A tale of two defectors: the importance of standing for evolution of indirect reciprocity

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Abstract

Indirect reciprocity occurs when the cooperative behavior between two individuals is contingent on their previous behavior toward others. Previous theoretical analysis indicates that indirect reciprocity can evolve if individuals use an image-scoring strategy. In this paper, we show that, when errors are added, indirect reciprocity cannot be based on an image-scoring strategy. However, if individuals use a standing strategy, then cooperation through indirect reciprocity is evolutionarily stable. These two strategies differ with respect to the information to which they attend. While image-scoring strategies only need attend to the actions of others, standing strategies also require information about intent. We speculate that this difference may shed light on the evolvability of indirect reciprocity. Additionally, we show that systems of indirect reciprocity are highly sensitive to the availability of information. Finally, we present a model which shows that if indirect reciprocity were to evolve, selection should also favor trusting behavior in relations between strangers.

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1. Introduction

Thirty-one years ago Trivers (1971) laid out his theory of reciprocal altruism, which has since become the standard explanation for the evolution of cooperation between unrelated individuals. After Axelrod and Hamilton (1981) formalized Trivers' argument using an evolutionary game-theoretic model of the repeated prisoner's dilemma, myriad elaborations have been published (for example Sugden, 1986; Boyd and Lorberbaum, 1987; Boyd, 1989; Nowak and Sigmund, 1993; Boerlijst et al., 1997). Although reciprocal altruism may account for most cooperative behavior between non-kin in the animal world, new models are needed to adequately capture the complexities and subtleties of human cooperation. With some exceptions (for example Dugatkin and Wilson, 1991; Pollock and Dugatkin, 1992; Enquist and Leimar, 1993), reciprocal altruism models require repeated interaction within stable dyads ignoring processes such as communication, mobility, and reputation, which are universal features of human sociality.

Alexander (1987) suggested indirect reciprocity as a framework for understanding large-scale human cooperation, which “involves reputation and status, and results in everyone in the group continually being assessed and reassessed.” Nowak and Sigmund (1998a, b) formalized Alexander’s argument using both a game-theoretic model and computer simulations to model indirect reciprocity as a donation game in which individuals never interact with the same partner twice. In their game-theoretic model, Nowak and Sigmund (1998a) introduce reputation as an image score which is a state variable: individuals are either good or bad, depending on whether or not they donated in the previous round. They introduce the Discriminator strategy (DISC) which donates to those who are good and refuses to donate to those who are bad. Nowak and Sigmund find that, even under conditions in which individuals never interact with the same partner twice, the DISC strategy can resist invasion by indiscriminate defectors (ALLD). However, when indiscriminate altruists (ALLC) are introduced, cooperation is destabilized and defection is the only evolutionarily stable strategy (ESS).

In this paper, we show that indirect reciprocity cannot be based on an image-scoring strategy when errors are
considered. However, if reputation is modeled as *standing* (Sugden, 1986), then indirect reciprocity can be evolutionarily stable. Like an image score, an individual’s standing can either be good or bad. However, the rules governing how standings are assigned differ from those for image scores. Image scores only reflect actions: an individual that donated in the previous round will have a good image score in this round, while an individual that refused to donate will have a bad image score. Standing, on the other hand, reflects intent as well as action. So, as with image scores, any individual that donated in the previous round will have good standing. Refusals to donate, however, are parsed into two types: those that are *unjustified* and those that are *justified*. A defection is unjustified when an individual refuses to offer help to a partner in good standing. A defection is justified when an individual refuses to offer help to a partner in bad standing. While an unjustified defection always brings with it bad standing, a justified defection will leave the actor’s standing unchanged.

The difference between image-score and standing is crucial. In Nowak and Sigmund’s model, an individual playing the *DISC* strategy will refuse to offer help to an individual playing the *ALLD* strategy. As a result, observers will assign the *DISC* a bad image score and thus will refuse to help him in the next round. Because an image score only captures behavior and not intent, an individual is punished for refusing to help defectors. In contrast, when reputation is based on standing, a refusal to help a defector does not tarnish one’s reputation, only refusing help to someone in good standing will.

Computing standings may require greater cognitive capacity than image scores because it requires both knowledge of others’ behavior as well as inferential knowledge of their intent. The increased cognitive demands of a standing strategy may shed some light onto the evolutionary precursors to the emergence of indirect reciprocity and explain the apparent limitation of this type of behavior to humans.

