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### Evolution of altruism: Exploring adaptive landscapes

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## Why conditional cooperators should play Prisoner's Dilemma games instead of opting out

Mathias Spichtig · Maurice W. Sabelis · Martijn Egas

**Abstract** The iterated Prisoner's Dilemma (iPD) game is commonly used as a metaphor to understand the evolution of cooperation. In its classic form this game includes strategies, such as conditional cooperators that take particular actions in response to actions of their opponent (e.g., Tit for Tat). This model has been extended by giving players a choice to join the game or not (e.g., Out for Tat). This optional game participation is thought to enhance cooperation for two reasons. First, 'Out for Tat' cooperators – relative to classic-type conditional cooperators – have a higher potential to invade defector populations. Second, defector populations can be invaded by strategies that always reject participating in iPD games, and these invaded populations can in turn be invaded by all types of cooperators. As a consequence, however, populations are rarely dominated by defectors, which weakens the direct advantage of 'Out for Tat' because opportunities for invading defector populations are rare. In this article, we study whether optional game participation favors the long-term evolution of cooperation and whether 'Out for Tat' strategies perform better than their 'Tit for Tat' analogues. In simulations that cover a broad range of PD games, actions of cooperation are sometimes increased in frequency due to optional game play when compared to actions in the classic form of the game. However, more often it is not. Moreover, we find that 'Out for Tat' strategies consistently underperform relative to classic-type conditional cooperators. We also find that there are various strategies effective in exploiting Out for Tat strategies and that strategies strictly avoiding iPD interactions are severe competitors of classic-type conditional cooperators, provided that avoiding PD games is sufficiently lucrative. Overall, we find little support for the hypothesis that optional game play catalyzes evolution of cooperation in iPD games.

## 1 Introduction

In iterated games, players may condition their actions on perceived behaviors in the course of the game. A well-known example of a conditional strategy is Tit for Tat, which imitates the previous action of its opponent (Axelrod and Hamilton 1981). Since the seminal paper by Axelrod and Hamilton (1981), the potential of various conditional strategies has been explored to explain the evolution of cooperation by direct reciprocity (Doebeli and Hauert 2005). Conditional play is usually tuned to the actions available in the game, but in fact it could also concern actions beyond the focal game, such as selection of opponents or performing actions alternative to the game ('optional game play'; Orbell and Dawes 1993; Vanberg and Congleton 1992; Batali and Kitcher 1995; Hauert et al. 2002a,b, 2007; Castro and Toro 2008; Mathew and Boyd 2009). Optional game play is particularly relevant to social network formation (Schuessler 1989; Ashlock et al. 1996; Hauk 2001; Pacheco et al. 2006a,b; Santos et al. 2006; Izquierdo et al. 2010) and spatial network patterning (Dugatkin and Wilson 1991; Enquist and Leimar 1993; Aktipis 2004; Le Galliard et al. 2005). Boyd and Mathew (2007; see also Mathew and Boyd 2009) discuss forms of optional game play in human societies. It is suggested to be a mechanism promoting the evolution of cooperation for reasons to be explained below (Batali and Kitcher 1995; Cant and Johnstone 2006).

The optional game play introduced by Vanberg and Congleton (1992) and analyzed more extensively by Batali and Kitcher (1995) is simple in that it attributes fixed identical payoffs to both players if either of them refuses to interact in a round of the iterated Prisoner's Dilemma (PD) game. The PD game is a two-player game in which personal incentive prevents the mutually beneficial outcome (Axelrod and Hamilton 1981; Doebeli and Hauert 2005). Players in the PD game have a choice between two actions: cooperation, or defection. The realized combination of actions determine the payoff for each player. The optional PD game of Vanberg and Congleton (1992) adds a third action that, when executed by either player, results in identical payoffs to both players and leaves no opportunity for counteraction. The choice of this action is 'non-social' as the opponent cannot influence the payoff of both players. The payoff of the third action is assumed to be in between those of mutual defection and mutual cooperation. The game termed 'semi-optional' by Batali and Kitcher (1995) corresponds to this situation where payoffs from PD games can be substituted with guaranteed payoffs for both players. These authors also considered a 'fully optional' game, where partners for PD games can be substituted. Thus, the semi-optional game allows a choice between interaction in the form of a PD game or not (further referred to as 'interaction choice'), whereas the 'fully optional' game allows a choice between potential partners (further referred to as 'partner choice'). This distinction is not only relevant conceptually, but also in terms of their effects on cooperation (Schuessler 1989; Santos et al. 2006; Hayashi and Yamagishi 1998). In this article we focus on interaction choice.

Batali and Kitcher (1995) distinguish two mechanisms explaining how interaction choice promotes evolution of cooperation in iterated games. The first mechanism is based on the non-social option as a payoff-effective alternative to defection, if the opponent is not cooperating. Conditional cooperators obtain higher payoffs from interactions with defectors if they stop playing PD games rather than playing repeated mutual defection interactions. These new conditional cooperators therefore have an advantage over conventional conditional cooperators such as Tit-for-Tat in directly invading

populations of (unconditional) defectors whenever opting out yields higher payoff than mutual defection.

The second mechanism opens an indirect route for the evolution of cooperation. Populations composed of defector strategies are unstable against strategies that avoid PD games altogether, because their payoff exceeds that of mutual defection. In turn, populations of strategies that strictly avoid PD games pose no (or at least smaller) invasion barriers to cooperator strategies. The invasion process of cooperator strategies in such populations is fairly analogous to the invasion process in the one-shot version of the PD game, analysed by Hauert et al. (2002b). Hence, this second mechanism promotes the evolution of cooperation by indirect invasion of conditional cooperators. Note that it is fundamental to the first mechanism that the game is iterated, whereas the second mechanism is shown to work in one-shot games as well (Hauert et al. 2002b).

In this article, we extend the work of Batali and Kitcher (1995) by analyzing the role of interaction choice in the evolution of cooperation. The first mechanism discussed above can be shown to be effective against unconditional defectors. Simultaneously, the second mechanism implies that defector strategies play minor roles over evolutionary time. Hence, we suspect that the second mechanism undermines the effect of the first on the evolution of cooperation. We quantify the effects elicited by interaction choice on the evolution of cooperation in iterated PD games. We study long-term evolution in finite populations of strategy sets with or without interaction choice. These sets contain all strategies that take (at most) the previous action of their opponent into account as a basis for conditional decisions. The importance of the two mechanisms to relative performances of conditional cooperators is investigated.

