Resolving the iterated prisoner's dilemma: theory and reality

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Abstract

Pairs of unrelated individuals face a prisoner's dilemma if cooperation is the best mutual outcome, but each player does best to defect regardless of his partner's behaviour. Although mutual defection is the only evolutionarily stable strategy in one-shot games, cooperative solutions based on reciprocity can emerge in iterated games. Among the most prominent theoretical solutions are the so-called bookkeeping strategies, such as tit-for-tat, where individuals copy their partner's behaviour in the previous round. However, the lack of empirical data conforming to predicted strategies has prompted the suggestion that the iterated prisoner's dilemma (IPD) is neither a useful nor realistic basis for investigating cooperation. Here, we discuss several recent studies where authors have used the IPD framework to interpret their data. We evaluate the validity of their approach and highlight the diversity of proposed solutions. Strategies based on precise accounting are relatively uncommon, perhaps because the full set of assumptions of the IPD model are rarely satisfied. Instead, animals use a diverse array of strategies that apparently promote cooperation, despite the temptation to cheat. These include both positive and negative reciprocity, as well as long-term mutual investments based on 'friendships'. Although there are various gaps in these studies that remain to be filled, we argue that in most cases, individuals could theoretically benefit from cheating and that cooperation cannot therefore be explained with the concept of positive pseudo-reciprocity. We suggest that by incorporating empirical data into the theoretical framework, we may gain fundamental new insights into the evolution of mutual reciprocal investment in nature.

Introduction

Helping behaviours, where an individual increases the direct fitness of a recipient, have to be incorporated into evolutionary theory with its emphasis on individual reproductive success (Darwin, 1859). The basic condition under which altruistic helping is under positive selection has been formulated by the theory of inclusive fitness (Hamilton, 1964a,b), where altruism pays as long as the benefit to the recipient times the degree of relatedness between the actor and recipient is larger than the direct fitness cost to the actor. In contrast, although the inclusive fitness concept also describes mutual helping for mutual direct fitness benefits, the individual decision rules are very diverse as all interacting individuals are both actors and recipients, and appropriate actions may depend on the actions of partners.

In some cases, cooperation occurs because both cooperator and recipient experience immediate, direct benefits from the interaction ('by-product mutualism', Brown, 1983). In other cases, however, cooperative behaviour involves an initial reduction in pay-offs to the actor (West *et al.*, 2007; Bshary & Bergmüller, 2008). Under these circumstances, cooperative behaviour may best be viewed as an investment, where the long-term benefits of investing accruing to the actor should outweigh the initial costs if the behaviour is to persist (Bergmüller *et al.*, 2007; Bshary & Bergmüller, 2008). Broadly speaking, there are two routes by which an actor

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might recoup their initial investment. First, actors may benefit as a by-product of the recipient's self-serving responses ('positive pseudo-reciprocity', where 'positive' implies fitness benefits to the investor, Connor, 1986; Bergmüller *et al.*, 2007; Bshary & Bergmüller, 2008). The key distinction between positive pseudo-reciprocity and by-product mutualism is that the former requires initial investments, whereas the latter does not (Bergmüller *et al.*, 2007; Bshary & Bergmüller, 2008). Second, actors may benefit via a costly return investment ('positive reciprocity', Hume, 1739; Trivers, 1971). In either scenario, the future benefits may arise because of the actions of the initial recipient ('direct' positive pseudo-reciprocity or 'direct' positive reciprocity) or because of the actions of a third party ('indirect' positive pseudo-reciprocity – also called social prestige – Zahavi, 1995; Roberts, 1998; or 'indirect' positive reciprocity, Alexander, 1987; Nowak & Sigmund, 1998). Although there is now plenty of evidence for the existence of communication networks where bystanders eavesdrop on interactions (McGregor, 2005), we will focus on cases where investors benefit from the acts of the recipients because almost all empirical examples of cooperation have used this framework.

Over the last decade, several authors have proposed that the vast majority of empirical examples of investments in nature fit the concept of positive pseudo-reciprocity, whereas proposed cases of reciprocity have been met with scepticism (Hammerstein, 2003; Stevens & Hauser, 2005; Stevens *et al.*, 2005; Henrich & Henrich, 2007; Clutton-Brock, 2009; Russell & Wright, 2009; Connor, 2010). Translated into game-theoretic pay-off matrices, solutions based on positive pseudo-reciprocity mean that the pay-offs fit the 'prisoner's delight' game (Binmore, 2004), where cooperative behaviour is the best option for each partner. In contrast, reciprocity has been based on the iterated prisoner's dilemma (IPD) game, where defecting is dominant over cooperating in each single round. Despite the widespread scepticism regarding the IPD framework, several recent empirical studies claim to provide evidence for reciprocity. Our aim is to assess both the likely pay-off matrix and the strategies employed by the animals in these studies to re-evaluate the potential importance of reciprocity for the evolution of cooperation.

