Published in Ethology 117, issue 4, 271-283, 2011
which should be used for any reference to this work

A General Scheme to Predict Partner Control Mechanisms in Pairwise Cooperative Interactions Between Unrelated Individuals

Redouan Bshary* & Judith L. Bronstein†

* Institute of Biology, University of Neuchâtel, Emile-Argand 11, Neuchâtel, Switzerland
† Department of Ecology and Evolutionary Biology, University of Arizona, Tucson, AZ, USA

Abstract

Recent years have seen an explosion in the diversity of partner control mechanisms hypothesised to stabilise cooperative behaviour among unrelated individuals. Game theory suggests numerous strategies, each with specific decision rules that allow cooperators to control a non-contributing partner. This diversity of hypothetical strategies seems likely to reflect diversity in the types of intraspecific cooperation and interspecific mutualism that exist in nature. It is therefore important to provide a framework that explains similarities and differences between the various hypothetical strategies and that predicts how key parameters that describe the natural history of natural systems favour different control mechanisms. We develop a novel unifying framework for pairwise interactions between unrelated individuals, in which we link specific control mechanisms to specific game structures. The latter are defined by unique combinations of the states of five parameters that describe investment, aspects of the payoff matrix, the number of interactions and partner choice. We find that specific control mechanisms potentially have utility in a limited number of game structures; conversely, each game structure may typically offer a few competing control mechanisms. Our framework offers theoreticians specific problems that await mathematical exploration, while at the same time offering empiricists guidelines for evaluating the game structure and corresponding control mechanisms in their systems.

Introduction

Helping between unrelated individuals remains a key topic in evolutionary biology. From the point of view of social evolution theory, helping unrelated individuals and thereby increasing their direct fitness can generally only be favoured by selection if it increases the actors' direct fitness as well (or e.g., in the case of sterile workers, their relatives' inclusive fitness because of direct fitness benefits) (Lehmann & Keller 2006; West et al. 2007). We call such mutual direct fitness benefits cooperation if it occurs within species and mutualism if it occurs between species (Bshary & Bergmüller 2008). A wide diversity of ecological parameters and cognitive mechanisms may promote or hinder stable cooperation. For example, low mobility, long life or strong between-group competition may facilitate stable cooperative behaviour (Lehmann & Rousset 2010). So do the cognitive abilities to recognise individuals, to remember their behaviour in the past interactions, and to show self-control to gain future benefits that more than compensate for current investment (Brosnan et al. 2010). Assumptions about ecological variables and cognitive abilities are implicitly integrated in another major tool used to tackle the issue of stable cooperative behaviour between

Correspondence
Redouan Bshary, Institute of Biology, University of Neuchâtel, Emile-Argand 11, BP 158, 2009 Neuchâtel, Switzerland.
E-mail:redouan.bshary@unine.ch

unrelated individuals: evolutionary game theory (Maynard Smith 1982).

Although fully applicable to few real-life examples, the standard game theoretical model of cooperation, the prisoner's dilemma game (Luce & Raiffa 1957), highlights both the advantages and the pitfalls of cooperative behaviour in many situations: mutual cooperative behaviour yields higher payoffs than mutual cheating, but cooperative behaviour may be vulnerable to exploitation by non-cooperative 'cheaters'. Payoffs represent an immediate cost-benefit analysis for alternative behavioural options. Payoffs affect the individuals' fitness by the sum of the immediate payoff value and the effects of the chosen behaviour on future payoffs because of its influence on the future behaviour of partners (Bshary & Bergmüller 2008). Most difficult to explain are behaviours that increase the immediate payoff to the recipient and decrease the immediate payoff to the actor relative to alternative behavioural options. We define such behaviours as 'investments'. For any investment, one must ask two related questions: how does this investment yield future benefits to the actor and hence an average net increase in inclusive fitness, and how does selection maintain that level of investment? While investments would appear to make cooperative behaviour vulnerable to exploitation, there is abundant evidence for cooperation and mutualism in nature that are based on investment by at least one partner (Bshary & Bronstein 2004; Sachs et al. 2004). Mutualism involves players from two gene pools, while cooperation involves players from one gene pool. While this difference makes conditions for stable mutualism less stringent than for stable cooperation (everything else being equal, Doebeli & Knowlton 1998; Bergstrom et al. 2003), the game theoretical approach allows us to treat them as a single problem in this article.

A first potential game theoretical solution for the persistence of cooperation between unrelated individuals (both of the same and different species) was provided by Axelrod & Hamilton (1981), who explored Trivers' verbal ideas on 'reciprocal altruism' (Trivers 1971) within an iterated version of the prisoner's dilemma. They found that a simple strategy called tit-for-tat emerged as a cooperative solution. Tit-for-tat players first interact cooperatively then copy the current behaviour of their partner in each subsequent round. Tit-for tat players can therefore reap the benefits of mutual cooperation when paired with a cooperative partner, while avoiding strong exploitation by an uncooperative partner. The controlling aspect of the strategy, i.e., the mechanism that causes cheating players to receive a lower total payoff than cooperative players when paired with a tit-for-tat player, is that only partners' cooperative behaviours are rewarded in the next round. Therefore, tit-for-tat like strategies have been termed 'positive reciprocity' (Clutton-Brock & Parker 1995).