## 2 The model

Dependent on the strategy set individuals play either iterated PD games (iPD) or iterated PD games with interaction choice (iPDI) for a fixed number ( $r$ ) of iterations. The PD game is a game of two actions: **D**efection and **C**ooperation. The two players simultaneously execute their actions. If either player in the PDI game chooses not to interact (i.e., executes interaction choice **I**) this enforces the payoff **O** upon executor and opponent. Thus, the payoff matrix for a single iteration of an iPDI game is:

	<b>C</b>	<b>D</b>	<b>I</b>
<b>C</b>	<b>R</b>	<b>S</b>	<b>O</b>
<b>D</b>	<b>T</b>	<b>P</b>	<b>O</b>
<b>I</b>	<b>O</b>	<b>O</b>	<b>O</b>

Payoffs in the matrix apply to a player whose action is indicated in the left column. The payoffs **R**, **S**, **T** and **P** result from the combinations of PD actions and follow the standard conditions:  $T > R > P > S$  and  $2R > T + S$ . The dilemma arises because payoffs of defection exceed those of cooperation ( $T > R$  and  $P > S$ ), whereas two players maximize their combined payoffs by mutual cooperation (per iteration because  $R > P$  and over iterations because  $2R > T + S$ ). We assume  $O < R$  to ensure an incentive for joining PD game interactions. The interaction choice is profitable if  $O > P$  and unprofitable if  $O < P$ . Resumptions of game interactions at a later moment remain an option.

Strategies of the iPD and iPDI set are represented by the codes:  $abc$  ( $a, b, c \in \{C, D\}$ ) and  $abcd$  ( $a, b, c, d \in \{C, D, I\}$ ). Action  $a$  is executed in the initial round. Actions  $b, c, d$  are executed if the action  $C, D$ , respectively  $I$  was perceived in the previous round. For example, the strategy  $CCDI$  starts with cooperation and thereafter imitates the opponent's last action. The iPD set contains  $2^3 = 8$  strategies and the iPDI set  $3^4 = 81$  strategies. Strategies of the iPDI set with the property  $a, b, c \in \{C, D\}$  are inactive with respect to interaction choice. Such strategies have an analogous strategy in the iPD set, e.g., the strategies  $CCDI, CCDD$  and  $CCDC$  are analogous to the iPD strategy  $CCD$ , i.e., Tit for Tat.

We assume strategies executing action  $I$  can sense the PD actions their opponents execute in the same round. In our opinion, a justified alternative is the game version in which strategies are not able to sense such intended PD actions whenever PD games are not played. However, in the alternative game, it is hard to define the motivation to resume PD interactions in later rounds for strategies that played action  $I$ . Therefore, we ignore this alternative game version.

To study evolutionary dynamics, populations of constant size  $N$  are assumed to evolve through a Moran birth-death process (1962; Nowak et al. 2004; Taylor et al. 2004). The process involves discrete time steps. First, payoffs are generated by assuming each individual plays the game with each of the  $N - 1$  other population members. The sum of these payoffs determines individual fitness. Second, one individual is chosen to produce one offspring clonally. For each individual, the probability to reproduce is proportional to its fitness. Third, a randomly chosen member of the population is removed and replaced by the newborn. Offspring mutate at a rate  $\mu$ , and mutants express each strategy phenotype of the set with equal chance.

For mutation-limited evolution,  $\mu \rightarrow 0$ , we employ the approach described by Fudenberg and Imhof (2006; Fudenberg et al. 2006), which approximates distributions of population compositions over infinite time. Due to the low rate of mutation assumed in this approach, the average time span between consecutive mutation events is of much higher order than the other relevant evolutionary time scales. The most relevant time scale thereby is the average time a mutant requires to go extinct or to reach fixation. Consequently, there is a separation of time scales because the population reaches fixation long before the next mutant appears. Populations therefore tend to remain in homogeneous states, i.e., composed of a single strategy. Heterogeneous states constitute of the (invader) mutant strategy and the resident strategy. The former either reaches fixation or goes extinct. Heterogeneous states occur too infrequently to affect any statistics we sample.

Evolution under finite mutation rates is explored using computer simulations. Generally, in these simulations the initial populations harbor a random set of strategies. For specific results (shown in Fig. 2-1d) homogeneous populations of the strategies  $DDD, DDDD$  (if  $O \leq P$ ) and  $IDII$  (if  $O > P$ ) are taken as initial populations. Simulations are performed for  $2 \cdot 10^8$  time steps. Statistics are sampled over the entire duration of these simulations.

A strategy's evolutionary potential depends on its ability to invade populations when rare, and on its relative invasibility when dominating the population. For mutation-limited populations we address these two aspects by the following probabilities: A) Invasiveness of strategy  $i$  is the average probability of mutants of this strategy to

reach fixation:  $\sum_x \rho_{xi} u_x$ , where  $\rho_{xi}$  is the probability of a mutant  $i$  to reach fixation in populations otherwise composed of strategy  $x$ , and  $u_x$  is the prevalence of a homogeneous population  $x$ . B) Invasibility is the average probability of mutants to reach fixation in populations otherwise composed of strategy  $i$ :  $s^{-1} \sum_x \rho_{ix}$  where  $s$  is the number of strategies in the set. Note: both probabilities consider invasions by individuals carrying strategy  $i$  as well, whereby the strategy of these individuals is generated by synonymous mutation.