The prisoner's dilemma – theory

The problem of reciprocal investments has been formalized by the prisoner's dilemma. The prisoner's dilemma describes a theoretical situation involving two players who each have the option to cooperate or defect (Luce & Raiffa, 1957; Fig. 1). Although collective pay-offs are greatest when both players cooperate, each player gains a higher individual pay-off from defecting irrespective of the partner's action. Conversely, an individual that cooperates when his partner defects experiences the

Player 1→	Cooperate	Defect
Player 2↓		
Cooperate	*R, R*	*T, S*
Defect	*S, T*	*P, P*

Fig. 1 The pay-off matrix (Player 1, Player 2) of a two-player game where each player has two behavioural options. In the prisoner's dilemma game, the sucker's pay-off (S), the worst pay-off in the game, is experienced when a player cooperates but his partner defects. P is the pay-off each player receives for mutual defection. R is the reward for mutual cooperation, and T, the highest pay-off in the game, is the temptation to defect when your partner cooperates. Thus, overall it holds that $S < P < R < T$. In the prisoner's delight game, the pay-offs change so that $R = S > T = P$, meaning that it is best to cooperate regardless of the partner's behaviour.

lowest pay-off in the matrix: the 'sucker's pay-off'. Mutual defection therefore represents both the Nash equilibrium (Nash, 1951) and the only evolutionarily stable strategy (ESS, Maynard-Smith, 1982) in one-shot interactions (Luce & Raiffa, 1957). In iterated games, defection is still an ESS but, under certain conditions, cooperative strategies can also invade. This is because, if players expect to meet again in subsequent rounds, they can adapt their behaviour to the behaviour of their partner in previous rounds: they can reciprocate (Hume, 1739; Trivers, 1971). Game theoreticians in economics realized in the 1950s that rational agents could use several strategies to achieve cooperation if the game consists of an infinite number of rounds (*folk theorem*, discussed in Binmore, 1998, 2005). Evolutionary theory subsequently contributed by placing the emphasis on strategies with increased ecological validity (Binmore, 1998) and by introducing uncertainty and errors. One particularly famous, conditionally cooperative strategy that has been proposed to yield stable cooperation in the IPD is tit-for-tat, which starts out cooperating and thereafter responds to whatever its partner did in the previous round (Axelrod & Hamilton, 1981). Adding a probability of errors yielded some slightly different dominant reciprocal strategies (e.g. contrite tit-for-tat, Sugden, 1986; Boyd, 1989; generous tit-for-tat, Nowak & Sigmund, 1992; Pavlov, Nowak & Sigmund, 1993). Tit-for-tat and these related strategies are similar in that behaviour is typically predictable and information about the last round is used to inform current decision-making. As such, these strategies have been referred to as 'cost-counting' or 'bookkeeping' strategies (Clutton-Brock, 2002, 2009).

The prisoner's dilemma – reality

Following these early theoretical developments, empiricists tried to find scenarios in the natural history of their study species that fitted the assumptions of theoretical models or designed experiments that were explicitly based on key assumptions of the theory (e.g. Fischer,

1980; Wilkinson, 1984; Milinski, 1987; Dugatkin, 1988). However, despite the apparent simplicity of the decision rules predicted by theoreticians, empirical evidence showing that animals use these rules remains rare and controversial. As a consequence, numerous authors have proposed that neither the IPD nor its many extensions (reviewed in Dugatkin, 1997) are useful for investigating cooperation and that reciprocal investment is likely to be rare in nature (Hammerstein, 2003; Stevens & Hauser, 2005; Stevens *et al.*, 2005; Henrich & Henrich, 2007; Clutton-Brock, 2009; Russell & Wright, 2009; Connor, 2010). The main arguments of these authors are that animals are unlikely to use tit-for-tat (or related) strategies because these strategies are cognitively rather demanding, and that simpler concepts like positive pseudo-reciprocity may often apply. In contrast, others have argued that the paucity of evidence for bookkeeping strategies may reflect the problems in defining the exact pay-offs of cooperating and defecting, as well as the empirical difficulties associated with demonstrating contingency of behaviour (McElreath *et al.*, 2003). Mismatches between theory and reality may also arise because the basic assumptions of the IPD model are rarely met. For example, the IPD model assumes that actors are forced to play with the current partner and only have the option either to cooperate or to defect. In reality, however, individuals may also employ other behaviours, such as punishment, to sustain mutual reciprocal investments, and may choose to terminate the interaction or select another partner (Noë, 2001; Cant & Johnstone, 2006). Furthermore, choosing to cooperate or defect need not be an all-or-nothing decision: in some situations, investment may be a continuous parameter rather than a binary choice (Roberts & Sherratt, 1998; Killingback *et al.*, 1999; Killingback & Doebeli, 2002). The existence of tit-for-tat, or related, strategies would then be hard to demonstrate because it is not intuitively obvious what constitutes a cooperative or a defective move. In IPD games, it is also commonly assumed players interact in sequential rounds where units of the same currency and magnitude are exchanged. This may also be improbable. For example, in several primate species, individuals reportedly exchange grooming for coalitionary support and other benefits (De Waal & Luttrell, 1988; Barrett & Henzi, 2001; Brosnan & De Waal, 2002; Gumert, 2007; Schino, 2007). Here, it would be difficult to demonstrate that individuals were using a precise accounting mechanism because it is not immediately obvious how to translate these various forms of investment into a single currency. Even if this were possible, it is doubtful that any nonhuman species would have the cognitive capacity to make these calculations and to remember the precise outcomes of interactions with several interaction partners over varying timescales (Stevens *et al.*, 2005).

