

## **The benefits of being seen to help others: indirect reciprocity and reputation-based partner choice**

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## **Abstract**

When one individual helps another, it benefits the recipient and may also gain a reputation for being cooperative. This may induce others to favour the helper in subsequent interactions, so investing in being seen to help others may be adaptive. The best-known mechanism for this is indirect reciprocity, in which the profit comes from an observer who pays a cost to benefit the original helper. Indirect reciprocity has attracted considerable theoretical and empirical interest, but it is not the only way in which cooperative reputations can bring benefits. Signalling theory proposes that paying a cost to benefit others is a strategic investment which benefits the signaller through changing receiver behavior, in particular by being more likely to choose the signaller as a partner. This reputation-based partner choice can result in competitive helping whereby those who help are favoured as partners. These theories have been confused in the literature. We therefore set out the assumptions, the mechanisms and the predictions of each theory for how developing a cooperative reputation can be adaptive. The benefits of being seen to be cooperative may have been a major driver of sociality, especially in humans.

## 1. Introduction

### 1.1 The benefits of being seen to help

Helping involves one individual paying a cost to benefit a recipient. The costs can be repaid in terms of indirect fitness if the helper and recipient are genetically related (Hamilton, 1964), or they can be repaid directly, for example if the recipient reciprocates (Axelrod & Hamilton, 1981; Trivers, 1971) or if the helper has a stake in the recipient's welfare (Aktipis et al., 2018; Queller, 2011; Roberts, 2005). Another way helpers might increase their direct fitness is by gaining a reputation for being helpful. A 'good' reputation may induce others to favour the helper in subsequent interactions. As a result, investing in a reputation for being seen to help others may be adaptive. This would potentially provide an explanation for helping others that goes beyond the domain of theories of kinship and direct reciprocity.

The best-known theory of how individuals might benefit from being seen to help others is indirect reciprocity, in which paying a cost  $c$  to benefit another by  $b$  makes the helper more likely to receive a reciprocal benefit from an observer, and thereby to make a net gain when  $b > c$  (Boyd & Richerson, 1989). A large number of theoretical models (e.g. (Nowak & Sigmund, 2005; Ohtsuki & Iwasa, 2005; Ohtsuki et al., 2009) and some experiments (e.g. (Milinski, 2016; Milinski et al., 2002b; Rockenbach & Milinski, 2006; Swakman et al., 2016) have studied this possibility. Unfortunately, reputation-building has tended to be equated with indirect reciprocity (Clark et al., 2020; Milinski et al., 2002b; Rand & Nowak, 2013; Whitaker et al., 2018; Yoeli et al., 2013). This focus has overshadowed the fact that indirect reciprocity is not the only theory for how individuals may get a return on a cooperative reputation. Different theories have been presented in the literature but have not always been clearly distinguished. We therefore set out the assumptions, mechanisms and predictions of the main theories for how developing a cooperative reputation can be adaptive. The psychological adaptations underlying reputation-based cooperation are considered elsewhere (Manrique et al, this volume).

We use the term 'reputation' where individuals use information acquired by observation or gossip to learn about and predict how another individual will behave in the future. There is a spectrum of ways in which the term 'reputation' has been applied in understanding cooperative behaviour. This spectrum can be seen in Figure 1 where we classify routes to cooperation using reputations. In the simplest sense, 'reputation' can be used to describe the observation of a

partner's behaviour. However, we prefer to follow typical practice and reserve the term for where third-party observation and/or gossip comes into play. As such, we consider reputations to be more than simply a record of an individual's behaviour that could have been gained by a partner in a dyadic relationship. This distinguishes 'reputation-based behaviour' from responses found within directly reciprocating partnerships, mutualisms or among kin. We therefore focus on helping behaviours that are performed outside of the context of repeated dyadic partnerships and on how individual reputations for being helpful mediate the emergence and maintenance of cooperative societies. Our focus is on humans where the concern for reputation appears most developed, but we have in mind a broader perspective encompassing other animals where some reputational concerns have been reported (Manrique et al. this volume).