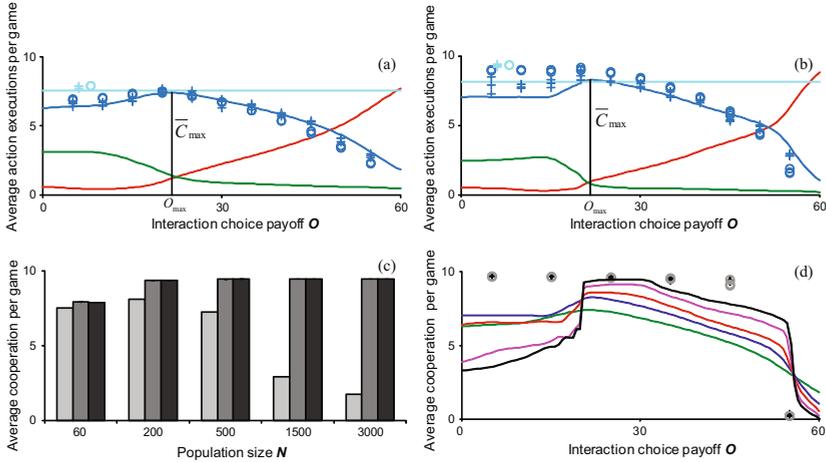
### 3 Results

#### 3.1 Game behavior

We start with observations on time-averaged game characteristics of populations of individuals playing either the iPD game or the iPDI game. For actions  $A \in \{I, D, C\}$ ,  $\bar{A}$  is the average number of executions per game over the observation time in iPDI populations.  $\bar{A}_I$  represents the corresponding average in iPD populations. Given a fixed PD payoff set, the averages  $\{\bar{I}, \bar{D}, \bar{C}\}$  are influenced by the payoff value  $\mathbf{O}$  selected a priori. Fig. 2-1a,b provide examples of the dependency of these averages on the payoff value  $\mathbf{O}$ , using population sizes of 60 (Fig. 2-1a) and 200 (Fig. 2-1b). The PD payoff values  $\{\mathbf{R}, \mathbf{S}, \mathbf{T}, \mathbf{P}\} = \{60, 0.01, 100, 20\}$  chosen for Fig. 2-1 are proportional to those of Axelrod and Hamilton (1981) except that an increment of 0.01 is added to the  $\mathbf{S}$  payoff to ensure positive chances for reproduction. This modification is unlikely to result in deviations from results obtained for the Axelrod and Hamilton payoffs (Fudenberg et al. 2006). For the mutation-limited case ( $\mu \rightarrow 0$ ), we found an overall increase of  $\bar{I}$  and a decrease of  $\bar{D}$  with increasing payoff  $\mathbf{O}$  (Fig. 2-1a,b). The values of  $\bar{C}$  display maxima in average executed cooperation,  $\bar{C}_{\max}$ , within the interval of  $\mathbf{O}$  values under consideration ( $\mathbf{S} \leq \mathbf{O} \leq \mathbf{R}$ ). In a systematic survey of PD payoff values (Fig. 2-2), a payoff value of interaction choice for which cooperation is maximal,  $\mathbf{O}_{\max}$ , is always found within  $(\mathbf{S}, \mathbf{R})$  for populations of sizes  $N = 60$  and  $N = 200$ . Fig. 2-1b shows that average cooperation in iPDI populations can exceed the value measured in iPD populations ( $\bar{C}_{\max} > \bar{C}_V$ ), a result also found for higher population sizes (compare  $\bar{C}_V$  in Fig. 2-1c [light grey bars] to  $\bar{C}$  in Fig. 2-1d [red, pink and black lines]). Average cooperation in iPDI can exceed that in the corresponding iPD population ( $\bar{C} > \bar{C}_V$ ) even under unprofitable interaction choice ( $\mathbf{O} < \mathbf{P}$ ). In our example, this observation applies to mutation-limited iPDI populations of sizes  $N = \{500, 1500, 3000\}$  (compare  $\bar{C}_V$  in Fig. 2-1c [light grey bars] to  $\bar{C}$  in Fig. 2-1d [red, pink and black lines]). In iPD populations average cooperation is highest for  $N = 200$  and decreases with increasing population sizes (light grey bars in Fig. 2-1c). In iPDI populations, average cooperation tends to decrease with increasing population size in the range of unprofitable interaction choice and, similarly, for very high interaction choice payoffs ( $\mathbf{O} \geq 55$ ; lines in Fig. 2-1d). Average cooperation in iPDI populations increases with population size for the remaining range of profitable interaction choice payoffs (lines in Fig. 2-1d). The consequent result is an increasing difference between

(increasing)  $\bar{C}_{\max}$  and (decreasing)  $\bar{C}_V$  with increasing population size (compare light grey bars in Fig. 2-1c with  $\bar{C}_{\max}$  in Fig. 2-1d).

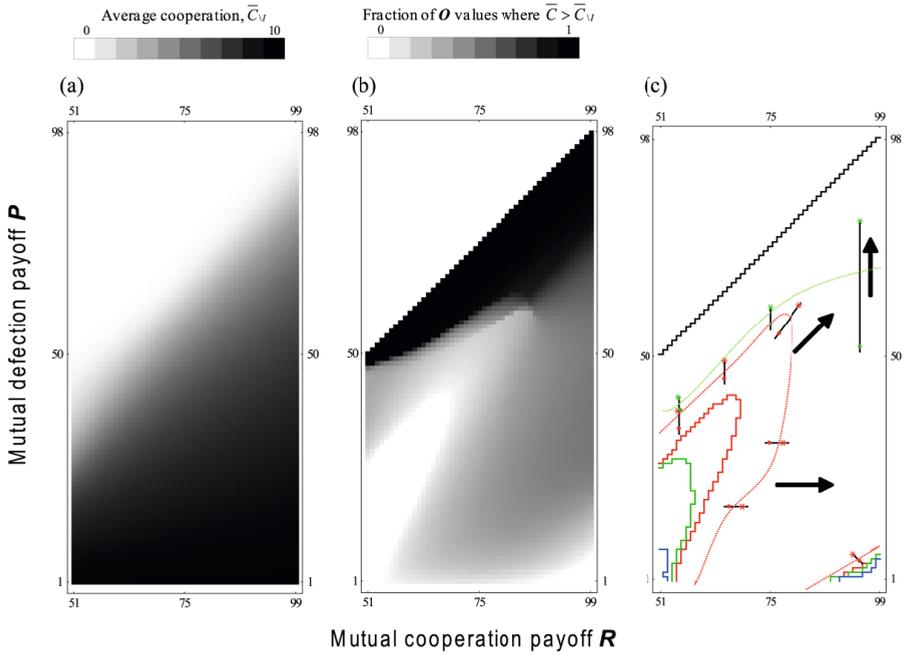
Simulation results under finite mutation imply that the described changes of  $\bar{C}$  and  $\bar{C}_V$  values can differ from values under limited mutation (Fig. 2-1a-d). Fig. 2-1a,b show values of  $\bar{C}$  and  $\bar{C}_V$  for simulations using  $\mu = 0.01$  ( $\circ$  symbols) and  $\mu = 0.001$  (+ symbols). In particular, at  $N = 200$  (Fig. 2-1b) the values of  $\bar{C}$  generated from these simulations were lower than  $\bar{C}_V$  for all explored  $O$  values while we find  $\bar{C}_{\max} > \bar{C}_V$  under limited mutation. In Fig. 2-1c,  $\bar{C}_V$  values were higher in the simulations of populations under finite mutation ( $\mu = 0.01$ ; intermediate and dark grey bars) than in corresponding mutation-limited populations and, unlike the mutation-limited case (light grey bars), we do not observe a strong decrease in  $\bar{C}_V$  with population size. Simulation results for  $N = 1500$  and  $\mu = 0.01$  showed average executions of cooperation of  $\sim 9.5$  ( $r = 10$ ) for both iPD populations (intermediate and dark grey bars in Fig. 2-1c) and iPDI populations (symbols in Fig. 2-1d) if  $O \leq 45$ , and observed  $\bar{C}$  values were markedly decreasing for higher interaction