Rather than relying merely on evidence for tit-for-tat (or related bookkeeping strategies) to evaluate the usefulness of the IPD framework, we focus on the pay-off consequences of cooperating and defecting depending on the partner's behaviour. To assess whether a situation resembles an IPD, it is necessary to consider whether players could theoretically benefit by exploiting cooperative partners, after having accounted for potential indirect fitness benefits of helping owing to relatedness. Where a player gains the highest fitness benefit from investing in a cooperative partner, then the situation does not resemble an IPD. Under these circumstances, the player only chooses to invest when that behaviour is ultimately self-serving and thus there is no temptation to cheat. Conversely, where players could theoretically gain the highest pay-off from exploiting a cooperative partner, then the situation has the key feature of a prisoner's dilemma in that individuals will be tempted to cheat ($T > R$, Fig. 1). As long as this latter condition is met, then cooperative behaviour must be an investment (it reduces immediate benefits relative to not cooperating) where net future benefits are contingent on (positive or negative) reciprocal return investments, leading to conditional strategies based on reciprocity.

Alternative strategies promoting reciprocal investment in iterated prisoners' dilemmas

Here, we discuss several recent publications, each claiming to provide evidence for cooperation based on reciprocal investment. For each case, we ask whether key features of interactions can be properly described with a game that resembles an IPD and, if so, what decision rules yield cooperative solutions.

Positive reciprocity

First, we highlight the example of predator inspection in fishes, which has been proposed to fit the positive pseudo-reciprocity concept (Hammerstein, 2003; Clutton-Brock, 2009) rather than the reciprocity concept as initially suggested (Milinski, 1987; Dugatkin, 1988; Milinski *et al.*, 1990). Under the positive pseudo-reciprocity concept, we would expect that neither fish can benefit from cheating by lagging behind during predator inspections with a cooperative partner. Instead, we would expect that the best (self-serving) response to a partner's investment (approach the predator) would be to approach a bit further than the partner as an optimal solution to the trade-off between information gain and predation risk, which enables the partner to approach even more closely in return and so on. In contrast to these predictions, the finding that groups of fish approach predators more closely than singletons suggests that there is no net benefit of predator inspection to singletons below some critical approach distance (Pitcher *et al.*, 1986), and it has also been demonstrated that fish can benefit by lagging behind a cooperative partner

(Milinski *et al.*, 1997; Krause *et al.*, 1998) and that a fish's tendency to approach a predator is often contingent on its partner's behaviour (Dugatkin, 1988, 1991; Milinski *et al.*, 1990; Külling & Milinski, 1992). In a recent study, Croft *et al.* (2006) established that female guppies (*Poecilia reticulata*) formed strong social associations with certain other females and were more likely to engage in predator inspection with these stable partners than with other fish in the population. Furthermore, dyads with the strongest association strength were more cooperative during predator inspections (more often exchanged the leading, more dangerous position while approaching the predator, Croft *et al.*, 2006). It has not yet been demonstrated that cheating by the preferred partner affects the cheated individual's partner preference. Nevertheless, these latter findings support two of the key theoretical predictions concerning the evolution of cooperation via reciprocal investments, namely that individuals repeatedly encounter one another and that cooperative individuals preferentially assort with cooperative partners, which may minimize the costs of defection (see Dugatkin, 1997; Wilson & Dugatkin, 1997). In addition, the results clearly suggest that cooperative behaviour cannot fully be understood without the concept of partner choice in a biological market (Noë, 1990, 2001; Noë *et al.*, 1991).

Perhaps, the most important open question is how pay-offs from being cheated by a laggard in a pair relate to outside options. The most obvious outside option is to perform solitary predator inspections, which is known to occur (see Magurran & Pitcher, 1987). If solitary inspections yield a higher pay-off than inspections with a laggard that would provide strong evidence for reciprocal solutions but even if the reverse was true, the demonstration that laggards have lower predation risk (Milinski *et al.*, 1997) shows that there are conflicts that do not fit the concept of positive pseudo-reciprocity. An alternative outside option is to switch to another partner for future inspections. Partner switching ends the game with the current partner and is hence not a reciprocal strategy but a sanction (Herre *et al.*, 1999; Kiers *et al.*, 2003). Unlike punishment or reciprocal defection, the controlling act of switching does not cause the partner to become more cooperative in future because, by definition, there is no future to the partnership. Nevertheless, we stress that introducing the option to switch only affects the strategic repertoire but not the pay-off matrix for the interaction itself. In conclusion, the findings so far strongly suggest that individuals can benefit from cheating a cooperative partner and that stable cooperation during predator inspection in fishes relies on conditionally cooperative strategies.