More recently, a large variety of additional concepts have been proposed to explain the evolutionary persistence of cooperation between pairs of unrelated individuals, both within and between species. These include by-product mutualism (Brown 1983), pseudoreciprocity (Connor 1986), indirect reciprocity (Alexander 1987), threat of reciprocity (Bshary & Bronstein 2004), parcelling (Connor 1995), punishment (Clutton-Brock & Parker 1995), sanctions (Herre et al. 1999), partner choice (Ferrière et al. 2002) and control over the duration of an interaction (also called power) (Johnstone & Bshary 2002). There has been some confusion in the literature regarding the precise definitions of these concepts and the extent to which they overlap (West et al. 2007; Bergmüller et al. 2007; Bshary & Bergmüller 2008). Nevertheless, while few cases of cooperation have been properly explored within a game theoretical framework, it appears that the most basic concepts have their corresponding real-life counterparts (Bshary & Bergmüller 2008). Therefore, questions arise about the relative importance of these mechanisms in nature. Several authors have argued that by-product mutualism and pseudoreciprocity are bound to be widespread because of their evolutionary stability, whereas any form of reciprocity should be rare in comparison, as any benefit in reciprocity is based on investment, constraining both its evolution and stability (Leimar & Connor 2003; Clutton-Brock 2009; Brosnan et al. 2010). However, the relative importance of these mechanisms might not hinge on evolutionary stability, but rather on the strategic options available to potential cooperators in nature. As we develop in this article, these strategic options can be deduced from the structure of the game that underlies the interaction.

The exercise should provide several important insights. First, it causally links game structures and control mechanisms in a single consistent framework. Second, it generates clear and mutually exclusive predictions about combinations of parameter states (game structures) and corresponding control mechanisms. Finally, it highlights key questions for future studies of game structures that are compatible with several alternative control mechanisms. Our key aim is to encourage empiricists to use game theoretical thinking when studying cooperation their systems. Modelling cooperation has become a world of its own, leading to many models that either seem to apply very specifically to humans, or that go far beyond the basic data that are still largely missing, or that address technical aspects minimally linked to real-life interactions. In 2009 alone, more than 50 theory papers on cooperation and altruism were listed in Web of Science. We do not attempt to review the theoretical literature. Instead, we focus on what we consider a key interest for field biologists, namely how the presence or absence of basic natural history parameters may affect cooperation.

Classification of the Various Concepts for Cooperative Outcomes in 2-player Interactions

Before we introduce our key parameters, we will briefly review the most basic concepts that have been proposed to explain cooperation between two unrelated individuals.

In response to confusion about the many game theoretical concepts and corresponding terms, Bshary & Bergmüller (2008) developed a simple classification scheme that distinguishes nine major partner control mechanisms that may underlie stable cooperative behaviour. These mechanisms are characterised by unique combinations of the states of four parameters, determined according to the answers to the following questions. (1) Does the act of cooperating require an investment? If there is no investment, then there is no problem of cheating, so no partner control is necessary (by-product mutualism; Brown 1983). If there is investment, one has to ask three more questions. (2) Do the benefits of an investment result from return investments ('reciprocity') or self-serving actions ('pseudoreciprocity')? (3) Do the benefits of an investment result from the behaviour of the recipient ('direct returns') or from the behaviour of a third party ('indirect returns')? Finally, (4) do the benefits of an investment result from a positive response of another individual, or from the absence of a negative response of another individual? In all, this scheme produces by-product mutualism and eight explanations for how investment in cooperation may be stabilised (i.e., control mechanisms): positive or negative, direct or indirect, reciprocity or pseudoreciprocity (Bshary & Bergmüller 2008). This classification scheme is illustrated in Table 1, which also shows how concepts of cooperation used in the literature can be defined using these four parameters. For example, 'punishment' as defined by Clutton-Brock & Parker (1995) is negative direct reciprocity, while 'sanctions' as used by Herre et al. (1999) constitute negative direct pseudoreciprocity. Note, however, that other authors have used the same terms in different ways.

A Decision Tree to Characterise Game Structures in Cooperative Interactions

We restrict ourselves to an analysis of interactions between two players. We extend an earlier study that investigated game structures in mutualisms (Bshary & Bronstein 2004), an approach that can easily be applied to intraspecific cooperation as well. The game structures can be described with a combination of

Table 1: Nine basic scenarios that may yield stable cooperation (net benefits to both players). The scenarios are described by unique combinations of the variables 'investment' (yes or no), 'costly return' (yes or no), 'returns from whom' (recipient = direct; third party = indirect) and 'nature of benefit' (reward = positive; avoidance of costs = negative). In the last column, we give names for the parameter combinations that fit definitions found in the literature (though possibly used with different meanings as well) and in brackets our composed definitions