**Fig. 2-1** Panels (a, b) show average executed actions  $\bar{I}$  (red),  $\bar{D}$  (green),  $\bar{C}$  (dark blue) and  $\bar{C}_V$  (light blue) as function of interaction choice payoff  $O$  in iPD populations and in iPDI populations of size (a)  $N = 60$  and (b)  $N = 200$ . Averages for mutation-limited populations are depicted by lines and simulation results (only  $\bar{C}_V$  and  $\bar{C}$ ) for populations at mutation rate  $\mu = 0.001$  and at mutation rate  $\mu = 0.01$  are depicted by ‘plus’ symbols and circles, respectively. Vertical lines indicate the payoff value  $O_{\max}$  with maximal average cooperation ( $\bar{C}_{\max}$ ) at  $\mu \rightarrow 0$ . Panel (c) gives average executed cooperation values  $\bar{C}_V$  in iPD populations of sizes  $N = \{60, 200, 500, 1500, 3000\}$ : Light gray bars give the  $\bar{C}_V$  values for mutation-limited populations, second and third bars give the average  $\bar{C}$  of three simulations of populations at rate  $\mu = 0.01$  (standard deviations across replicas tend to be too small for the resolution of the graph). In one set of these simulations, the initial populations were randomly composed (medium-gray bars) and in the other set, the initial populations were homogeneously composed of  $DDD$  (dark-gray bars). Panel (d) average executed cooperation  $\bar{C}$  as function of interaction choice payoff value  $O$  for mutation-limited iPDI populations of different sizes (color code follows  $N = \{60, 200, 500, 1500, 3000\} \rightarrow \{\text{green, blue, red, pink, black}\}$ ). Additionally, the panel shows average cooperation (‘pluses’ and ‘circles’) in simulated populations of size  $N = 1500$  and at rate  $\mu = 0.01$ . In these simulations, initial populations were randomly composed (‘plus’ symbols) or initial populations were homogeneously composed (‘circle’ symbols) of  $DDDD$  (if  $O < P$ ) or of  $IDII$  (if  $O > P$ ). Parameters:  $R = 60$ ,  $S = 0.01$ ,  $T = 100$ ,  $P = 20$ ,  $r = 10$ ; per condition set, three replica simulations were performed.

choice payoffs (right-most symbols in Fig. 2-1d). These values were higher than the corresponding  $\bar{C}_{\max}$  value for the mutation-limited case ( $\sim 9.1$ ; as can be read from the pink line in Fig. 2-1d). In general, we did not recover the decrease of  $\bar{C}_V$  to  $\sim 2.9$  nor the marked decrease of  $\bar{C}$  for the range of unprofitable  $O$  values found for populations of the same size evolving under limited mutation (Fig. 2-1c,d).

In order to investigate to what extent average cooperation in iPDI populations can exceed that in iPD populations, we recorded whether  $\bar{C}_{\max} > \bar{C}_V$  across a systematic sample of PD values (using  $N = 60$ ). The payoff values of  $S$  and  $T$  were kept 0.01 and 100, respectively,  $P$  was varied between 1 and  $R - 1$  and  $R$  was varied between 50 and  $T - 1$ . For the mutation-limited case ( $\mu \rightarrow 0$ ), Fig. 2-2a shows  $\bar{C}_V$  values for the range of payoff values under consideration and Fig. 2-2b shows the fractions of the range of



**Fig. 2-2** The data in the three panels are given on the grid of  $\{P, R\}$ -values for which data were generated (see main text); upper left corners are empty because PD games assume by definition that  $P < R$ . Panel (a) shows average cooperation,  $\bar{C}_V$ , in iPD populations of size  $N = 60$  and  $\mu \rightarrow 0$ . The scale ranges from 0 to 10 as the game is played for ten rounds ( $r = 10$ ). For the conditions of panel (a), panel (b) shows the fractions of the interval  $O \in [S, R]$  for which average execution of cooperation is higher in iPDI populations than in iPD populations ( $\bar{C} > \bar{C}_V$ ). Panel (c) shows the parameter regions (bordered by solid lines towards the bottom left corner and bottom right corner) where  $\bar{C} < \bar{C}_V$  for all  $O \in [S, R]$  under limited mutation ( $\mu \rightarrow 0$ ) for the population sizes  $N = 60$  (red solid line, corresponding to the border of white areas in panel (b)),  $N = 200$  (green solid line) and  $N = 500$  (blue solid line). Under the finite mutation used in simulations ( $\mu = 0.01$ ), dotted lines represent hand-sketches of the corresponding parameter regions where  $\bar{C} < \bar{C}_V$  for all  $O \in [S, R]$  (green dotted line:  $N = 200$ , red dotted lines:  $N = 60$ ). These sketches are based on simulations performed for values of  $\{P, R\}$  indicated as straight black lines. Asterisks mark the beginning in ascending direction (indicated by arrows) of  $\{P, R\}$ -combinations along the lines for significant  $\bar{C} > \bar{C}_V$  (see appendix for the condition of significance). Solid dots mark the beginning of  $\{P, R\}$ -combinations in descending direction along the lines for significant  $\bar{C} < \bar{C}_V$ . Other parameters:  $T = 100$ ,  $S = 0.01$ .