The pay-offs experienced by individuals while mobbing predators are likely to be very similar to those that occur during predator inspections. Specifically, approaching and harassing a predator imposes costs on the mobber (in terms of opportunity costs, energetic expenditure and increased risk of predation, Curio *et al.*, 1983; FitzGibbon,

1994; Regelmann & Curio, 1986; Sordahl, 1990). Individuals might personally benefit from mobbing predators if this allows them to gain information about the predator (Curio, 1978; FitzGibbon, 1994). However, at least some of the proposed benefits of mobbing (including alerting conspecifics to predator presence and the predator leaving the vicinity) also accrue to individuals that do not participate (Curio, 1978) meaning that this situation often has the same pay-offs as an *n*-player prisoner's dilemma, where individuals can theoretically benefit by not participating. Several lines of evidence exist demonstrating that individual decisions to approach and harass predators are contingent on the behaviour of others (Curio & Regelmann, 1985; Regelmann & Curio, 1986; FitzGibbon, 1994). More recently, the decision rules underpinning contributions during predator mobbing have been experimentally investigated. Using trios of pied flycatcher (*Ficedula hypoleuca*) pairs, Krams *et al.* (2008) demonstrated that neighbours behave reciprocally during sequential predator-mobbing events. In this study, nest boxes were established in a triangular distribution so that each pair's nest was equidistant from its two neighbours' nests. An artificial predator was then placed at A's nest whereas B was temporarily removed from the territory. Pair B were therefore unable to mob the predator at A's nest, while C could help A. After receiving help from C but not B, pair A were more likely to mob predators at C's nest than at B's nest. Furthermore, if the predator at C's nest was removed, such that A could choose to help B without foregoing delivering aid to C, A still refused to help B. Thus, pairs appeared to be sensitive to their neighbours' behaviour in previous mobbing situations and only helped those neighbours that helped them in the past, whereas current mobbing behaviour of neighbours did not play a role. This represents a cooperative solution to an IPD that appears to be based on a form of positive reciprocity (Wheatcroft & Price, 2008).

Some authors disagree with this interpretation. In a subsequent rebuttal, Russell & Wright (2009) argued that pairs gain a net benefit from joining neighbours to mob predators because predators in the vicinity are also a threat to their own brood. Thus, in this situation, the benefit of investing in mobbing is not contingent on future reciprocation, and the results can be explained by positive pseudo-reciprocity (Russell & Wright, 2009). Along with Wheatcroft & Krams (2009), we disagree with this rebuttal. If each pair could gain the highest pay-off from mobbing a predator regardless of what its neighbours did, then each pair should mob predators regardless of their neighbours' previous behaviour. Russell & Wright (2009) argue that the reason that A mobbed at C's, but not B's, nest is that pair A have no experience of mobbing predators with B and therefore assume that pair B do not mob predators. As mobbing in smaller groups is likely to involve higher risks of injury and/or death (Hamilton, 1971), pair A might not risk

mobbing predators at B's nest if they do not expect B to join in. Again, however, the data do not seem to support this assertion. In the experiment, pair A decided not to mob at B's nest while B were already mobbing a predator. It therefore seems unlikely that A's decision not to help was based on an expectation that pair B would not mob predators. To evaluate this criticism, the experiment could be modified to allow A experience of mobbing both with B and with C, but to then prevent one of the pairs from assisting A. This design would help to disentangle these currently confounding explanations. In addition, to correctly interpret the results of this study, it will be necessary to better define the fitness pay-offs associated with mobbing and not mobbing predators at neighbours' nests in this species. Based on the available evidence so far, we cannot properly evaluate the animals' decision rules. To demonstrate a tit-for-tat solution, it would also be necessary to perform a further experiment where, after a round of defection and counter-defection, one pair helps the other and then to find that the recipient pair is willing to 'forgive' earlier defection by helping in return. Nevertheless, we argue that the results as they currently stand are strongly suggestive of conditional cooperation and hence fit an IPD scenario.

Laboratory experiments using Norway rats (*Rattus norvegicus*) have also provided convincing evidence of positive reciprocity in a nonhuman species. In a recent experiment, Rutte & Taborsky (2008) placed pairs of rats in cages that were each divided into two compartments by a wire mesh. Each rat was sequentially given the opportunity to pull a stick that moved a platform baited with food into its partner's half of the cage. Thus, the pulling rat paid a cost for its partner to receive a food benefit. Each rat's propensity to pull was tested, first for a cooperative partner and then for an uncooperative partner. The results showed that rats were more likely to pull the stick to provide for a partner that had pulled for them in previous interactions. While suggestive of conditional cooperation, decisions were not based on precise accounting because rats often pulled the stick, even for uncooperative partners (Rutte & Taborsky, 2008). In a subsequent study, Viana *et al.* (2010) designed an experiment where rats received pay-offs (in food or tail pinches) that exactly fitted the IPD pay-off matrix. The authors found that rats strategically modified their behaviour according to the strategy played by their partner in an IPD game. When faced with a stooge that played tit-for-tat, rats were more likely to cooperate than when faced with a stooge that played a pseudo-random strategy (pseudo-random stooges cooperated, unconditionally, with 50% probability in each round) (Viana *et al.*, 2010). The fact that rats' tendency to cooperate was contingent on the partner's behaviour is difficult to reconcile with the positive pseudo-reciprocity concept. Instead, these studies indicate that rats are able to find stable cooperative solutions to an IPD based on positive reciprocity.

