but not in the one-shot game. In repeated versions of a symmetrical 2×2 game, the sufficient condition for a dilemma is that, in the underlying one-shot game, there is a Nash equilibrium that is not system optimal. In addition to the social dilemmas, this is true for the games Turn-Taking Dilemma, TT-Route Choice, and TT-Deadlock, that is, each game with $S + T > \max(2R, 2P)$. Whereas this variant of the Prisoner's Dilemma can also be seen as a social dilemma, the other two one-shot games do not hold a dilemma because their Nash equilibria are strict and Pareto efficient. Therefore, in the classification of Rapoport, the payoff rankings of these two games are assessed "almost trivial."

However, in repeated setups of all the three games, players might take turns to persistently exploit the system optimum while sharing the payoffs evenly among each other. Of course, such a solution would imply a Pareto-improvement compared to the persistently played one-shot Nash equilibrium (itself the only Nash equilibrium of the definitely repeated game), hence the dilemma. This can be best illustrated by the payoff matrix for a twice played symmetrical 2×2 game

$$\begin{array}{cc} & \begin{array}{cccc} CC & CD & DC & DD \end{array} \\ \begin{array}{c} CC \\ CD \\ DC \\ DD \end{array} & \begin{pmatrix} 2R & R+S & S+R & 2S \\ R+T & R+P & S+T & S+P \\ T+R & T+S & P+R & P+S \\ 2T & T+P & P+T & 2P \end{pmatrix} \end{array}. \qquad (2)$$

The three games (TT-Dilemma, TT-Route Choice, and TT-Deadlock) have in common that $T > R$ and $P > S$. It follows that the solution (DD, DD) is the unique and strict Nash equilibrium. In contrast to the one-shot game, this strict equilibrium is Pareto-dominated by the solutions (CD, DC) and (DC, CD), because there both players receive $S + T > 2P$. It is worth noticing that the repeated Turn-Taking Dilemma possesses a particularly interesting feature: its Nash equilibrium is twice Pareto-dominated. Hence, there are three solutions of interest: (1) the strict equilibrium, (2) mutual cooperation without anticoordination efforts required, but still Pareto-dominated by (3) turn-taking, which is Pareto-efficient, but requires temporal anticoordination.

We call this dilemma situation PCD, because an efficient solution requires partial cooperation instead of full cooperation. Whereas here we only use the pure possibility of taking-turns as argument to illustrate the existence of a social dilemma in repeated games, we refer to other works that investigate how turn-taking can emerge and be maintained (Neill 2003; Browning and Colman 2004; Helbing et al. 2005; Kaplan and Ruffle 2007; Stark et al. 2008; Tanimoto 2008). Interestingly enough, turn-taking in repeated games of PCD combines the game theoretical problems of cooperation and anticoordination (see also Neill 2003). A similar argument holds for another form of partial cooperation, namely interior mixed strategies. Although they are not as efficient as coordinated turn-taking, a Pareto-improvement can still be achieved (the next section contains a corresponding quantification). PCDs are indicated by red payoff matrices in Figure 1.

PCD in Evolutionary Games

So far, we have derived the notion of PCD games with respect to their relevance for repeated interactions. In the following, we will argue that this classification is also meaningful in evolutionary game theory. Particularly in evolutionary biology, the evolution of cooperation under natural selection remains a not fully understood, scientific topic. Here, cooperation means that an individual has a genetic trait that makes it help another individual at a certain cost (in terms of reproductive fitness) to itself. In the standard model (see left matrix in eq. 1), every cooperator induces exactly the same benefit b, independent of the number of cooperators in the population. Qualifying this strong assumption, Hauert discussed the possibility of synergistic and discounting effects in N-person social dilemmas (Hauert et al. 2006). Implementing this concept into the framework of symmetrical 2×2 games, we obtain the left matrix in equation (3). The parameter w determines whether cooperation has synergistic effects ($w > 1$), discounting effects ($w < 1$), or none of both ($w = 1$). By specifying $\gamma > \beta = b > 0$ and $\beta - \gamma = -c$, we find the according implementation of the synergy/discounting-concept into the standard cooperation model (right matrix in eq. 3).