Investment	Costly return	Returns from whom	Nature of benefit	Terms from literature
No	No investment → no conditionality	–	Own behaviour	By-product mutualism
Yes	No (by-product benefits)	Recipient (direct)	Reward (positive)	Pseudoreciprocity (direct positive Pseudoreciprocity)
Yes	No (by-product benefits)	Recipient (direct)	Avoidance of costs (negative)	Pseudoreciprocity, Sanctions, Power (Direct negative Pseudoreciprocity),
Yes	No (by-product benefits)	Third party (indirect)	Reward (positive)	Social prestige (Indirect positive Pseudoreciprocity)
Yes	No (by-product benefits)	Third party (indirect)	Avoidance of costs (negative)	Pay-to-stay (Indirect negative Pseudoreciprocity)
Yes	Yes	Recipient (direct)	Reward (positive)	Reciprocity, tit-for-tat, Pavlov (Direct positive reciprocity)
Yes	Yes	Recipient (direct)	Avoidance of costs (negative)	Punishment (Direct negative reciprocity)
Yes	Yes	Third party (indirect)	Reward (positive)	Indirect reciprocity (Indirect positive reciprocity)
Yes	Yes	Third party (indirect)	Avoidance of costs (negative)	Strong reciprocity, Policing (Indirect negative reciprocity)

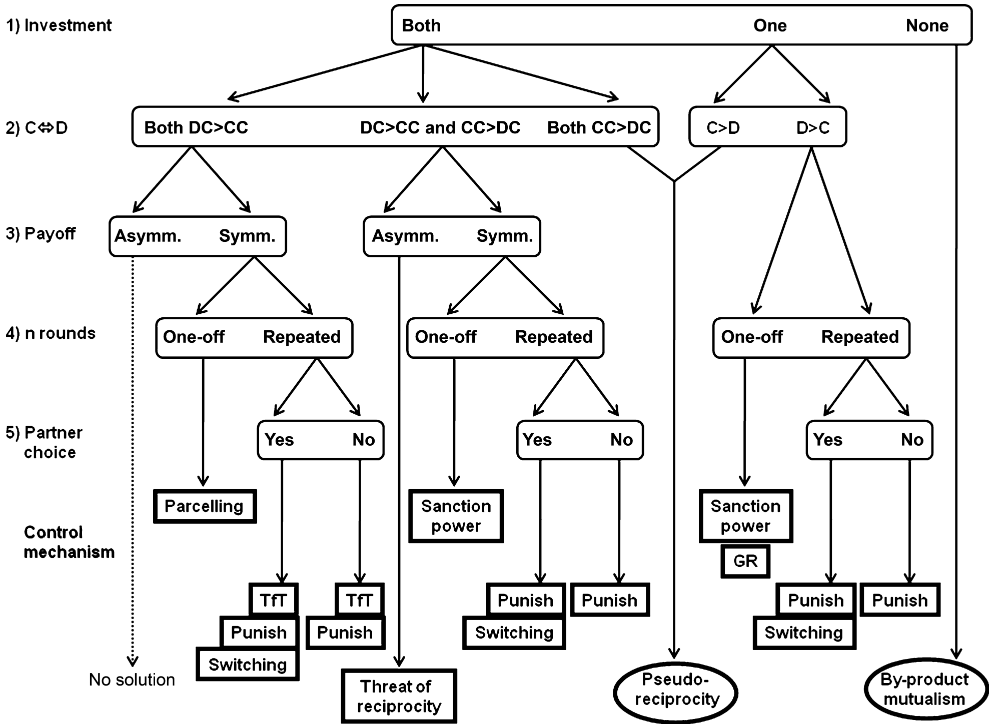

Fig. 1: A framework that defines various game structures of two-player interactions by the parameter states of the variables 'investment', 'C⇔D' (the relative payoffs of Cooperating or Defecting), payoff (rather symmetrical or rather asymmetrical), 'n rounds' (between the same two players, one-off or repeated) and 'partner choice' (present or absent), and which links each game structure to specific partner control mechanisms. The control mechanisms are defined in the text and Table 1. 'Switching': short hand for partner switching. TFT: tit-for-tat like reciprocity = direct positive reciprocity. GR, Generalised Reciprocity.

states of several parameters (Bshary & Bronstein 2004), five of which are relevant here for our main analysis: (1) Investment: does one player, both players, or neither player invest in the interaction? (2) Relative payoffs of cooperating and defecting: on average, does cooperating yield a higher payoff than defecting irrespective of the partner's preferred behaviour, or does the reverse apply? (3) Payoff symmetry: are the payoffs relatively symmetrical for both players, or is there a strong asymmetry? (4) Number of interactions: do partners interact only once or repeatedly? (5) Partner choice options: does one, both, or neither of the players have access to alternative partners? The resulting general framework for game structures is best illustrated as a decision tree with five steps, each representing the binary state of one particular parameter (Fig. 1). We can then move along the decision tree and ask, for each parameter state combination, which strategies and their corresponding control mechanisms could potentially promote cooperation.

It is important to note that there is a hierarchical order in the five parameters we discuss, from most basic to more specific. Sometimes, answers concerning the states of more basic parameters make answers to more specific parameter states irrelevant in the sense that the latter do not have to be considered to understand how stable cooperation may be achieved. The explanations will be given in the text, while Fig. 1 illustrates what state combinations of more basic parameters make the evaluation of more specific parameter states irrelevant.

In an extension of our decision tree, we will then introduce a sixth parameter, namely whether the pairwise interaction takes place in the presence or absence of a communication network. In a communication network, bystanders may eavesdrop on interactions and use the gained information for behavioural decisions in future interactions with previously observed partners (McGregor 1993, 2005). Behavioural decisions could therefore be guided by observations ('information', Roberts & Sherratt 2007) rather than by personal experience.