Negative reciprocity: reciprocal investment under the threat of punishment

The original prisoner's dilemma model assumes that interactions are symmetrical in that both players have the same behavioural options (cooperate or defect). In reality, however, this assumption is rarely fulfilled. Instead individuals often differ, sometimes markedly so, in their resource holding potential or dominance. In the context of an IPD-like game, such differences may be important because dominant players may be able to punish defecting partners. Punishment has similar pay-offs to cooperating: it involves a short-term investment that is only repaid if the punished individual responds by re-investing in the punisher (cooperating) (Clutton-Brock & Parker, 1995). Empirical evidence that punishment may promote mutual reciprocal investments in a situation that resembles an IPD comes from work on cleaner fish (*Labroides dimidiatus*). These fish hold small territories on coral reefs and provide a cleaning service to other reef fish (clients) by removing skin ectoparasites (Grutter, 1996). Although cleaners gain nutritional benefits from eating client ectoparasites, they prefer to eat client mucus (Grutter & Bshary, 2003), resulting in a conflict between cleaner and client. Cleaners regularly cheat clients, and clients often terminate the interaction in response (Bshary & Grutter, 2002). Cleaners occasionally work together in mixed-sex pairs to clean a joint client (Bshary *et al.*, 2008). This situation resembles an IPD for the male and female cleaner fish, because only one cleaner can gain the benefit associated with biting the client, although both individuals share the cost of the interaction being terminated when the client is bitten. A game theoretic analysis demonstrates that mutual defection is one ESS for almost the entire parameter space (Bshary *et al.*, 2008). However, cleaner fish pairs find a cooperative solution. This solution is not based on reciprocal alternation of mucus feeding. Instead, male cleaners, that are larger than and dominant to their female partners, aggressively chase females that cheat in joint inspections (Bshary *et al.*, 2008). As a consequence, females behave more cooperatively (feed more against their preference) in future interactions (Raihani *et al.*, 2010) and, during pair inspections, males can cooperate at a very similar level as when they inspect alone (Bshary *et al.*, 2008). Cooperative outcomes are thus conditional, depending not on males 'rewarding' cooperative females but on males reducing the pay-offs of cheating females. By working together rather than alone, cleaners may gain access to a greater number of clients because clients preferentially visit cleaning stations with pairs of cleaner fish (Bshary & Schäffer, 2002). Furthermore, as females are punished into behaving very cooperatively but not forced into joint client inspections, we can assume that the usual outcome of joint inspections is mutually beneficial for both males and females and therefore rule out the possibility that females are coerced into a

suboptimal strategy. This is only possible because, unlike the standard prisoner's dilemma model, in this system, to cooperate is not an all-or-nothing event. Instead, cleaners can choose a variable level of investment that may be expressed as the ratio of parasites eaten divided by the number of mucus bites (Bshary *et al.*, 2008).

'Friendships': reciprocal investment based on emotional bookkeeping

In other species, reciprocal investment may occur without precise bookkeeping strategies. This might be particularly common in species that live in socially complex environments, where individuals interact with several different partners and trade different commodities and resources (Cheney *et al.*, 2010). Under these circumstances, investments are not easily converted into one universal currency and return investments may often be delayed. For example, in several nonhuman primate species, positive correlations exist between grooming and support received in agonistic encounters, food sharing, tolerance, sex and access to infants (De Waal & Luttrell, 1988; Barrett & Henzi, 2001; Brosnan & De Waal, 2002; Gumert, 2007; Schino, 2007), which has prompted the suggestion that grooming may be exchanged either for itself or for several other benefits in primate societies. Support for this idea comes from experiments where the conditional nature of the interaction can be explored. For example, in an experiment using captive long-tailed macaques (*Macaca fascicularis*), Hemelrijk (1994) showed that individual A was more likely to support B after B had groomed A, but not when A had groomed B or when no grooming had occurred. This study demonstrates that, at least in this species, support in agonistic encounters is contingent on previous grooming received. In a similar study using wild baboons (*Papio hamadryas ursinus*), Cheney *et al.* (2010) showed that females were more likely to approach a conspecific following a playback of this individual's recruitment call if they had had a prior grooming interaction with the caller, rather than a prior agonistic interaction with the caller. Because approaching in response to hearing a recruitment call is indicative of willingness to support the caller in an agonistic interaction, this finding was interpreted as suggestive evidence for contingent positive reciprocity in baboons.

Despite evidence for conditional behaviour in some contexts, however, the vast majority of studies in nonhuman primates fail to demonstrate that defection by one individual leads to reciprocal defection from its partner. Here, along with others (Gomes *et al.*, 2009; Schino *et al.*, 2009), we stress the importance of considering the time frame over which reciprocal investment can occur. Considering too short a time frame can cause researchers to erroneously rule out positive reciprocity, if return investments occur over a longer time frame than that considered (Gomes *et al.*, 2009). This is especially pertinent when individuals do not reciprocate in the

same currency that they received. For example, grooming can only be reciprocated with support when support is needed. As such, trading grooming for support will almost inevitably involve a temporal delay. Rather than immediate, sequential reciprocal investments, it has been proposed that nonhuman primates typically engage in long-term patterns of exchange with familiar partners (De Waal & Luttrell, 1988; De Waal, 2000; Kappeler & Van Schaik, 2006), in much the same way as it is proposed that humans invest in friends (Silk, 2003; Hruschka & Henrich, 2006; Majolo *et al.*, 2006; Henrich & Henrich, 2007; Gomes *et al.*, 2009). So-called 'attitudinal' reciprocity (De Waal, 2000) differs from cost-counting or 'calculated' reciprocity (De Waal & Luttrell, 1988) in that the former depends on an animal having a positive emotional attitude towards an interaction partner, whereas the latter requires individuals to remember who did what and when. As attitudinal reciprocity is thought to be less cognitively demanding than calculated reciprocity, it might therefore serve as a simpler proximate mechanism for sustaining mutual investment in interactions where the return investment is likely to be delayed and/or in a different currency (Gomes *et al.*, 2009; Schino & Aureli, 2009; Schino *et al.*, 2009).