## **1.2 A spectrum of reputation**

In Figure 1, we show schematically how individuals might develop reputations for helping, and how others might respond to these reputations in a manner that makes reputation-building adaptive. Following (Roberts & Sherratt, 2007) we distinguish the selective pressures behind why an individual A helps individual B in the presence of individual C. These mechanisms can be divided into whether they act primarily through the actual benefits to the recipient(s) or through the information that the helping act conveys. We discuss each of these in turn.

The first selective pressure on A's helping is via the benefits to B, which may mean that the recipient B, or a third party C, are more likely to provide a return benefit to A. These routes to cooperation are direct reciprocity (Trivers, 1971) and indirect reciprocity (Boyd & Richerson, 1989) respectively. Indirect reciprocity is based on the 'observer' picking up cues, either by their own observation or via gossip, which increase their likelihood of paying a cost to benefit the original actor. As the name implies, it is explicitly based on reciprocation of the costs and benefits of helping. This is a crucial point: indirect reciprocity is not a catch-all term for benefitting through third parties.

In between the concepts of direct and indirect reciprocity is the possibility that individuals could pick up cues of how others have behaved (perhaps by eavesdropping (Covas et al., 2007)) so that they can then use this to inform their helping decision when they meet the observed party for directly reciprocal interaction. This strategy has been termed Observer Tit-for-Tat (OTFT) by (Pollock & Dugatkin, 1992) in one of the leading game theoretical papers to explicitly consider

the role of reputations. Some confusion has arisen here because (Alexander, 1987) referred to indirect reciprocity as “direct reciprocity occurring in the presence of others”. Although OTFT encapsulates Alexander’s verbal description, it is not a strategy of indirect reciprocity: individuals with good reputations benefit from directly reciprocal interactions.

The second selective pressure we consider is that by being helpful, individuals reveal information about themselves. It may then pay to invest in reputations so as to be seen to be helpful. In this sense, reputations for helping function as signals, where signals are defined as phenotypic traits adapted to change the behaviour of a receiver in a way that is beneficial to the signaller (Maynard Smith & Harper, 2003). We note that the receiver of the signal may or may not be the recipient of the act of help, and that the ‘help’ need not strictly even be beneficial to anyone (Sozou & Seymour, 2005) to function as a signal, although we are concerned here with signals that do help others. The idea that help is selected for as a signal contrasts with typical models of help which work through the benefits to recipients (e.g. (Axelrod & Hamilton, 1981; Nowak & Sigmund, 1998). To put this in other words, indirect reciprocity could be conceived as involving individuals changing the behaviour of others so that they are more likely to help them. However, this conception does not change the basic nature of indirect reciprocity as involving reciprocation. In contrast, signal receivers do not simply reciprocate a helpful act, but change their behaviour in a way that is beneficial to the signaller yet does not necessarily incur a net cost to the signal receiver. This means that signalling models of help (Gintis et al., 2001) are formulated in a fundamentally different way than models based on reciprocity.

We focus in this paper on how a signal receiver may be more likely to choose the signaller for mutually beneficial interactions. This process was initially defined as ‘competitive altruism’ by (Roberts, 1998) through comparison with the term ‘reciprocal altruism’ (Trivers, 1971). The term has been widely adopted (e.g. (Barclay, 2004, 2013; Barclay & Willer, 2007; Böhm & Regner, 2013; Hardy & Van Vugt, 2006; Herrmann et al., 2019; Macfarlan et al., 2012; Roberts, 2015a; Van Vugt et al., 2007)). Nevertheless, here we follow (Sylwester & Roberts, 2010) in using the more descriptive term ‘reputation-based partner choice’ (RBPC). When specifically referring to the escalation of pro-social behaviour due to competition for partners, we use the term ‘competitive helping’ (Barclay, 2011; Raihani & Smith, 2015) to avoid the term ‘altruism’ which is reserved by some biologists for where there is a net lifetime fitness cost (West et al., 2007).

The role of partner choice is integral to the concept of competitive helping, and this provides a link with the theory of Biological Markets (Barclay, 2016; Noë & Hammerstein, 1994) which has been developed to understand, for example, between-species mutualisms. We illustrate this in Figure 1 as a dimension representing whether individuals have a choice of partner.