$\mathbf{O} \in [\mathbf{S}, \mathbf{R}]$  where  $\bar{C} > \bar{C}_V$ . Whereas for most of these  $\{\mathbf{R}, \mathbf{P}\}$  combinations the condition  $\bar{C} > \bar{C}_V$  respectively  $\bar{C} < \bar{C}_V$  is dependent on the choice of payoff  $\mathbf{O}$  there is a range of combinations with  $\bar{C} > \bar{C}_V$  for all payoffs  $\mathbf{O} \in [\mathbf{S}, \mathbf{R}]$ , as well as two distinct parameter regions with  $\bar{C} < \bar{C}_V$  for all payoffs  $\mathbf{O} \in [\mathbf{S}, \mathbf{R}]$ . The range with  $\bar{C} > \bar{C}_V$  for all  $\mathbf{O}$  comprises the collection of  $\{\mathbf{R}, \mathbf{P}\}$  combinations along the upper edge of Fig. 2-2b, i.e.,  $\mathbf{P} \sim \mathbf{R}$ . In iPD populations these conditions are most stringent for the evolution of cooperation (see Fig. 2-2a) as the extra gain from mutual cooperation is small relative to the payoff of mutual defection. For most of the  $\{\mathbf{R}, \mathbf{P}\}$ -combinations studied we find  $\mathbf{O}_{max} > \mathbf{P}$ , i.e., the  $\bar{C}_{max}$ -value is observed when the interaction choice is profitable. Exceptions with  $\mathbf{O}_{max} < \mathbf{P}$  are found only for a few combinations with  $\mathbf{P} \sim \mathbf{R}$ . We consider scrutiny of this anomaly as irrelevant because under such conditions average cooperation is very low in iPD populations (Fig. 2-2a) as well as in iPDI populations.

Fig. 2-2b shows two distinct parameter regions with  $\bar{C}_{max} < \bar{C}_V$ , i.e., where interaction choice has an overall negative effect on the occurrence of cooperation. In mutation-limited populations, the size of these regions seems to decrease with increasing population size (compare solid lines in Fig. 2-2c). In a set of simulations, we assessed the boundary of transition from  $\bar{C}_{max} < \bar{C}_V$  to  $\bar{C}_{max} > \bar{C}_V$  in population at  $\mu = 0.01$  along selected lines of  $\{\mathbf{P}, \mathbf{R}\}$ -values (dotted lines in Fig. 2-2c; the assessment procedure is described in Appendix 2-1). The results for  $N = 60$  in Fig. 2-2c (compare dotted and solid lines in red) imply that the regions with  $\bar{C}_{max} < \bar{C}_V$  are larger at  $\mu = 0.01$  than at  $\mu \rightarrow 0$ . For  $N = 200$ , the regions with  $\bar{C}_{max} < \bar{C}_V$  at  $\mu \rightarrow 0$  (solid green lines) seem fused into one region covering the majority of the  $\{\mathbf{P}, \mathbf{R}\}$  shown in Fig. 2-2c (green dotted line) at  $\mu = 0.01$ . The results in Fig. 2-2c suggest an increase of the discussed type of parameter regions if mutation rates are changed from  $\mu \rightarrow 0$  to  $\mu = 0.01$ . Moreover, opposite to the pattern observed in mutation-limited populations at the finite rate of  $\mu = 0.01$  the sizes of the regions with  $\bar{C}_{max} < \bar{C}_V$  seem to increase by this increase of population size (compare dotted lines in Fig. 2-2c). In the mutation-limited case, the decline of the regions with increasing population size is in accordance with the observation of increasing differences between  $\bar{C}_{max}$  and  $\bar{C}_V$  with increasing population sizes (as described above, see Fig. 2-1c,d). At  $\mu = 0.01$ , such a decrease of  $\bar{C}_V$  with population size is absent (intermediate and dark grey bars in Fig. 2-1c). This observation is in agreement with the fact that the regions in Fig. 2-2c (dotted lines) seem to grow with population size.

## 3.2 Strategy interactions

In this section we discuss details of strategy dynamics that we find relevant for the interpretation of the results described above.

### 3.2.1 Mutation-limited populations

The conditional cooperator of the iPD set is Tit for Tat (coded as *CCD* in our notation of strategies; see the Model section). Observed prevalences of cooperation can be

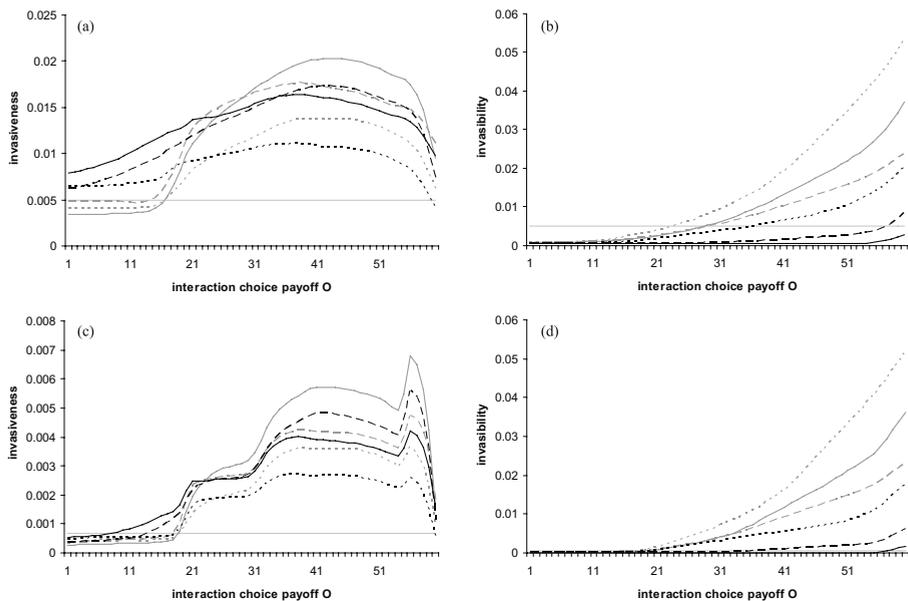
largely attributed to this strategy. The iPDI set contains three strategies analogous to Tit for Tat, *CCDI*, *CCDD* and *CCDC*, and three further conditional cooperators, *CCII*, *CCID* and *CCIC*. The latter three employ interaction choice in response to defection and we refer to them as Out for Tat strategies (Hayashi and Yamagishi 1998). Observed cooperation in iPDI populations can be largely attributed to these six conditional cooperator strategies.