Nevertheless, we note that the concept of friendship or attitudinal reciprocity still implies conditionality of behaviour that needs to be demonstrated. Cheating by one individual may not immediately lead to cheating by the partner, but prolonged cheating should lead to a degradation of the friendship and a reorientation towards alternative allies. Thus, as in the predator inspection example, partner choice (negative pseudo-reciprocity) may play an important role in stabilizing reciprocal investments but this remains to be demonstrated. Furthermore, if there are no obvious alternative allies in the group, partners might be stuck with each other and their fitness then becomes interdependent (Roberts, 2004). Cooperation among interdependent partners is best explained with the concept of positive pseudo-reciprocity rather than with the reciprocity framework. Thus, the verdict seems to be quite open at the moment.

Unconditional cooperation (or positive pseudo-reciprocity?)

As a final empirical example, we consider the case of pairs of zebra finches (*Taeniopygia guttata*) that cooperate more or less unconditionally when paired with their familiar partner in a situation with an IPD pay-off matrix, while being more likely to defect when interacting with an unfamiliar conspecific (St-Pierre *et al.*, 2009). In this study, captive zebra finches were placed in a choice chamber where they could choose to perch in front of either a high or a low cup. Initially, both birds could gain the highest pay-off (in grains of food) from perching in front of the higher of the two cups (the 'by-product mutualism' treatment). In a subsequent treatment, the

pay-off matrix was then changed to approximate an IPD, such that each bird could gain the highest pay-off from perching in front of the lower cup (defecting) regardless of what its partner chose. Although zebra finches were equally likely to cooperate with both familiar and unfamiliar conspecifics in a game with a by-product mutualism pay-off matrix, the strategy in the game with an IPD pay-off matrix depended on whether the birds were playing with their social partner or an unfamiliar conspecific. With unfamiliar partners, zebra finches initially tended to cooperate; however, cooperation quickly broke down if one finch defected. When interacting with their social partner, however, zebra finches seemed to 'forgive' occasional defection by their partner, with the result that individuals invested apparently unconditionally in one another (St-Pierre et al., 2009).

These results prompt us to ask why familiarity with the social partner should have such a large bearing on decision rules in this experiment. One possibility is that because male and female social partners work together during a breeding season to raise offspring (Zann, 1996), each individual's fitness may be tied in with the survival of its social mate because reproductive success depends on biparental care ('interdependence', Roberts, 2004). In the most extreme case, the death of one partner, the current reproductive success of the surviving individual would be severely affected (S. Griffith, unpublished). Under these circumstances, an individual's best option might actually be to opt for the cooperative three grain/three grain solution because the two extra grains to be gained from cheating would cause a reduction in direct fitness owing to the losses incurred by the partner. Thus, individuals might derive benefits from investing in their social partner that are not contingent on any costly return investment, arising instead by enabling a self-serving response from their partner – to provide better care for the joint offspring. If this were the case, then the results obtained in this study might best be explained with the concept of positive pseudo-reciprocity, rather than positive reciprocity.

Conclusion and future directions

Defending the prisoner's dilemma pay-off matrix

The results from these empirical studies may not decisively show that individuals use tit-for-tat (or related) decision rules. However, we argue that the aspect of mutual investment that is contingent on the partner's return investment behaviour cannot be dismissed in most presented studies. Consequently, we argue that it is important to distinguish between the IPD-type problem (that cooperation has to be based on mutual investments) and precise bookkeeping solutions. The latter may indeed by rare whereas the former more abundant than currently appreciated. We think that several scientists currently dismiss reciprocal investment too easily

just because evidence for tit-for-tat (or related) strategies is rare and often debatable. Rather than considering alternative decision rules that allow cooperative solutions to an IPD-type situation, these authors tend to propose that the pay-off matrices for the disputed case studies do not fit the prisoner's dilemma game but the prisoner's delight game (Binmore, 2004) and cooperation can therefore be explained with the concept of positive pseudo-reciprocity.