We now consider indirect reciprocity and RBPC in more detail.

## **2. Indirect Reciprocity**

### **2. 1 Theoretical basis.**

Indirect reciprocity has been reviewed elsewhere (Nowak & Sigmund, 2005; Okada, 2020) so we focus here on the basic structure of indirect reciprocity theory and models to allow comparison with other theories of reputation-based cooperation (Figures 1 & 2). Indirect reciprocity occurs when one individual pays a cost to benefit another, and then an ‘observer’ pays a cost to benefit the original donor. For simplicity, we include in the term ‘observer’ those who witness the helping as a third-party (Roberts, 2008) and those who are recipients of ‘gossip’ about it (Sommerfeld et al., 2007). Provided the benefits exceed the costs then a helper makes a net profit via the observer (Boyd & Richerson, 1989). This process is best understood by comparison with direct reciprocity: whereas direct reciprocity involves one individual paying a cost to benefit a second individual, in indirect reciprocity the reciprocal donation comes from an observer. Indirect reciprocity, like its direct counterpart, works when cooperators are rewarded and defectors are sanctioned. This principle was applied to repeated games with changing partners by (Kandori, 1992).

Much of the theoretical work on indirect reciprocity has involved computer simulation of strategies. Among these, a well-known candidate was ‘image scoring’, a simple mechanism in which a reputation index was incremented when individuals donated and decremented when they did not (Nowak & Sigmund, 1998). However, this strategy is not evolutionarily stable because it does not allow for ‘justified defections’ when individuals meet non-cooperators (Leimar & Hammerstein, 2001; Panchanathan & Boyd, 2003). Defecting on a defector harms an individual’s image score, meaning that the unhelpful individual will not be helped by a third-party. This weakness means that individuals are incentivized to reward all players, regardless of whether they cooperate, simply to protect their own reputation. Cooperation can collapse as a

result. A prior solution to this problem is if individuals use a 'standing' strategy (Sugden, 1986), whereby justified defection is still rewarded by third-parties. An extension of this approach, analyzing a large number of possible strategies (Ohtsuki & Iwasa, 2006), found that 'stern-judging' was most successful (Pacheco et al., 2006; Santos et al., 2018). This strategy helps helpers and (crucially) sanctions defectors; essentially what (Kandori, 1992) showed.

## **2.2 Empirical Evidence**

Whilst most interest in indirect reciprocity remains theoretical, experiments have provided evidence that people give preferentially to those with positive image scores ((Milinski et al., 2001; Seinen & Schram, 2006; Semmann et al., 2004; Wedekind & Milinski, 2000). Indirect reciprocity has since been considered as the main reason why individuals, especially humans, care about being seen to help others. Some authors have also argued that indirect reciprocity provides the selective pressure behind the evolution of language and morality (Nowak & Sigmund, 2005; Ohtsuki & Iwasa, 2006; Santos et al., 2018). However, indirect reciprocity theory requires that people discriminate between justified and unjustified defection, and although there is some evidence for this (Swakman et al., 2016), other studies have failed to find such an effect (Milinski et al., 2001; Samu et al., 2020; Yamamoto et al., 2020). Evidence of indirect reciprocity in real-world settings has also been claimed (Lange & Eggert, 2015; Yoeli et al., 2013). However, a review of the evidence for indirect reciprocity finds that there is less evidence for indirect reciprocity in experimental and in real-world settings than is typically thought (Roberts 2021); see also (Bshary & Raihani, 2017; Raihani & Bshary, 2015) for critiques).

## **4. Reputation-based partner choice**

### **4.1 Theoretical basis**

The concept of RBPC emerged from modelling which showed how generosity and choosiness can co-evolve (Sherratt & Roberts, 1998). RBPC is based on conceptualizing individuals in a social group making decisions about interaction partners, for example a bird choosing a mate; or a person choosing a friend. It posits that individuals invest in cooperative reputations so that they will be more likely to be chosen for profitable partnerships (Roberts, 1998; Van Vugt et al.,

2007). This approach contrasted with that of reciprocity within set partnerships where cooperation was seen as being difficult to evolve.