We exemplify strategy interactions in the iPD set using the parameter conditions of Fig. 2-1. In iPD populations, unconditional defector (*DDD*) and Tit for Tat (*CCD*) are the strategies with highest average abundances. Strategy *DDD* replaces *CCD* as the most prevalent strategy for  $N > 983$ . The prevalences of the other six strategies over time are marginal and fixation of *CCD* mutants in *DDD* populations is consequently the usual process by which *CCD* populations are established. The fixation probability of *CCD* mutants in *DDD* populations is smaller than  $N^{-1}$  for population sizes  $N > 881$ , i.e., the mutants have a lower chance to reach fixation than a mutant neutral to *DDD* in populations above this size. *CCD* populations are most likely to be replaced by unconditional cooperator mutants (*CCC*). These two strategies are mutually neutral and have a respective fixation probability of  $N^{-1}$ . The invasiveness (defined in the Model section as the average probability of a mutant to reach fixation) of *CCD* decreases with increasing population size  $N$ , whereas established populations of *CCD* increase in stability with population size (high stability means low invasibility as defined in the Model section). These two effects together result in a maximal average prevalence of *CCD* and in  $\bar{C}_V$  at an intermediate population size ( $N = 166$ ; note that  $\bar{C}_V$  is highest at  $N = 200$  in Fig. 2-1c [light grey bars]).

In iPDI populations, either of the Tit for Tat analogues *CCDI* and *CCDD* has the highest average frequency of the six conditional cooperators at  $\mathbf{O}_{max}$  in the PD payoff matrices and population sizes explored in Fig. 2-2. These two strategies are the most prevalent conditional cooperators over the entire range of conditions of Fig. 2-1. The lower prevalences of the third Tit for Tat type strategy *CCDC* (and similarly *CCIC*) is due to the fact that various strategies can exploit the characteristic that these strategies respond to action *I* by cooperation. We use invasiveness and invasibility to identify the reason for the dominant prevalence of the conditional cooperators *CCDI* and *CCDD*. In Fig. 2-3 we show for populations of  $N = \{200, 1500\}$  invasiveness and invasibility values of the six conditional cooperators along the same cline of  $\mathbf{O}$  values as in Fig. 2-1. The Out for Tat strategy *CCII* and the Tit for Tat analogue *CCDI* are distinct only in their reaction to perceived defection, the same applies to pairs  $\{CCID, CCDD\}$  and  $\{CCIC, CCDC\}$ . Any difference in invasiveness or invasibility of each of these pairs of strategies can be attributed to the different response to perceived defection. Invasiveness tends to be higher under profitable interaction choice for all conditional cooperators (Fig. 2-3a,c). Either of the Out-for-Tat strategies *CCII* or *CCID* has the highest invasiveness in the range of profitable  $\mathbf{O}$  values except when small (Fig. 2-3a,c). The overall increase of all invasiveness values with increasing  $\mathbf{O}$  values from unprofitable to profitable suggests that this increase is partly attributable to increased and effective confrontations with populations of strategies against which they do not employ *D*, e.g., the conditional cooperators themselves and certain loners (i.e., strategies that avoid PD games). The invasion of loner-dominated populations is one way by which conditional cooperators are favored by interaction choice (see introduction section). Invasibility values increase for all strategies with increasing  $\mathbf{O}$  value (Fig. 2-3b,d). The increase is already marked for the Out for Tat strategies at unprofitable  $\mathbf{O}$  values whereas invasi-

bility values of *CCDI* and especially of *CCDD* remain virtually unchanged over a range of profitable  $O$  values (Fig. 2-3b,d). Hence, the Out for Tat strategies pay for the increased invasiveness under profitable interaction choice by an increased instability of the populations they establish. For certain profitable  $O$  values, invasiveness of Tit for Tat analogues such as *CCDD* is lower than corresponding values of Out for Tat strategies (Fig. 2-3a,c). However, the lower invasibility values of the Tit for Tat analogues (Fig. 2-3b,d) imply that population dominance states of these strategies tend to last longer. The net effect is higher prevalence of the Tit for Tat analogues *CCDI* and *CCDD*.

To illustrate the weaknesses of the Out for Tat strategies we consider their interaction with strategy *DCDD* in more detail: this strategy plays an action sequence of **D-C-D-C...** against conditional cooperators, and receives the payoff  $(T + O + T + O + \dots)$  against the Out for Tat strategies and the payoff  $(T + S + T + S + \dots)$  against the Tit for Tat analogues. The strategy exploits both conditional cooperator types in the first round and thereafter in every second round. In order to pursue sequential exploitation the strategy *DCDD* executes **C** in the in-between rounds. This behavior triggers the response **C** in the conditional cooperators we defined in our model. When playing against the Out for Tat strategies the plays of **C** by *DCDD* are countered by action **I** resulting in the payoff  $O$  (for both strategies). When playing against the Tit for Tat analogues the strategy *DCDD* is exploited (i.e., the strategy receives the lowest payoff



**Fig. 2-3** Invasiveness values (panels **a**, **c**) and invasibility values (**b**, **d**) of the Out for Tat strategies  $\{CII$  (continuous gray line),  $CCID$  (coarse broken gray line),  $CCIC$  (fine broken gray line) $\}$  and the Tit for Tat analogues  $\{CCDI$  (continuous black line),  $CCDD$  (coarse broken black line),  $CCDC$  (fine broken black line) $\}$  as a function of interaction choice payoff  $O$ . Straight light gray lines indicate value  $N^{-1}$  (i.e., fixation probability of a neutral invader strategy). Population size in panel (**a**) is  $N = 200$  and in panel (**b**) is  $N = 1500$ . Other parameters as in Fig. 2-1.