The steps are explained in quite some detail, and empirical examples are given as illustrations for game structures and corresponding control mechanisms. Colleagues familiar with the field may find the logic illustrated in Fig. 1 quite self-explanatory.

Step 1: Who Invests?

At this step, we distinguish among three scenarios: either both partners, one partner or neither partner invests, i.e., behaves such that their immediate payoff is reduced compared to alternative behaviours. Some forms of cooperative behaviour involve no investment at all. These behaviours increase the actor's immediate payoff and ultimately its direct fitness relative to alternative behavioural options, independently of the recipient's behaviour. This condition, in which cooperative behaviour is entirely self-serving, has been termed by-product mutualism (Brown 1983). Many authors have used the shorthand 'mutualism' for this scenario, which is very unfortunate given that this term has already been defined in the 19th century as cooperation between species (Bronstein 2003). Coordinated hunting by pairs of jackals or between groupers and moray eels provide good examples of by-product mutualism: if both individuals cheat by not contributing to hunting, each receives no food. A single individual may hunt successfully with low probability, while joint hunting yields significantly increased hunting success (Lamprecht 1978; Bshary et al. 2006). As mutual cooperation is the best option for both players, it is not necessary to proceed any further on our decision tree (Fig. 1); that is, we do not need to know any further aspects of the game structure to understand that by-product mutualism will be the mechanism underlying stable cooperative behaviour. Other interesting issues certainly remain: for example, partner choice may still be important (Leimar & Connor 2003), as one potential partner might provide higher by-product benefits than another. However, no partner control mechanism is needed to ensure a positive payoff compared to the alternative of not interacting, even if an individual is paired with a low-quality partner. We do not consider this form of cooperation further, focusing instead on cases where cooperation involves an investment on at least one side of the interaction.

If there is investment, one has to determine whether one or both players invest. Unilateral investment sets up an asymmetric situation in which the partner that invests may be able to defect (i.e., to gain the benefit of cooperation while skipping the investment). Bilateral investment, in turn, sets up a symmetrical situation in which either partner can defect.

Step 2: The Relationship Between Cooperating and Defecting in the Behavioural Response to an Investment

The second step in characterising the game structure of a cooperative interaction is to assess how an investment may yield return benefits to the investor in the future (Fig. 1). In one scenario, the investment leads to a predictable, self-serving behaviour by the recipient or by a third party (e.g., an observer) that happens to benefit the investor as a by-product of its actions. If these by-product benefits are higher than the costs of the investment, the game is classified as positive pseudoreciprocity (Table 1) (Connor 1986; Bshary & Bergmüller 2008). A good empirical example is the mutualism between leafcutter ants and fungi that they 'farm' (i.e., cultivate and feed upon, Mueller et al. 2005). Ants invest in this mutualism by providing leaves as a substrate for the fungi to grow upon and by pruning pathogenic organisms from the fungal colony. These behaviours allow the fungi to self-servingly grow healthy colonies in association with ants, yielding by-product benefits to the ants as they harvest fungi for food. Because the fungi's response to the ants' investment is self-serving, 'C' (the payoff from cooperating, i.e., growing) is by definition larger than 'D' (the payoff from defecting, i.e., not using the ants' help to grow). Therefore, investors (ants) do not risk being cheated by the partners (fungi), as cheating would be spiteful as defined by Hamilton (1964): it would reduce the direct fitness of the fungi themselves. The evolutionary stability of positive pseudoreciprocity is easy to understand. As with by-product mutualism, we need to proceed no further on the decision tree (Fig. 1).

The issue of stability in cooperation and mutualism becomes more complex as soon as there is investment upon which at least one partner is tempted to cheat, i.e., cases in which a reduction of investment would be beneficial in the absence of retaliatory actions of the partner. For example, a plant may benefit from redirecting the resources necessary for nectar production into growth or reproduction (Brandenburg et al. 2009), as long as the pollinators do not respond in a way that reduces that plant's fitness (e.g., by abandoning it). If pollinators do not discriminate between cooperative plants (those providing normal nectar quantities) and cheating ones (those providing reduced nectar), cooperative plants lose in competition with cheaters. Therefore, for cooperation to persist, pollinators must monitor the behaviour of the plants, and partner control mechanisms such as the power to terminate interactions with plants prematurely (Cresswell 1999) are expected that will reduce plant cheaters' fitness. In other words, partner control mechanisms are retaliatory actions that enforce investment.

Interactions with enforced investment can have one of three combinations of payoffs for the two players: (1) One player gains a higher payoff from defecting on a cooperative partner, while the other player's best option is to cooperate as long its partner cooperates; (2) both partners gain a higher payoff from defecting on a cooperative partner; or (3) strategic options are asymmetric, in that one player benefits from cheating while the other player lacks any option to cheat its partner because it does not invest in the partner. We will now separately explore how these three states of parameter 2 (investment), in combination with the other parameters, influence the applicability of partner control mechanisms.