We think that such reinterpretation pushes the concept of positive pseudo-reciprocity to a point where its enormous usefulness (see Bergmüller et al., 2007; Bshary & Bergmüller, 2008) is diminished. This is because the concept of positive pseudo-reciprocity should not be seen simply as a null hypothesis. Rather, its original definition includes a key assumption that has to be demonstrated: the investment must *enable* the recipient to perform self-serving behaviour that benefits the investor as a by-product (Connor, 1986). If this investment is necessary to enable recipients' self-serving responses, then it follows that actors cannot benefit from 'cheating' by withholding the investment. Thus, under the positive pseudo-reciprocity concept, individuals cannot benefit from reducing investment below the optimal cost/benefit ratio because this, by definition, would reduce the benefits they accrue as a by-product (Bshary & Bronstein, 2011). This assumption does not hold for several examples that are now explained with the concept of positive pseudo-reciprocity. In pied flycatchers, it not the help received during previous encounters with predators that *enable* pairs to mob predators at a neighbour's nest; rather, it is the attention of each party towards its partner's behaviour that necessitates reciprocal investments. Similarly, in primates, it is not receiving grooming that *enables* the partner to subsequently defend the groomer nor does defence enable a partner to give grooming. In a long-term interdependence scenario, one could argue that repeated failure to help a partner may eventually reduce the partner's rank or survival and hence prevent it from providing return services, leading to self-serving mutual support. If relationships are short term, or if partner switching is an option (i.e. long-term interdependency is low), it is mutual conditionality that necessitates investment. Mutual investments that arise owing to partner vigilance fit a prisoner's dilemma pay-off matrix. The fact that the best response to a conditional investor is to invest in return should not be confounded with positive pseudo-reciprocity; it is the essence of cooperation based on watchful strategies.

Determining pay-off matrices

Having defended the general idea of reciprocity, we agree that a key challenge has been, and will remain to be, the determination of the exact pay-off matrix (Dugatkin, 1988). For example, we note that a pay-off matrix exists where players do best to exploit cooperative partners, but

where the best response when faced with a cheating partner is to cooperate (this is called the snowdrift, hawk-dove or chicken game, Maynard-Smith, 1982; Sugden, 1986; Doebeli & Hauert, 2005). Finding ways to distinguish between snowdrift games and games with IPD pay-offs will remain a key challenge for empiricists. Determining precise pay-off matrices will be even more complex in many cases of intra-specific cooperation where individuals are related, meaning that indirect fitness benefits also have to be incorporated for the calculation of pay-offs. While in this context the advantages of controlled laboratory conditions cannot be dismissed, we strongly advocate designing ecologically valid experiments wherever possible (e.g. Milinski, 1987; Krams *et al.*, 2008; Cheney *et al.*, 2010). Presenting captive animals with arbitrary tasks to test cooperative tendencies (e.g. Hauser *et al.*, 2003; Rutte & Taborsky, 2008; St. Pierre *et al.*, 2009; Viana *et al.*, 2010) may mean that the biological significance of positive results is hard to interpret. At the same time, failure to provide evidence for cooperation in artificial reciprocity tasks (e.g. Stevens & Stephens, 2004; Melis *et al.*, 2008; Brosnan *et al.*, 2009) does not necessarily mean that reciprocity would be similarly absent under natural conditions. A profitable approach in future studies may be to carefully consider whether selection is likely to have favoured reciprocity in that species and, if so, under which circumstances it may be found, before designing experiments that test for reciprocity in precisely that context.

It is ironic that of the two recent studies that seemed to have precisely used the pay-off matrix of an IPD game, one of these (the study on the zebra finches) may have yielded results that are best described with mutual positive pseudo-reciprocity. In theoretical models, the numbers are a measure of changes in fitness, whereas the same numbers in food units do not necessarily translate into similar changes in fitness if the fitness of interacting partners is interdependent. Roberts (2004) remarked that the aspect of interdependency could be captured with a reinterpretation of the '*r*' in Hamilton's formula (rB − C > 0): as an approximation, helping an unrelated individual could be beneficial if the benefits for the recipient times the degree of dependency, '*d*', is higher than the cost (i.e. dB − C > 0). If dependency interpreted in this way is high, food pay-offs that seem to fit an IPD pay-off matrix would not properly reflect fitness consequences for interdependent partners. Thus, it may well turn out that in the zebra finch example, pair partners would (under natural conditions) play a prisoner's delight game, whereas unfamiliar individuals would experience an IPD (yielding mutual defection, at least in the laboratory experiment).

Perspective-taking and pay-off matrices

To determine whether an interaction is best explained with the concept of positive pseudo-reciprocity or with the concept of positive reciprocity, we advise considering the pay-offs that accrue from investing and not investing (cheating) to each player in the interaction. In many cases, it may be the case that one player can benefit from cheating whereas the partner cannot. Where one or both players can benefit from cheating, then watchful strategies are likely to evolve. Conversely, if neither player can benefit from reducing or withholding investment, then we may expect unconditionally cooperative strategies to evolve. Thus, we emphasize that the concept used to explain the interaction may depend on which player's perspective is taken. We outline this viewpoint with some empirical examples.

The interaction between seed-producing plants and the seed-eating animals that disperse the seeds (Herrera, 2002) may be explained with the concepts of positive pseudo-reciprocity or by-product mutualism, depending on whether one takes the perspective of the plant or the animal. The plant invests resources into making seeds that are attractive to some animals. This enables a self-serving response from the animal that eats the seed and later disperses it via defecation. Because the plant makes an initial investment in the interaction, but there is no potential to benefit from reducing this investment, we can explain the plant's investment with the concept of positive pseudo-reciprocity. The animal, on the other hand, simply eats the seed and later defecates: there is no investment and the benefits to the plant are a by-product of the animal's own self-serving behaviour. Thus, from the animal's point of view, seed-dispersal behaviour is an instance of by-product mutualism.