$$\begin{array}{c c} & \begin{array}{cc} C & D \end{array} \\ \begin{array}{c} C \\ D \end{array} & \begin{pmatrix} (1+w)\beta-\gamma & \beta-\gamma \\ \beta & 0 \end{pmatrix} \end{array} \qquad \begin{array}{c c} & \begin{array}{cc} C & D \end{array} \\ \begin{array}{c} C \\ D \end{array} & \begin{pmatrix} wb-c & -c \\ b & 0 \end{pmatrix} \end{array}. \tag{3}$$

The question is now: what are the different scenarios when we consider synergistic and discounting effects of cooperation based on the standard model? For this purpose, let us systematically vary the parameter w: For $w \in [(b+c)/2b, (b+c)/b]$, which includes $w = 1$, we regain the traditional Prisoner's Dilemma game with $2R > S + T$. Hence, to a certain extent, this model covers both synergistic and discounting effects. However, increasing w above $(b+c)/b$, the game effectively transforms into a Stag Hunt game. That means if synergistic effects are strong enough, defection is not anymore a dominant strategy. In evolutionary terms, we derive a bistable system in which both strategies are evolutionarily stable against each other. Most interestingly, the remaining three possible games, generated by a discounting factor $w < (b+c)/2b$, are exclusively the PCDs. For $w \in [c/b, (b+c)/2b]$, we find a Turn-Taking Dilemma. For $w \in [0, c/b]$, the payoff ranking is the one of TT-Deadlock. By the same reasoning, we obtain that values $w < 0$ result in the TT-Route Choice game. This means that in all these scenarios we address the evolutionary problem of cooperation (helping behavior that induces a fitness-benefit to the recipient and a fitness-loss to the helping individual), but in different environmental scenarios. Note further that the three PCDs possess a dominant strategy, just like the standard cooperation model. When, for example, considering replicator dynamics (strategies that are more successful than average increase their share in the population, see e.g., Hofbauer and Sigmund 1998; Taylor and Jonker 1978) in infinite, well mixed populations (interactions occur between random individuals), a stable population would consist of defectors only. However, what makes these games worth considering besides the standard cooperation model is that too many cooperators may reduce overall fitness. For example, a group (be it in the sense of group selection, spatial clusters, or similar) consisting of cooperators only is not the most successful group, but one in which cooperators and defectors coexist persistently would have the highest group fitness. Let us quantify the fitness of a group as the expected payoff π of a random interaction between two group members

$$\pi = 2x^2 R + 2x(1-x)(S+T) + 2(1-x)^2 P. \tag{4}$$

In this equation, x is the frequency of cooperators in the group. π has its maximum at

$$x^* = \frac{2P - (S+T)}{2[(R+P)-(S+T)]}, \tag{5}$$

where $0 < x^* < 1$, because $S + T > \max\,[2R, 2P, (R+P)]$ by the definition of PCDs. Let us remark that the value of x^* also corresponds to a mutually optimal mixed strategy, that is, if every player cooperates with probability to the amount of x^*, the outcome is system-optimal and characterized by equal expected payoffs. This is in contrast to the individually optimal strategy, which is $x = 0$. For the Prisoner's Dilemma, $x^* = 1$, that is, only full cooperation would be mutually optimal. Due to the fact that x^* is intermediate in PCDs, the conceptual difference to "classical" social dilemmas becomes obvious: we do not ask the question how cooperation can achieve evolutionary stability, but how an "efficient" coexistence of strategies can stabilize (compare to general results in finite systems Antal and Scheuring 2006). In fact, similar questions are addressed by many researchers seeking for explanations regarding the huge biodiversity (Kerr et al. 2002; Doebeli et al. 2004; Reichenbach et al. 2007) and variation in cooperation (Kurzban and Houser 2005) and helping efforts (Field et al. 2006). The game "rock-paper-scissors," where three strategies dominate each other in a cyclic fashion, is then most often used as paradigmatic model (Czaran et al. 2002; Kerr et al. 2002; Reichenbach et al. 2007). However, this game requires at least three strategies and may straight-forwardly promote coexistence (see also Claussen and Traulsen 2008). Contrarily, PCDs could be used to investigate the emergence of coexistence states where evolutionary dynamics is expected to drive the system into dominance of only one specific behavior (in line with the considerations in Imhof et al. 2005).