Situation 1

We can denote the situation in which one player gains a higher payoff from defecting on a cooperative partner while the other player's best option is to cooperate as long its partner cooperates as 'player 1: DC > CC, player 2: CC > DC', with DC standing for Defecting on a Cooperating partner, and CC standing for Cooperating with a Cooperative partner. Such a situation might apply to interactions between the cleaner fish *Labroides dimidiatus* and predatory species that solicit inspection ('clients'). Cleaners remove ectoparasites from other reef fish but prefer to eat mucus (Grutter & Bshary 2003). This constitutes cheating, as it is costly to the host compared to the alternative of not interacting. In the absence of partner control mechanisms, cleaners would therefore be mucus-scraping cheaters rather than ectoparasite-feeding mutualists (DC > CC). Conversely, Trivers (1971) proposed that predatory clients benefit from leaving cleaners alive instead of eating them because the repeated benefits of having ectoparasites removed are larger than the one-time benefit of caloric intake through eating the cleaner (CC > DC). We now explore steps 3–5 of our decision tree under these payoff conditions.

Step 3: Payoff Asymmetries

Payoffs may often vary along a continuum. For simplicity, however, we only deal with the two extremes to introduce a binary choice in our decision tree. One extreme is that payoffs are very similar for both partners: e.g., if both cooperate, each gains 10% of its daily energy requirements, whereas if both cheat, each gains nothing. The other extreme is that payoffs are very asymmetric: e.g., cheating by one partner causes minor losses to the other, while in the reverse case, the cheated individual loses its life. Highly asymmetric payoffs are found in some ant defence mutualisms, for example. In one well-known case, ants tend aphids that produce nutrient-rich excretions (honeydew). A cheating aphid would be one that produced little, or less nutritious, honeydew; in contrast, an ant that cheated would be one that consumed the aphid rather than tending it. Under such asymmetric payoff conditions, stable cooperative behaviour may be achieved if the player that could kill its partner (the ant in this example) is the one that receives a higher payoff if it cooperates as long as its partner cooperates (CC > DC): an aphid can be consumed only once, but the caloric gains from doing so might soon be outweighed by the repeated benefits of honeydew-feeding. Ant-defended species would benefit from producing less honeydew as long as ants cooperate (DC > CC). However, the potential prey should behave cooperatively just because of the 'threat of reciprocity' (Bshary & Bronstein 2004): if it cheated, it would have more value as an immediate prey item, at which point the predator would have effectively terminated the game (Hammerstein & Hoekstra 1995). As a consequence, predators do not have to hold their partners in check. Therefore, no further information about other parameters (*n* interactions, choice options) is necessary to understand such interactions with asymmetric payoffs. The threat of reciprocity may promote stable cooperative behaviour under these conditions.

If payoffs are more or less symmetrical without threats to immediate survival from defection, further information on the number of interactions and partner choice is needed to assess how players may be able to control their partner's behaviour to make them behave cooperatively.

Step 4: *n* Interactions

We distinguish between repeated interactions between the same two players (typically viewed as a game with a certain probability of having a next interaction (Axelrod & Hamilton 1981) and one-off ('one shot') interactions. If interactions are one-off but the payoffs are a function of the duration of an interaction, then players may be able to terminate an interaction prematurely if the partner cheats. Under these conditions, control over the interaction's duration, termed 'power' in the economic literature (Bowles & Hammerstein 2003), may be sufficient to promote a cooperative outcome (Johnstone & Bshary 2002), if the accumulation of cooperative benefits during a prolonged interaction yields a higher total benefit than a quick cheat. For example, non-predatory clients often terminate an interaction prematurely in response to cheating by a cleaner fish (Bshary & Grutter 2002), and cleaners cooperate more to avoid premature endings of interactions (Bshary & Grutter 2005). While the cleaner-non-predatory client interactions provide a potential example for the use of power, the strategic options for cleaners and clients are asymmetric, as the non-predatory clients lack any option to cheat cleaners. We do not know of an example in which both partners invest, the payoffs are such that 'CC > DC' applies to one player and 'DC > CC' to the other, the payoff consequences are quite symmetrical, and individuals meet only once. If such a game structure were found in nature, we predict that power would be the mechanism used to yield stable cooperative behaviour.

If interactions are iterated, a further question is whether players, in particular the individuals that risk being cheated, can choose their partners.

Step 5: Partner Choice

Partner choice potentially exists if an individual may select a partner from among two or more potential partners. Partner choice has been identified as a potentially important parameter for payoff distribution among partners in biological market theory (Noë et al. 1991; Noë & Hammerstein 1994). Biological market theory views cooperation as an exchange of goods or services between traders that typically belong to two different classes, as defined by the product they offer for exchange: nutrition for transport, nutrition for protection, etc. (Bronstein 2001). If the class of cooperators (CC > DC) is rare relative to the class of potential defectors (DC > CC), the former may choose among individuals belonging to the latter. As a consequence, cooperators may use a decision rule such as 'if the partner cooperates, then keep it, but if the partner cheats then switch to a different partner'. Cheaters would thus end up without a partner. Several models show that the risk of losing a partner may promote cooperative behaviour under such conditions (Ferrière et al. 2002; McNamara et al. 2004; Foster & Wenseleers 2006; Johnstone & Bshary 2008). For example, individual ant-tended lycaenid butterfly larvae may benefit from reducing the quantity or quality of nutritional secretions they produce for ants, as their production reduces fitness ('DC > CC', Axén & Pierce 1998). While the ants have an interest in protecting reward-producing larvae from predators ('CC > DC'), they are the mobile partner with choice options. They can therefore leave any larva that produces little or no substance and search for more rewarding partners elsewhere. In conclusion, partner switching provides a partner control mechanism that can provide stable cooperative behaviour in this particular game structure.