RBPC theory has some key assumptions.

- (1) Individuals vary in quality and/or intentions as potential social or sexual partners.
- (2) Individuals perform helpful acts that provide public information which others can observe to judge quality and /or intentions (signals)
- (3) Individuals can choose their partners for further interactions (individuals may play one or both roles).

Individuals benefit from choosing partners who are either high quality or have good intentions (i.e. they are both able and willing to confer benefits; Barclay, 2013). We then infer that those seen to be most helpful will either assortatively partner with each other (in the case of social selection (Lyon & Montgomerie, 2012; Nesse, 2009; West-Eberhard, 1983)) or will be preferentially selected by sexual partners (in the case of sexual selection). This hypothesis of assortative pairing arises from models of the correlation between generosity and choosiness (McNamara et al., 2008; Sherratt & Roberts, 1998). Once paired, individuals form a cooperative relationship which may be of direct reciprocity, by-product benefits, or other mechanisms involving interdependence between the two partners. The signaller benefits from their investment in signalling and the receiver of the signal benefits from being choosy. Figure 2(b) illustrates these processes in a simple case and where signallers are also receivers and where receivers are also recipients.

Where individuals compete for access to partners, RBPC theory proposes that displays of increasingly costly behaviour will be used as signals to attract the best partners, hence helping is 'competitive' because what matters most is how much one helps relative to others (Roberts, 1998; Barclay, 2004, 2013; van Vugt et al., 2007). In this way, helpful acts that are not directly reciprocated can be explained not as part of a system of indirect reciprocity, but as ways of enhancing a reputation which, through assortative partner choice, will lead to profitable relationships. RBPC theory provides a functional explanation for helping when the benefits arising from increased access to profitable partnerships exceed the costs of investing in a reputation (e.g., Barclay, 2011).



RBPC theory assumes that individuals honestly signal their quality as a strategic investment which changes receiver behavior (Maynard Smith & Harper, 2003). When RBPC theory was developed, the best-known theory of honest signalling was Zahavi's Handicap Principle (Grafen, 1990; Zahavi, 1975; Zahavi, 1977, 1997). This theory encapsulates the idea that the cost of a trait (or 'handicap') ensures its honesty because only the highest quality individuals can afford such a cost. It was applied to sexually selected traits such as the classic peacock's train, but also to helping (Zahavi, 1995). Zahavi's idea was that competition over prosocial behaviours such as mobbing predators led to increased 'social prestige'. RBPC theory built on the concept of honest signalling, but stressed the role of signals in choosing partners for cooperative interactions, and not their role in competing for social prestige. More recently the term 'handicap principle' has been disfavoured relative to the more generic 'costly signalling theory' (Gintis et al., 2001). We prefer to use the term 'honest signalling' rather than 'costly signalling' to avoid the misconception that the cost itself makes signalling systems honest. Signal honesty arises when the marginal benefits differ, typically between types such as low and high quality individuals (Lachmann et al., 2001; Penn & Számadó, 2020).

The use of helping as a costly signal of quality has since been formalized in a game theoretic framework (Gintis et al., 2001). This holds that there will be a separating equilibrium at which high quality types signal whilst low quality types do not. Cooperative reputations then allow observers to correctly deduce the underlying quality of the signaller (Bliege Bird & Smith, 2005). The use of helping as a costly signal of quality means that selection acts on how well the signal functions to change the behaviour of receivers, and not via the fitness effects of benefits given to recipients. Indeed it has been shown that 'costly but worthless' gifts may be the product of selection (Sozou & Seymour, 2005), such as an investment of time (Seymour & Sozou, 2009). If it pays high quality types to signal (and low quality types not to) then this can lead to unconditional helping instead of direct reciprocity (Lotem et al., 2003).