Evolution of Partial Cooperation

As a first step to investigate the possibility of stable coexistence in PCDs, let us consider the "Five rules for the Evolution of Cooperation" (Nowak 2006), that is, five evolutionary concepts that, under certain circumstances, can effectively change the strategical situation (the game) compared to a single, binary interaction. The five concepts are direct and indirect reciprocity, kin selection, group selection, and network reciprocity (refer to the Discussion of this article to find some comments on criticisms related with these concepts). In Nowak (2006), these concepts are valuably simplified by implementing them into the standard cooperation model. In a subsequent work, these mechanisms were applied to an arbitrary Prisoner's Dilemma game and, among others, the conditions for stability of coexistence within this payoff ranking was derived (Taylor and Nowak 2007). It is found that the concepts of kin selection, group selection, and network reciprocity can lead to stable coexistence if $S + T > R + P$, that is, in the discounting region ($w < 1$). Direct and indirect reciprocity cannot lead to stable coexistence. But do these results also hold for discounting factors beyond the Turn-Taking Dilemma? As derived in Nowak (2006), we can illustrate the effects of kin selection, group selection, and network reciprocity on a symmetrical 2×2 game

$$\begin{array}{ccc} & C & D \\ C & (1+r)R & S+rT \\ D & T+rS & (1+r)P \end{array} \qquad \begin{array}{ccc} & C & D \\ C & (n+m)R & nS+mR \\ D & nT+mP & (n+m)P \end{array}$$

$$\begin{array}{ccc} & C & D \\ C & R & S+H \\ D & T-H & P \end{array}, \tag{6}$$

where r is the relatedness coefficient (mostly defined as probability of two individuals sharing a gene, i.e., $r \in [0, 1]$), n, m are group size and number of groups, respectively, and $H = [(k+1)(R-P) + S - T]/[(k+1)(k-2)]$, with the degree of the network $k > 2$ (note that these results are obtained in the limit of weak selection). Evolutionary dynamics lead to stable coexistence of behaviors if none of the behaviors is evolutionarily stable. The conditions, under which this is fulfilled in the payoff rankings of the three PCDs, can be found in Table 1, repeating and extending the results of Taylor and Nowak (2007). If a condition cannot be met in the respective payoff matrix, this impossibility of stable coexistence is indicated by dashes. For group selection, this happens because $m/(m+n)$ can only vary between 0 and 1, thereby violating the according (not shown) conditions. At first glance, this result seems surprising as a mixed group of cooperators and defectors performs better than a group of defectors. However, this mechanism bases on individual reproduction and not on the reproduction of groups. Because, in contrast to the Turn-Taking Dilemma, a cooperator in any group is less fit than a defector in any group, higher-level selection favors defection (compare with Traulsen and Nowak (2006)). For network reciprocity, the condition to be hold is the same for all three games, that is, the one displayed for the TT-Dilemma. In networks with $k > 2$, F_D is always positive in the games TT-Deadlock and TT-Route Choice,

Table 1. Conditions for stable coexistence of strategies in the three partial cooperation dilemma games (TT-Dilemma (TT-D), TT-Deadlock (TT-DL), TT-Route Choice (TT-RC)) for kin selection (KS, with relatedness r), group selection (GS, with group size n and number of groups m), and network reciprocity (NR, where $F_D = k^2(P-S) - k(R-S) + S + T - R - P$, $F_C = k^2(P-S) - k(R-S) + S + T - R - P$ and $k > 2$ denotes the number of neighbors per individual in the network). Direct and indirect reciprocity cannot lead to stable coexistence.