If there is no partner choice, then cooperators may still be able to prevent potential defectors from cheating in a repeated game if they are able to punish cheating of their partners. Punishment as defined by Clutton-Brock & Parker (1995) is a behaviour that reduces the immediate payoffs of both the actor and its target. Punishment functions because the target's best option is to behave more cooperatively during future interactions, thereby avoiding further costs, while the actor is more than compensated for its investment through the change of the target's behaviour. We are not aware of an example in which this parameter state combination (both partners invest, 'DC > CC' for one player and 'CC > DC' for the other, repeated interactions, no partner choice) applies. If one were found, punishment would provide a partner control mechanism that promotes stable cooperative behaviour.

Situation 2

In the second situation, we explore, both partners would gain a higher payoff from defecting on a cooperative partner (both DC > CC). This situation fulfils a critical assumption of the prisoner's dilemma game, in which the payoffs are constructed such that the payoff in any single round is maximised if one defects, irrespective of the partner's choice of behaviour.

Step 3: Payoff Asymmetries

Highly asymmetric payoff structures cannot yield cooperative solutions, as one player would invariably kill its partner and the game would be over. Therefore, only more symmetrical payoff structures, in which cheating by one player does not cause the death of the partner, are possible.

Step 4: *n* Interactions

If interactions are one-off but the payoffs are a function of the duration of an interaction, then players may be able to terminate an interaction prematurely if the partner cheats. Under these conditions, parcelling of the exchanges and continuation of the interaction that is contingent on the partner delivering may promote a cooperative outcome (Connor 1995). A good example for parcelling is the egg trading in the hermaphroditic hamlet fish (Fischer 1988). In principle, one player could offer all its eggs (which are costly to produce) to the partner for fertilisation, then the partner could reciprocate. However, in such a sequential one-off game, the initial investor risks that the partner will swim off after fertilising the eggs, in search of an individual willing to provide eggs for fertilisation in exchange for receiving eggs for its own fertilisation. In fact, hamlet fish do not release all eggs at once, but rather in small parcels, with partners alternately taking the female and the male role (Fischer 1988). Parcelling of the eggs and alternating release transforms a one-off interaction into one with iterated decisions. Therefore, it is better to return investments to elicit further investments than to cheat and to lose time and energy while searching for a new partner.

Alternatively, individuals interact repeatedly, a scenario for which we have to explore the effect of partner choice options.

Step 5: Partner Choice Options

If there is no partner choice, then we have a combination of parameter states as in the iterated prisoner's dilemma (Axelrod & Hamilton 1981): both players invest, DC > CC applies to both players, payoffs are symmetrical, and interactions are iterated. Cooperative solutions to this game structure are traditionally predicted to be tit-for-tat like: investment by one player causes the partner to invest in return ('positive reciprocity'). Several cases of animal cooperation, including predator inspection in fishes, blood provisioning in false vampire bats and grooming in mammals, have been interpreted as tit-for-tat like cooperation (reviewed in Dugatkin 1997). While all these examples have been challenged (Hammerstein 2003), further examples have emerged more recently (reviewed in Raihani, N. J. & Bshary, R., submitted). One example, pair inspections of clients by cleaner wrasses, provides evidence that an iterated prisoner's dilemma may be solved with asymmetric punishment rather than tit-for-tat (Bshary et al. 2008; Raihani et al. 2010).

If there is partner choice, cheating by one player could still lead the cheated individual to respond with cheating or with punishment. However, now there is also the alternative of terminating the relationship, in which case both players have to look for a new partner. Searching and finding a new partner probably incurs opportunity costs and search costs, which would have to be balanced against the potential gains to be made from finding a more cooperative partner. It has been argued that long-term exchanges of services like grooming in primates are cases of reciprocity in which cheating would lead to partner switching (Schino & Aureli 2008). Theories that show that the risk of losing a partner may promote cooperative behaviour (Ferrière et al. 2002; McNamara et al. 2004; Foster & Wenseleers 2006; Johnstone & Bshary 2008) need to be expanded to specify the conditions under which switching is better than positive or negative reciprocity and vice versa.

Situation 3

In this situation, strategic options are asymmetric, in that one player benefits from cheating (D > C) while the other player lacks any option to cheat its partner because it does not invest in the partner. For example, when cleaner fish *L. dimidiatus* interact with non-predatory clients, the cleaners still prefer client mucus over ectoparasites (Grutter & Bshary 2003), while non-predatory clients have no means to exploit a cleaner fish because they do not eat small fishes. Under these conditions, we can skip step 3 regarding payoff asymmetries of cheating, as one player cannot cheat. To determine possible game structures, we only need to ask whether interactions are one-off or repeated and whether or not there is partner choice (steps 4–5 of our decision tree).