In formalizing RBPC as a two-stage process, we implicitly assume that a helper's actions can predict future ability or willingness to help. Such a relationship seems reasonable if signals reflect physical ability which remains stable over time; or if the stake that one individual has in another is stable (Barclay et al., this volume); or alternatively if there is a cost to behavioural flexibility (McNamara & Barta, 2020). We also assume that helping improves an individual's reputation, although Dumas et al. (this volume) show how this can be context-dependent. Further development of the RBPC approach should consider more explicitly the range of joint-

action games, since these can lead to either enhancement or suppression of cooperation (McNamara & Doodson, 2015).

## **4.2 Sexual selection**

Sexual selection is a process in which individuals compete for matings, often by producing signals of quality (such as the iconic peacock's train). A cornerstone of the concept of competitive helping was that just as individuals might compete for social partners using signals of cooperation, so these signals might also be used in competition for sexual partners. Helping might be a sexually selected signal revealing differences in quality. This theory remains outside of the mainstream cooperation literature but has been supported by several studies (see below).

## **4.3 Signalling intentions**

An alternative or additional hypothesis is that costly investments might be honest signals of *intent*. That is, those who develop a reputation for helping might be more likely to be more cooperative and so may be preferred as partners (Roberts 1998; Van Vugt, Roberts, and Hardy 2007; Barclay 2013; Barclay 2015; Silk 2002; Bliege Bird and Smith 2005). The notion that reputations might signal future intent (rather than underlying quality) has been stated verbally by several of these authors, and has been applied in multiple contexts like food sharing (Bird et al., 2018) has only recently been developed theoretically (Barclay & Barker, 2020; Quillien, 2020; Roberts, 2020); these models add an important dimension in understanding how reputations can be rewarded. Several studies support the idea that there are signalling benefits of generosity – that those who are more generous are trusted more (Diekmann et al., 2013; Fehrler & Przepiorka, 2013; Przepiorka & Liebe, 2016). One issue with costly signalling as an explanation for helping is that the theory fails to predict what costs should be spent on – whether on helpful acts or simply wasteful ones. This problem of 'equilibrium selection' might be solved if cues of cooperative behaviour have evolved into signals (Biernaskie et al., 2018).

## **4.4 Evidence for RBPC**

We consider that evidence for RBPC requires:

- (1) Actors invest in a reputation by helping more when their contributions are made public to potential partners (but see below);

- (2) Those who give more are more likely to be chosen as partners;
- (3) Those investing in a reputation and chosen as partners have higher net payoffs.

Experimental studies have used a two-stage design: first a game where individuals may signal by contributing more to potential partners, then a game where they can interact with a chosen partner. Several studies have used this design (Barclay & Willer, 2007; Hardy & Van Vugt, 2006; Sylwester & Roberts, 2010). Such studies show that contributions in social dilemmas increase not only when they are made public, but also further, when people are told that partners may be chosen for later interactions. The strategy of investing in a cooperative reputation reaps rewards in that better contributors obtain more profitable partnerships. Other experimental economic games have also been employed, e.g. both Chiang (Chiang, 2010) and Debove and colleagues (Debove et al., 2015) found ultimatum game players prefer partners who make more generous offers and that this can result in fairness. A link between charitable or blood donation and reputation has been found by for example (Bereczkei et al., 2007; Milinski et al., 2002a) and between blood donation and generosity (Lyle et al., 2009). Furthermore, competition for partners leads individuals to share honest gossip about others (Giardini et al, this volume). There is evidence that generosity is displayed publicly (Smith et al., 2003), but whether individuals do choose the most cooperative others as alliance partners seems context-dependent (Smith & Apicella, 2020). In fact the prediction that individuals will ostentatiously display higher generosity is simplistic, since it may then be apparent that the helper is motivated by strategic gains rather than a cooperative disposition. There is evidence that people either don't help when it is public or hide their beneficent acts from others (Raihani & Power, 2021).

Generosity is well known to be a desirable trait in mate choice (Miller, 2007). A few experimental studies have also found evidence that helping is used as a display to attractive members of the opposite sex (Farrelly et al., 2007; Iredale et al., 2008) is deemed attractive (Barclay, 2010; McAndrew & Perilloux, 2012), or results in higher mating success (Arnocky et al., 2017). Yet despite this, sexual selection is rarely invoked in explaining cooperation, and a high profile review does not include it as one of the routes to cooperation (Nowak, 2006). An analysis of online charity donations reveals that when males make large donations to attractive female fundraisers, other males respond in kind, providing field evidence for competitive helping in which helpful acts are used as a display to attract partners (Raihani & Smith, 2015).