**S** while the Tit for Tat analogues receive the highest payoff **T**) each time it plays **C**. With increasing payoff value **O** strategy *DCDD* is an increasingly effective invader of the Out for Tat strategy populations. For the parameters used in Fig. 2-1, the fixation probability of *DCDD* mutants in Out for Tat populations is larger than  $N^{-1}$  for all chosen **O** values, but against the Tit for Tat analogues it is smaller than  $N^{-1}$ .

Average cooperation  $\bar{C}$  observed under profitable interaction choice conditions can practically be attributed to *CCDI* and *CCDD* populations at the larger population sizes ( $N = \{1500, 3000\}$ ) in Fig. 2-1c, e.g., prevalence is 42% for each strategy (Fig. 2-1 conditions and  $\{\mathbf{O}, N\} = \{25, 1500\}$ ) whereas the combined prevalence of the remaining conditional cooperators is 5%. We attribute high prevalence of the strategies *CCDI* and *CCDD* to their stability to invasions (low invasibility in Fig. 2-3b,d). At these population sizes no fixation probabilities of the strategies in *CCDD* populations exceed  $N^{-1}$  for  $\mathbf{O} < 55$ . The marked increase in  $\bar{C}$  observed for these population sizes (blue and pink line in Fig. 2-1d) is at the critical point of interaction choice profitability ( $\mathbf{O} \approx \mathbf{P}$ ). The fixation probability of strategy *DIIC* in *CCDD* populations exceeds  $N^{-1}$  for  $\mathbf{O} \geq 55$  (strategies with this characteristic can be found for lower **O** values for *CCDI*; see the prompt increase of the invasibility of *CCDI* in Fig. 2-3d). The group of cooperator strategies  $\{CCII, CCID, CCIC, CCDI, CCDD, CCDC, CCCI, CCCD, CCCC\}$  which contains the conditional cooperators are mutually neutral because they always cooperate with each other. In the range  $\mathbf{O} \geq 55$ , non-cooperators such as *DIIC* begin to replace the cooperators as most effective invaders of *CCDD* populations. The resulting lowered stability of *CCDD* populations against invaders such as *DIIC* coincides with the marked decrease in  $\bar{C}$  observed in Fig. 2-1c. Our interpretation of this decrease is that interaction choice is too attractive as alternative to the PD game.

### 3.2.2 Finite mutation

In contrast to the mutation-limited case, assuming finite mutation rates implies that other strategies are likely to interfere in evolutionary interactions between the resident strategy and the invader strategy (Traulsen et al. 2006). To investigate to what extent this may affect the results, we performed simulations with mutation rates of 0.01 and 0.001 (Figs. 2-1 and 2-2). We explain the results first for the iPD simulations, and then turn to the iPDI simulations.

Average cooperation under finite mutation rates was higher than under mutation limitation. We no longer found the marked decrease in cooperation level with high population size (Fig. 2-1c). The strategy *CCD* was the most prevalent strategy in all performed iPD simulations shown in Fig. 2-1. We conjecture that in our simulations finite mutation stabilized populations of *CCD* against invasion by the unconditional cooperator *CCC*. For  $N = \{60, 200\}$  and  $\mu = 0.01$ , we observed repeated dynamics of *CCD* reaching dominance status followed by (temporal) loss of the strategy during the course of simulations (using the parameter values of Fig. 2-1). These dynamics were not observed for  $N = \{500, 1500, 3000\}$ , i.e., strategy *CCD* became and remained dominant over the course of the simulations. Note that this observation applied to both forms of initial populations, i.e., a random sample from the strategy set, or a homogeneous *DDD* population. Applying these different initial populations had no discernable effect on observed average cooperation  $\bar{C}_V$  for the selected population sizes (compare

second columns to respective third columns in Fig. 2-1c). For  $N \geq 200$ ,  $\bar{C}_V$  values were at  $\sim 9.5$  (Fig. 2-1c) and therefore much higher than in corresponding mutation-limited populations (compare first columns to second, third columns in Fig. 2-1c). As discussed above, the strategy *DDD* shows highest average prevalence in such mutation-limited populations of sizes  $N = \{1500, 3000\}$ . The observed  $\bar{C}_V$  of  $\sim 9.5$  for simulations initiated with homogeneous *DDD* populations suggests that this strategy was ineffective in maintaining its dominance. We interpret this result as an indication that the dynamics of populations under limited mutation and under finite mutation of  $\mu = 0.01$  markedly differ from each other.

In the iPDI simulations, the Tit for Tat analogues *CCDI* and *CCDD* were the most prevalent among the conditional cooperators in all performed iPDI simulations of Fig. 2-1. For  $N = 1500$ , the corresponding  $\bar{C}$  value was also at  $\sim 9.5$  for a broad range of unprofitable and profitable  $O$  payoff values (symbols in Fig. 2-1d). The height of this average indicates that *CCDI* and *CCDD* had the highest prevalences of all strategies in the simulations over these  $O$  payoff values. The corresponding  $\bar{C}$  values for  $\mu \rightarrow 0$  and for unprofitable interaction choice are clearly lower in Fig. 2-1d (pink line). For the range of unprofitable interactions choice, we therefore retrieved the observation of iPD that cooperation is rather rare at  $\mu \rightarrow 0$  and the most frequently executed action at  $\mu = 0.01$ . The low values of  $\bar{C}$  at the upper end of the  $O$  values  $\geq 45$  (symbols in Fig. 2-1d) indicate that conditional cooperators were not the most prevalent strategies in the simulations over these payoffs. The lines in Fig. 2-1d show that the marked drop in  $\bar{C}$  is also observed for mutation-limited populations, but at the higher values of  $O \geq 55$ .

## 4 Discussion

We investigated the evolution of cooperation in the PD game when a non-social action, i.e., opting out of the game, is added as an alternative to the social interaction of playing the PD game. If it is more beneficial than mutual defection, the option to avoid social interactions is argued to promote the evolution of cooperation via two routes (Vanberg and Congleton 1992; Batali and Kitcher 1995). First, it can result in conditional cooperators (the Out for Tat strategies) better suited to invade populations dominated by unconditional defectors than conditional cooperators that respond with defection (the Tit for Tat analogues). Second, (conditional) cooperators can indirectly invade defector-dominated populations by invading populations dominated by non-social strategies (loners) which in their turn invaded defector-dominated populations (Hauert et al. 2002a,b, 2007; Castro and Toro 2008; for a critical evaluation of this invasion route see Mathew and Boyd 2009). The presence of effective invaders of defector dominated populations – the loners – cast doubt on the relevance of the first route. The focus of this discussion is if the advantage of the Out for Tat strategies as invader is effectuated.