As with the case above, some interactions may be explained with the concept of positive pseudo-reciprocity or with the concept of positive reciprocity, depending on which player's perspective is taken. Possible examples include cleaner fish interacting with predatory clients (e.g. giant moray eels, *Gymnothorax javanicus*). Clients approach cleaning stations when they are parasite ridden. Thus, although predatory clients could potentially eat cleaners, they benefit from foregoing a foraging opportunity because this enables cleaners to perform the cleaning service not only now but also in the future (Trivers, 1971). The interesting twist is that whereas predatory clients benefit in the long run from enabling a cooperative cleaner to continue its inspections, the cleaner's pay-offs are different as it is tempted to cheat by biting clients. Thus, it seems that clients cannot benefit from exploiting cooperative cleaners, but cleaners could benefit from exploiting cooperative clients. To ensure cooperative behaviour from the cleaners, predatory clients must therefore adopt a watchful strategy: they should try to eat cheating cleaners (although they are not otherwise tempted to cheat). Although the exact pay-offs for cleaner–predator interactions are yet to be evaluated, our predicted pay-off structure makes the case that investments that are explained by positive pseudo-reciprocity can, under specific circumstances, be coupled

with watchfulness if one player is tempted to cheat. Similar pay-offs may exist in some ant protection mutualisms (reviewed in Bshary & Bronstein, 2004) where the ants are potential predators of their partner species, as in the case of aphids or homopterans. In these mutualisms, ants face similar pay-offs to the predatory clients in the previous example. They invest by letting the partner species live, which is ultimately self-serving as long as the partner produces enough food. As was the case with the cleaner fish, however, the partner species may be tempted to defect because they often benefit from producing less or lower quality food for the ants. To ensure cooperation, the ants must therefore adopt a watchful strategy: they defect by eating the partner if the partner does not invest enough.

It may be the case that several empirical examples that have been explained with the concept of positive pseudo-reciprocity (and hence were assessed as a prisoner's delight game) may only have accounted for the perspective of one player. The partner, on the other hand, may experience a prisoner's dilemma pay-off matrix. We suggest that failure to distinguish between the different pay-offs accruing to players may result in the interaction being explained with the concept of positive pseudo-reciprocity, when the assumptions of this concept are in fact only met from one player's perspective. We advocate considering the pay-offs accruing to each partner in an interaction to determine whether there is a temptation for one or both players to cheat.

Summary

1 Although it is unlikely that the entire set of assumptions of the IPD will be fulfilled in any real-world interaction, the assumptions about the pay-off matrix may apply to several real-world situations.
2 Cooperative solutions to an IPD-like pay-off matrix require positive or negative reciprocity (or negative pseudo-reciprocity if partner choice is possible).
3 Cost-counting strategies, like tit-for-tat, as solutions to an IPD-like pay-off matrix seem to be rare outside humans. However, the popular concept of positive pseudo-reciprocity cannot be applied to such a pay-off matrix and instead fits the prisoner's delight pay-off matrix.
4 Pseudo-reciprocity is not a null hypothesis to explain investments but requires researchers to demonstrate that the investment by one player *enables* the partner to perform a self-serving response.

Acknowledgments

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Glossary

Altruistic behaviour: behaviour that reduces the direct fitness of the actor but increases the direct fitness of the recipient.

Attitudinal reciprocity: mutual exchange of investments based on positive emotional attitudes towards partners, rather than a mental score sheet of who did what and when.

By-product mutualism: a cooperative interaction without investments towards other individuals.

Calculated or cost-counting reciprocity: mutual exchange of investments based on precise accounting of who did what and when.

Coercion: a player is forced into a social interaction with another player that yields a lower pay-off than not interacting at all.

Cooperation: the outcome of a social interaction between two or more members of the same species that results on average in net direct fitness benefits to each player.

Defection: behaviour that confers increases immediate pay-offs to the defector but which reduces the immediate pay-offs of the partner.

Evolutionarily stable strategy: a strategy which, if adopted by a population of players, cannot be invaded by another, initially rare strategy.

Glossary (continued)

Iterated prisoner's dilemma: identical to the one-shot prisoner's dilemma but players encounter the current partner again with a nonzero probability.

Nash equilibrium: a set of strategy choices adopted by players in a game of two or more players where each player knows the equilibrium strategies of the other players and no player can profit from changing his own strategy.

Negative pseudo-reciprocity (sanctions): occurs when the failure to invest by one player enables the partner to make a self-serving response that harms the noninvesting player as a by-product. A good example is switching partners in response to cheating from the current partner.

Negative reciprocity (punishment): behaviour that reduces the immediate pay-offs of the actor and the recipient. The punisher's pay-off losses can be regained if the punished individual modifies its behaviour in future interactions in a way that increases the punisher's pay-offs.

One-shot prisoner's dilemma: a theoretical situation involving two players who each have the option to cooperate or to defect. Defection always yields a higher pay-off than cooperating irrespective of the partner's behaviour.

Positive pseudo-reciprocity: an investment by one individual *enables* or *enhances* a self-serving response from the recipient. The self-serving response benefits the investor as a by-product.

Positive reciprocity: in investment by one individual precipitates a costly return investment from the recipient. Benefits to investors are contingent on receiving return investments from recipients.

Prisoner's delight: a theoretical situation where each player gains the highest pay-off from cooperating regardless of the partner's behaviour. The highest pay-off in the matrix occurs when both players cooperate.