## **4.5 Indirect reciprocity vs reputation-based partner choice**

Having described the processes of indirect reciprocity and of RBPC we compare their domains, assumptions, requirements and predictions. Some key differences between indirect reciprocity and RBPC are summarized below and in Figure 2.

**4.5.1. The structure of interactions.** RBPC is explicitly based on a two-stage model of cooperative interactions in which individuals first build up cooperative reputations and then choose partners for further interactions (Figure 2). The significance of this structure with two separate stages each involving different processes and having different payoffs is that whereas reciprocity must be evolutionarily stable within multiple rounds of donation games, RBPC can involve a loss in one stage (building a reputation by helping) in order to make a profit in a second stage involving a different kind of game (a mutually beneficial pairwise relationship).

**4.5.2. The role of signalling.** Signalling works when it changes a receiver's behavior (Maynard Smith & Harper, 2003). Receivers may or may not be recipients of any benefits resulting from the costs invested in a signal. RBPC theory explicitly incorporates signaling theory. In contrast, there has been some confusion in the literature about the relationship between indirect reciprocity and signalling. The image scoring model has been explicitly described as involving Zahavi's Handicap Principle (Ferriere, 1998; Nowak & Sigmund, 1998, 2005). It has been said that in indirect reciprocity individuals "produce a costly signal which triggers assistance" (Doebeli & Hauert, 2005) and that this can explain behaviours such as the competition for status described by Zahavi in Arabian babblers (Zahavi, 1997). Of course, donating in indirect reciprocity is costly, but models such as that of image scoring explicitly model it as operating through the transfer of benefits to a recipient and do not include or require any signalling function. Indirect reciprocity is therefore entirely independent of Zahavi's Handicap Principle: there is no condition dependence or communication of differences in quality. Help that is indirectly reciprocated need be no more Zahavian than that which is directly reciprocated. It could be argued that donation acts as a signal in indirect reciprocity, however the most parsimonious interpretation is that models of indirect reciprocity work through individuals picking up cues which provide information that is fed into the strategy of how to respond (Figure 1).

**4.5.3. Who benefits from the help.** Indirect reciprocity can only work when donations provide a benefit to the recipient. In RBPC, it is important to distinguish the receiver of the signal and the

recipient of the donation. These may be the same or different individuals. Furthermore there may actually be no benefit to any other individual (Bolle, 2001; Power, 2017; Sosis, 2004; Sozou & Seymour, 2005). A good example of helping as a signal with no benefit is where people contribute to step-level public goods games even when their contribution makes no additional effect on the provision of the public good: they just seem to be motivated to be seen to be contributing (Van Vugt & Hardy, 2009). Similarly, donating in economic games regardless of benefit has been dubbed 'ineffective altruism' to contrast with 'effective altruism' in which philanthropic acts are encouraged to have maximum impact.

**4.5.4. Selective benefit to the helper.** In both indirect reciprocity and RBPC, individuals invest in a reputation in order to make a net direct fitness benefit. The difference is that in indirect reciprocity the benefit comes via a reciprocal donation game whereas in RBPC the benefit comes via a mutually beneficial relationship. In the case of choosing a sexual partner, the benefits of investing in a good reputation and being chosen by a good partner may come through increased breeding success. This is not a form of reciprocity.

**4.5.5. Conditionality.** For any form of cooperation to work there must be some form of assortment: cooperators must interact more with other cooperators. In reciprocity, this happens through discrimination, whereas in RBPC it works through assortative partner choice. Indirect reciprocity is explicitly conditional in that it can only operate where individuals help those who help others and do not help those who do not help others. RBPC has no such conditionality. Individuals help others as a signal of abilities and/or cooperativeness (Samu & Takács this volume). They benefit from then being more likely to be chosen for profitable partnerships. The issue of conditionality is a key reason why indirect reciprocity cannot explain acts that cannot be conditional upon whether the recipient has donated, such as when giving to charity.