Step 4: *n* Interactions

If interactions are one-off, cooperative outcomes may still be possible if any of the three following conditions is met. The first condition is that the payoffs are a function of the duration of an interaction, and the cooperator can terminate the interaction prematurely if the partner defects. This power to terminate the interaction may suffice, in particular if cheating does not yield much more per time unit interaction than cooperating does ('low temptation' to cheat; Johnstone & Bshary 2002). Second, the potential cheater may have to make the first move, which may then be accepted or rejected by the partner. The partner's option to reject a bad offer is a control mechanism that has been termed a sanction

(Herre et al. 1999; Kiers et al. 2003). For example, yucca plants are pollinated by highly specialised insects (yucca moths) that also lay eggs in the flowers; the offspring of the pollinators consume some of the developing seeds. Yuccas cannot influence how many eggs yucca moth females lay in flowers while pollinating. However, in some yucca species, the plant evidently can evaluate the number of larvae in single fruits and can selectively abort fruits in which larvae would destroy the majority of seeds (Pellmyr & Huth 1994). The negative effect of sanctions on the cheating partner is a by-product of a self-serving act: the plant aborts a heavily infested fruit if it can shift its resources into maturing ones with more seeds. Therefore, one could call a sanction pseudo-punishment, so the control mechanism that stabilises cooperative behaviour is negative pseudoreciprocity (Bshary & Bergmüller 2008). A third condition that has been proposed to yield stable cooperation in one-off interactions is that individuals use their current experience for decision-making in future interactions with third parties (Pfeiffer et al. 2004; Hamilton & Taborsky 2005). In such 'generalised reciprocity', an actor helps if it has received help from any other individual in its previous interaction in the role of a recipient, and the actor does not help if it has not received help from any other individual. The decision to help is thus completely independent of the recipient's identity and past behaviour, but rather is based on the actor's general experience. While there is experimental evidence for the use of generalised reciprocity in rats under laboratory conditions (Rutte & Taborsky 2007), empiricists are challenged to find the game structure for generalised reciprocity in nature.

If there are potentially repeated interactions, the question about partner choice must be addressed.

Step 5: Partner Choice

In a repeated game with asymmetric strategic options, partner choice may promote cooperative outcomes if the cooperator is able to choose between (and switch) partners. If players that lack the option to cheat can move around freely and choose with whom they interact, they can evolve a simple strategy that keeps their partners in check: 'keep a partner as long as it cooperates, and switch to a new partner for the next round if the current one cheated'. This decision rule may force chosen players to refrain from cheating their partner simply because of the risk of not having a partner in the next round (Ferrière et al. 2002; Johnstone & Bshary 2008). In the absence of partner choice, potential victims may hold their partners in check if they can punish any acts of cheating. Both cases exist in the cleaning mutualism involving *L. dimidiatus* (Bshary & Grutter 2005). Non-predatory client species with access to several cleaner territories (cleaning stations) are likely to return to the same station for their next inspection if the last service they received there was of good quality, whereas they are likely to switch to another cleaning station if the last quality of service they received there was poor (Bshary & Schäffer 2002). Resident client species, which are characterised by small territories/home ranges and hence only have access to the local cleaning station (without the option to choose among cleaners), chase cleaners if the latter cheat; cleaners respond by giving them particularly high-quality service during the next interaction (Bshary & Grutter 2002). Experiments suggest that both leaving and aggression make cleaners behave more cooperatively (Bshary & Grutter 2005). In conclusion, negative reciprocity and partner switching are partner control mechanisms that may promote cooperative behaviour in repeated games with asymmetric strategic options.

Introducing the Parameter 'Communication Networks'

All control mechanisms introduced until now rely on personal experience of the actor with a given partner. However, it has been proposed that as long as interactions take place in the presence of bystanders (in a communication network), these bystanders can reach an optimal behavioural decision not only through experience but also by gaining information about the partner prior to interactions. It has been proposed that observers use the information to attribute an 'image score' (Alexander 1987; Nowak & Sigmund 1998) or a 'social prestige' (Zahavi 1995; Roberts 1998; Lotem et al. 2003) to the interacting partners. The score is positive/high if the interacting partners cooperated and negative/low if they cheated. An individual's decision to cooperate or to cheat will then depend on the score of its partner. If one witnessed that the current partner cooperated with someone else, then one may cooperate, while if the current partner was observed cheating someone else, then one may cheat. Under these circumstances, the benefits of investing in an individual A are not because of the behaviour of individual A but accrue 'indirectly', because of the behaviour of an observing individual B during future interactions. If all behaviours classify as investments, then the concept of indirect reciprocity applies (Nowak & Sigmund 1998; Leimar & Hammerstein 2001). If observers choose cooperating individuals for self-serving reasons (i.e., they expect a benefit to their choice relative to other potential partners), the concept of indirect pseudoreciprocity also applies (called 'social prestige' or 'competitive altruism' by Zahavi 1995; Roberts 1998; Lotem et al. 2003).

If a communication network exists and only one player invests, the non-investing partners may use indirect pseudoreciprocity to maximise their payoffs. A communication network exists in the cleaning mutualism involving *L. dimidiatus*, which has more than 2000 interactions per day (Grutter 1997). Thus, cleaners often inspect one client while another potential client is waiting or approaching. These bystanders apparently observe the outcome of ongoing interactions, as they typically invite inspection in the absence of conflicts but avoid the cleaner if it cheats its current client (Bshary 2002; Bshary & Grutter 2006). This client decision rule is self-serving because clients simply benefit from seeking cooperative cleaners and avoiding cheating cleaners. At the same time, the decision rule sets the stage such that cleaners benefit from giving current clients an extraordinary quality of service if bystanders are watching, not because the current clients will return a benefit, but indirectly, because the bystanders will choose to interact with the cleaners. Cleaners indeed behave more cooperatively when observed (Bshary 2002; Bshary & Grutter 2006).