On average, higher occurrence of cooperation in populations with interaction choice (iPDI) to that in corresponding populations without this choice (iPD) is found under limited mutation and at the highest population sizes (compare light grey bars in Fig. 2-1c with  $\bar{C}_{\max}$  in Fig. 2-1d). Such higher occurrence was not found in corresponding simulations with finite mutation rates, i.e., cooperation was

highly prevalent under iPD and iPDI (compare intermediate/dark grey bars in Fig. 2-1c with plus and dot signs in Fig. 2-1d). Finite mutation frequently generates defector strategies. These defectors can prevent (neutral) invasions of unconditional cooperators into populations dominated by conditional cooperators – like Tit for Tat in iPD or one of the six conditional cooperators of iPDI. Under limited mutation, such invasions are an important cause for the demise of (conditional) cooperator-dominated populations. If such demise of cooperator-dominated populations is virtually absent – a situation that occurs in some simulations – then the advantages of Out for Tat strategies as invader of defector-dominated populations hardly take effect. Hence, the supposed advantage of the Out for Tat strategies (Batali and Kitcher 1995) as invader plays a secondary role in (large) populations under finite mutation. Note that the stabilization of cooperation by high mutation rate is a phenomenon also described (Traulsen et al. 2009) for the system of Hauert et al. (2007). Also for this system, this effect of mutation is independent of interaction choice (compare Fig. 2b,c of Traulsen et al. 2009).

The results on invasiveness describe the advantage of the Out for Tat strategies as invaders under limited mutation (Fig. 2-3a,c). The advantages are highest at intermediate interaction choice payoff values, i.e., where interaction is attractive but not too attractive as an alternative to playing the PD game. The invasiveness of all conditional cooperators is highest in this range of  $O$ -payoffs (Fig. 2-3a,c) and this range coincides with the range where average cooperation is highest ( $\bar{C}$  around  $\bar{C}_{\max}$  in Fig. 2-1a,b,d). Hence, we explain this finding by the second route of indirect invasion, i.e., invasion of these strategies into populations dominated by loners (and cooperators), not by invasion of populations dominated by defectors. Furthermore, the conditional cooperators with the highest prevalence were almost always Tit for Tat analogues. In the case of limited mutation, we explain this observation with the higher invasibility of the Out for Tat strategies (Fig. 2-3b,d) that is due to certain strategies being effective in exploiting the Out for Tat strategies. These strategies are also contained in the behavioral variants regularly generated by finite mutation. This explains why certain Tit for Tat analogues are the most prevalent cooperators in the simulations with finite mutation. In our study, the advantage of the Out for Tat strategies as invaders is more than compensated by a disadvantage in withstanding invasions.

The high invasibility of the Out for Tat strategies (Fig. 2-3b,d) could be an artifact of our choice of strategy set. For example, the exploitation of our type of Out for Tat strategies by strategy *DCDD* is avoided by ‘grim trigger’ Out for Tat strategies that ‘grimly’ forego all future interactions after the opponent defected once. Hence, the weaknesses of our type need not be a characteristic of Out for Tat strategies. Interaction choice might be more efficient in promoting the evolution of cooperation with Out for Tat strategies that do not have the weaknesses of our type. The ‘grim trigger’ Out for Tat strategies are contained, e.g., in the set of strategies defined around the strategies which (can) condition on the previously received payoff. Each strategy from this set is determined by an initial action and a reaction to each of the four payoffs. Hence, this set contains  $(3 \times 3 \times 3 \times 3 =)$  729 strategies, a number that would be feasible for an analysis like ours. A study of this large set would allow a more comprehensive insight on the effect of interaction choice on the evolution of cooperation.

## 4.1 Conclusion

Under limited mutation and large  $N$ , we retrieve the positive effects of interaction choice on the evolution of cooperation in iterated PD games proposed by Batali and Kitcher (1995): conditions can be found where cooperation is more common with interaction choice than without and the effect of interaction choice on the evolution of cooperation was largest where defector-dominated populations constitute real invasion barriers for Tit for Tat (large  $N$  and limited mutation). However, under finite mutation this barrier was largely offset in our simulations. Continuous domination of conditional cooperators was – aside of invading loner-dominated populations – the main reason why the advantage of the Out for Tat strategies as invaders was hardly effective. Indeed, cooperation evolved also when other cooperators than the Out for Tat strategies dominate. Improved abilities as invader are only one element of success. What also counts, is how the Out for Tat strategies we considered withstand invasion. Possibly ‘grim trigger’ Out for Tat strategies differ in this respect and this is why we propose a more definitive analysis of the effects of interaction choice on the evolution of cooperation by studying strategy sets that include ‘grim trigger’ Out for Tat strategies.

## Appendix 2-1

In Fig. 2-2c, we provide an assessment if  $\bar{C}_{max} < \bar{C}_I$  or  $\bar{C}_{max} > \bar{C}_I$ . The assessment was performed using the following procedure. For a set of conditions  $\{R, S, T, P, r, N\}$ , the intervals  $[S, P]$  and  $[P, R]$  are both divided into 20 identical sections. The edge values of these subintervals are used for the set of  $O$  values. Per set of conditions, we run 8 replica simulations of iPD populations and 123 replica simulations of iPDI populations (3 per  $O$  value). For a set of conditions and for interaction choice payoff  $O'$ , the value  $\bar{C}_{O'}$  is the average execution of cooperation averaged over the three replicas. The value  $sd_{O'}$  is the corresponding standard deviation. The value  $\bar{C}_I$  is the average execution of cooperation averaged over the eight replica iPD simulations. Average cooperation in iPDI populations is considered significant lower than in the iPD populations if  $\bar{C}_{O'} + sd_{O'} < \bar{C}_I$  for all  $O'$ . Average cooperation in iPDI populations is considered significant higher than in the iPD populations if  $\bar{C}_{O'} - sd_{O'} > \bar{C}_I$  for at least one  $O'$ .

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