**4.5.6. Partner choice.** The theory of indirect reciprocity involves no partner choice. However, it can be extended so that individuals can select who to give to (Ghang & Nowak, 2015; Roberts, 2015b). This can have a crucial effect in making the simple strategy of image scoring more stable because partner choice (or recipient selection) avoids the problem of whether image scorers would enhance their own reputation at the cost of discrimination by giving to non-donors. However, indirect reciprocity cannot be extended to involve choosing a partner for repeated interaction since this would become direct reciprocity (Roberts, 2008) because individuals would then be helping in order to be more likely to receive a directly rather than an indirectly reciprocated benefit.

RBPC explicitly involves partner choice for profitable relationships. The process may be likened to a biological market (Noë & Hammerstein, 1994), although a market is based on trade between two different classes of individuals, those buying and those selling goods or services, whereas in mutual partner choice, all “suppliers” are also “consumers”. The key concepts of buyers and sellers and of shifting trading prices with supply and demand have helped elucidate behaviour such as where baboons exchange grooming for access to infants (Barrett et al., 2000). Biological Market Theory (BMT) has been developed and reviewed in (Barclay, 2011; Barclay, 2013; Barclay, 2016). Both BMT and RBPC emphasize the importance of partner choice. Where BMT differs from RBPC is that it is not explicitly about signalling: individuals make offers so as to be chosen as partners, but BMT is based on those offers being competitive in a marketplace. It is not about making offers that signal information, it is about making offers that provide benefits to recipients: for example in the baboon grooming system, more subordinate females need to spend longer grooming others to get access to infants (Barrett et al., 2000). One way to think of this is that BMT assumes buyers and sellers will maximize profits within a single ‘game’ scenario, whereas signalling assumes a combination of two ‘games’ the first in which players make a strategic loss so as to gain in second game when chosen as a partner for trade.

**4.5.7. Constraints.** It has been recognized that those with cooperative strategies may not always have the resources to cooperate. These so-called ‘phenotypic defectors’ have been included in models of IR and actually stabilize cooperation by maintaining discrimination in the system (Lotem et al., 1999; Sherratt & Roberts, 2001). Differences in state have also been considered by (Leimar & Hammerstein, 2001). Such differences between individuals are integral to the theory that individuals can choose between potential partners of differing quality (Roberts, 1998).

**4.5.8. Dynamics.** A corollary of choosing between partners on the basis of their reputations for helping is that those potential partners may then compete to be chosen. The prediction that this competition will lead to escalation in helping behaviour lies behind the theory of ‘competitive altruism’ (McNamara et al., 2008; Roberts, 1998; Roberts & Sherratt, 1998; Sherratt & Roberts, 1998). This kind of escalation has been demonstrated in experimental economic games (Barclay, 2004; Barclay & Willer, 2007; Sylwester & Roberts, 2010) and in charitable donations (Raihani & Smith, 2015). Importantly, this escalation shows that RBPC is explicitly built to deal

with graded helping behavior, either because individuals can vary the amount of help they give or because choosers evaluate the number of helping acts when decisions are binary.

#### **4.5.9 Humans and other animals.**

We have focused on reputation-based helping in humans whilst maintaining a broader theoretical perspective encompassing other animals. But is indirect reciprocity and / or RBPC found in non-human animals? There are a few examples of reputational concerns in non-human animals. For example, cleaner fish *Labroides dimidiatus* behave cooperatively towards client fish by removing ectoparasites when observed by bystanders (Bshary & Grutter, 2006). We do not know of specific examples of indirect reciprocity in non-human animals, and the examples that there are seem better explained as cases where individuals invest in a positive reputation and benefit from being chosen as a partner. It does seem that a concern for reputation is much more common in humans than in other animals. One hypothesis is that whilst signals of quality may be common in non-human animals in the contexts of aggression and courtship, the signals of intent involved in cooperative interactions may be more stable when supported by the human capacities for language and gossip (Roberts, 2020)(other authors, this volume).