If both players invest, indirect reciprocity can stabilise investments in a communication network. Evidence is currently restricted to humans (Wedekind & Milinski 2000). The classic experiment explicitly sets up the game as one-off encounters between individuals, precluding any direct reciprocity. The importance of indirect reciprocity in a repeated game structure and in games with partner choice has not yet been tested.

Indirect forms of cooperation based on image scoring could in principle be integrated in our scheme by introducing the sixth parameter 'communication network; yes or no'. However, the tree would become very complicated. In the absence of networks, the solutions remain as depicted in Fig. 1. If interactions take place in a communication network, for every game structure, either indirect pseudoreciprocity or indirect reciprocity becomes potential partner control mechanisms, but individuals may still alternatively use the control mechanisms depicted in Fig. 1. The issue of competing alternative control mechanisms will be a key topic in the discussion.

Discussion

We began with the observation that current theoretical developments concerning stable cooperation are far ahead of empirical knowledge. However, if we ignore modelling details, there are just nine basic game theoretical concepts and partner control mechanisms that may explain how stable cooperative behaviour may be achieved. The importance of these various concepts should depend on how often the conditions that allow the successful use of a specific control mechanism are found in nature. Those conditions can be specified according to the course of the interaction between partners. We therefore attempted to characterise various game structures in terms of unique combinations of the states of initially five parameters and went on to discuss an extension with a sixth parameter. For each combination of parameter states, we discussed how individuals may prevent partners from cheating.

A key result from this exercise is that we can link each control mechanism to a limited number of specific game structures. A more general implication is that both empiricists and theoreticians need to investigate what 'outside options' an individual potentially has to the observed course of action (Cant 2010): could it in principle switch partners, how easy would that be, and how likely would it be that a new partner behaves differently? Variation in levels of cooperation typically promotes stable cooperation (McNamara & Leimar 2010). Concepts are typically studied in isolation and the conditions for stable cooperation specified (Nowak 2006). Our framework shows that often, several control mechanisms could potentially be used in the same game. Recently, theoreticians have started to evaluate the conditions under which one control mechanism may be superior over alternatives (Roberts 2008; Izquierdo et al. 2010; Hilbe & Sigmund 2010). More such analyses are needed to make predictions about the empirical relevance of competing concepts. For example, while we explained that indirect (pseudo-) reciprocity could be used as control mechanisms in many different game structures, empirical evidence is currently very limited. Is this because indirect (pseudo-) reciprocity may lose against alternative mechanisms available for any given game structure because of costs linked to cognitive demands (which may even constrain its use in many species; Brosnan et al. 2010), or have we merely overlooked these control mechanisms until now? In favour of the latter hypothesis, we note that there is plenty of evidence for communication networks and eavesdropping on interactions at least in vertebrates in competitive contexts (McGregor 2005). Thus, increased awareness of these concepts among empiricists studying cooperative interactions may generate more widespread evidence. Similar questions arise with respect to punishment, as this control mechanism could be used at least in theory in several game structures (Fig. 1), while cognitive constraints may prevent common usage (Brosnan et al. 2010).

Conclusions

We hope that empiricists will find our framework a useful starting point to consider game theoretical questions in their systems, and that it may encourage theoreticians to explore for each game structure the conditions that may favour one control mechanism over the alternatives. Our framework joins several recent reviews (Sachs et al. 2004; Lehmann & Keller 2006; Bergmüller et al. 2007; West et al. 2007; Bshary & Bergmüller 2008; Clutton-Brock 2009; Leimar & Hammerstein 2010) that point to the many routes apart from strategies in prisoner's dilemma type games to stable cooperative behaviour between unrelated individuals. As the concepts used in the cooperative breeding literature can be translated into the more general cooperation concepts presented here (Bergmüller et al. 2007), our scheme is also valid for empiricists working on cooperatively breeding species. The large variety of game structures discussed here should allow empiricists to match their detailed observations on the natural history of their system to potential partner control mechanisms without oversimplifying too much. Our five parameters – investment, relative payoffs for cooperating and defecting, payoff asymmetries between partners, number of interactions and partner choice – can be assessed in many cases, as can the potential role of image scoring in a communication network. The parameter state combinations yield predictions about the control mechanisms that yield cooperative behaviour, amenable for further testing. Empiricists should also be aware that several game structures may occur within their study system, and hence several control mechanisms may be used, as is the case in marine cleaning mutualism (Bshary 2010). Also, the temptation to cheat may vary from one situation to the next, depending for example on whether future interactions are expected to be frequent or infrequent (Oates et al. 2010). Thus, our dichotomous approach is a simplification, but we believe it provides a valid starting point. With more empirical studies on game theory, we can both refine the framework presented here and build a data set that will eventually reveal the relative importance of the various concepts for cooperative behaviour in nature.

Acknowledgements

RB is funded by the Swiss Science Foundation. We thank Ralph Bergmüller, Rufus Johnstone and Andy Russell for discussions, and Emily Jones, Ralph Bergmüller and two referees for valuable comments. Furthermore, we thank Ana Pinto for designing Fig. 1.

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