	TT-D	TT-DL	TT-RC
KS	$\frac{P-S}{T-P} < r < \frac{T-R}{R-S}$		$r > \frac{P-S}{T-P}$
GS	$\frac{P-S}{R-S} < \frac{m}{m+n} < \frac{T-R}{T-P}$	–	–
NR	$F_D < 0 < F_C$	–	–

because $S + T > R + P$ and $P > \max(R, S)$, thereby violating the condition. This result is rather intuitive as, in contrast to the TT-Dilemma, a cluster of cooperators performs worse than a cluster of defectors. Only for kin selection, there is a range of r leading to stable coexistence in all three games of PCDs (direct and indirect reciprocity are left out of the discussion because in none of the scenarios stable coexistence of strategies can emerge).

Discussion

Related to the well-known subclass of social dilemmas, we speak of a dilemma in repeated games if equilibrium play might lead to a solution that is not system optimal. Among the symmetrical 2×2 games, this is additionally true for variants of the Prisoner's Dilemma, the Route-Choice game, and Deadlock that lie within the "turn-taking phase." We call them PCDs because these games bear a dilemma situation both in repeated and evolutionary games that can only be resolved by partial cooperation. In repeated games, partial cooperation might be realized by coordinated turn-taking or the application of intermediate mixed strategies. Both variants are forms of (partial) cooperation that yield a payoff improvement for both players (compared to the strict Nash equilibrium in definitely repeated games).

In evolutionary biology, where individual payoff gains contribute to the reproductive fitness of its genotype, another form of partial cooperation plays an important role: stable coexistence of cooperative and noncooperative strategies. A genotype that maintains such a coexistence (think of different roles in ant colonies or the differentiation in eukaryotic microorganisms and similar forms of cooperation, see Wingreen and Levin 2006) might be advantageous, but it remains a challenge for evolutionary biologists to completely understand how such forms are protected against "cheating," that is, other organisms that profit from cooperation but contribute less cooperation themselves, or how the efficient level of phenotypic variation can be maintained. Therefore, in evolutionary game theory, PCDs are even relevant when considering one-shot games, that is, interactions without the possibility of turn-taking or similar, memory-dependent strategies.

Whereas instances of PCDs have been discussed in previous works (Schüßler 1986; Kreps et al. 2001; Neill 2003; Helbing et al. 2005; Kaplan and Ruffle 2007; Stark et al. 2008), we here provide a concise conceptualization of the general kind of dilemma. For symmetrical 2×2 games, we show that PCD games translate to the standard model of biological cooperation when considering discounting effects of helping efforts. Consequently, we derive the conditions for stable coexistence dependent on the strength of evolutionary mechanisms at work, thereby complementing recent findings (Taylor and Nowak 2007). We find that only kin selection can explain the maintenance of partial cooperation when a dilemma of partial cooperation is present. Group selection and network reciprocity are not able to resolve such kind of dilemma. We are convinced that there is room for new thoughts on realistic mechanisms that are able to explain diversity in a wide range of evolutionary scenarios, especially in PCDs.

Some concepts that are applied in this work have been and still are subject to a scientific dispute. In particular, the multilevel selection approach (leading to the group selection concept) (Traulsen and Nowak 2006) and the role of spatial structure (leading to the network reciprocity concept) is sometimes proposed to be identical to kin selection (see particularly Lehmann and Keller (2006), West et al. (2007) and references therein). In our view, it is semantically rather productive than misleading to distinguish between different sources of indirect fitness benefits. In situations in which differences in genetical relatedness can be cancelled out, the mechanism to explain why cooperation is selected for should not be "kin selection." Apart from this semantic argument, in this work it quantitatively proved valid to distinguish between the concepts: they transform the dilemma in different ways and lead to differing results (see (Traulsen 2010) for more mathematics on this issue).

Although widely neglected by the literature so far, the games exhibiting a PCD could widen the range of models describing complex scenarios of reality without increasing the complexity of the model (they base on a simple symmetrical 2×2 game). Our conjecture is that applying the idea of PCDs into respective models and experimental setups will lead to new and relevant insight regarding the evolution of cooperation in biological systems and human society. In particular, we reckon advances in investigations on the huge biodiversity, phenotypic variation, and heterogeneity of social behaviors in nature.

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