**4.5.10. Evolution.** The initial evolution of indirect reciprocity, like direct reciprocity, is likely to depend upon reciprocators being close kin (Axelrod & Hamilton, 1981). It can be speculated that RBPC could have evolved from a system in which those seeking partners eavesdropped on cues. Once audiences attend to a cue of quality or intent, signalers will start investing in displaying that cue. This kind of process has been modelled by (Biernaskie et al., 2018). In this way, honest signals that have evolved from related cues could evade the equilibrium selection problem whereby costly signals could evolve to be non-cooperative (Gintis et al., 2001).

## **5. Discussion**

We have reviewed the essential features of different functional explanations for how individuals benefit from being seen to help others. We have argued that although indirect reciprocity has been the focus of much interest, it is just one possible explanation for reputation building. Indirect reciprocity has sometimes been wrongly used as an umbrella term for benefits arising through third parties. Just as individuals may benefit in ways other than direct reciprocity from

recipients of help, so they can also benefit in ways other than indirect reciprocity from third parties. A set of other theories, which might be united under the label of ‘strategic signalling’, offer explanations for why individuals might benefit from being seen to be helpful.

We have emphasized the role of partner choice in driving such signalling. We suggest that more research should be directed towards the theoretical underpinnings and empirical evidence for reputations as signals that are used in partner choice, as opposed to what strategy to play in indirect reciprocity games. This work may have broader significance in assessing whether the use of language and gossip, and the development of moral systems are indeed tied to indirect reciprocity, as has been suggested, or whether they have a function in choosing partners.

More empirical work is needed that clearly distinguishes indirect reciprocity from reputation based partner choice. One experiment suggested that RBPC is more effective in inducing strategic reputation building than is IR, and can thereby provide a more robust mechanism for maintaining cooperation in social dilemmas (Sylwester & Roberts, 2013). This is consistent with the hypothesis that where reputations are really important is when making decisions about partnerships. In Table 1 we set out some of the differences which may allow us to distinguish between systems of IR and of RBPC.

**Table 1.** Expected differences between reputation systems based on indirect reciprocity (IR) versus reputation-based partner choice (RBPC)

	IR	RBPC
Can individuals choose partners?	Optional	Integral
How many rounds are required?	Multiple, for reciprocation	A single two-stage round can be sufficient
Do helpers interact again with the recipient?	No (becomes direct reciprocity)	Not required
Must the “helping” benefit the recipient?	Yes	Not required
Are the return benefits costly to confer?	Yes	No
What are return benefits based upon?	Helper’s past actions	Helper’s inferred future value



Do individuals differ in quality and/or intentions?	Not assumed	Yes
Do the theories take account of constraints?	Can be incorporated as 'phenotypic defectors'	Helping can honestly signal quality within constraints
Do helping acts escalate in magnitude?	No	Yes

Theoretical interest in indirect reciprocity has focused on solving the problem of why individuals cooperate might with each other even when they never meet again. As a result, indirect reciprocity has come to be seen as the primary explanation for why individuals might benefit from cooperative reputations. However, the formalization of indirect reciprocity makes it an unlikely solution to real world issues such as how cooperation is sustained in large, fluid societies. In such societies it is unlikely that individuals who never meet again will nevertheless know the reputations of those with whom they will have one-off interactions. In contrast, the RBPC approach came out of formalizing how animals interact socially and form relationships. We have argued that we are more likely to invest in a reputation in the context of choosing partners for cooperative relationships than we are to follow the indirect reciprocity rule of 'help those who help others'. We therefore argue that the RBPC approach may be more productive in practice for explaining how acts of apparent selflessness such as donations to charity, heroism in humans or courtship feeding in birds are integral to long term social and sexual partnerships with repeated interactions. It may be that whilst theoretical focus within the cooperation literature has been on solving the hardest problems, real world behaviour may be explicable by the simpler processes of choosing among partners that display their qualities and intentions.

### **Authors' contributions**

GR wrote the m.s. with contributions from all authors.

### **Competing interests**

NR is the author of the 2021 book, *The Social Instinct: How Cooperation Shaped the World*

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