In this paper, we reanalyze only Nowak and Sigmund’s model (1998a) of binary-valued image scores. Their other paper on the subject (1998b) models image scores taking on values from −5 to +5. In that model, any donation increments one’s image score by one unit, while any refusal to donate decrements one’s image score by one unit. When image scores take on this range of values, rather than binary values, Nowak and Sigmund find that the image-scoring strategy, although not an ESS, can persist for long periods of time. Leimar and Hammerstein (2001), using computer simulations, argue that, even when taking on a range of values, an image-scoring strategy cannot evolve. Their criticism revolves around assumptions of population structure and the role of genetic drift. As in this paper, they find that the standing strategy is evolutionarily stable.

2. Image scoring fails when errors occur

Although not evolutionarily stable, cooperative regimes based on image scoring can persist. (Nowak and Sigmund, 1998a) When the initial frequency of image scorers is sufficiently high, selection takes the population to a mixture of image scorers and indiscriminate altruists. When this equilibrium is reached, the defectors have been driven to extinction and selection is neutral with respect to image scorers and indiscriminate altruists. Eventually, the population drifts below a critical threshold of image scorers and defectors invade and quickly go to fixation. Once this has occurred, image scorers cannot reemerge unless one considers another process such as group selection. However, Nowak and Sigmund’s (1998a) claim that indirect reciprocity can be based on an image-scoring strategy hinges completely on the assumption that agents never commit errors. That is, individuals that intend to cooperate always do so and those that intend to defect always do so. In this section, by introducing errors, we show that cooperation based on image scoring cannot evolve; the defect equilibrium is reached quickly and deterministically.

We reanalyse Nowak and Sigmund’s model (1998a) after adding errors. Agents interact in an infinite, unstructured population. All agents begin with an image score of good. In the first round of social interaction, each agent acts as a potential donor to a randomly selected partner. If a donation is offered, the donor’s image score is good in the next round and his fitness is decremented by c while the recipient’s fitness is incremented by b. It is assumed that b > c > 0. If no donation is offered, the image score of the donor is bad in the next round and the fitness of both the donor and the recipient remains unchanged. Subsequent rounds of social interaction occur with probability w (0 ≤ w < 1).

Errors are introduced with the parameter ε, which denotes the probability of an intended donation failing. We ignore the reciprocal case of an agent accidentally donating when he intended not to. Additionally, we only consider errors of which both donor and recipient are aware. We distinguish these implementation errors from *perception* errors in which the donor believes that she donated while the recipient perceives that there was no donation. Perception errors add sufficient complexity to render analytic results intractable. However, Leimar and Hammerstein (2001) have run computer simulations considering both types of errors.

Like Nowak and Sigmund (1998a), we consider three strategies: indiscriminate altruist (*ALLC*), indiscriminate defector (*ALLD*), and the image-scoring discriminator (*DISC*). The frequencies of these strategies are denoted by x1, x2, and x3, respectively. *ALLC* always donates and *ALLD* never donates. Discriminators attend to their partner’s image score, donating to those
who are good and withholding donations from those who are bad. The DISC strategy is ‘nice’ in that it always attempts to donate in the first round.

Employing similar analytic techniques as Nowak and Sigmund (1998a), we find that the addition of errors results in the rapid and deterministic success of defectors (Fig. 1).\(^1\) This result is in stark contrast to the model without errors in which cooperation can persist indefinitely if the initial frequency of Discriminators is sufficiently high.

The addition of errors has a dramatic effect on the evolutionary dynamics along the ALLC–DISC edge. Recall, when errors are not considered, selection is neutral with respect to altruists and discriminators in the absence of defectors. When errors are added, there exists a stable, polymorphic equilibrium at which both ALLC and DISC are present. The frequency of DISC at this equilibrium is given by

\[ x_3 = \frac{c}{bw(1-z)} \]  

(1)

When errors do not occur, in the absence of defectors, everyone has a good image score and no one ever withholds donation. Thus, selection cannot distinguish between indiscriminate altruists and discriminators. When errors occur, indiscriminate altruists and discriminators respond differentially to error-committers, which then activates selection, leading to the stable, polymorphic equilibrium.

To understand this change in dynamics, first consider the case in which ALLC is common. The DISC strategy is favored by selection because it can, without cost, withhold aid from previous error-committers. When in the role of donor with a recipient who committed an error in the previous round, ALLC will donate, and thus have a good image score, while DISC will not, and thus have a bad image score. In this one interaction ALLC pays a cost \(-c\), which DISC does not. In the subsequent round, as DISC is rare, both the good ALLC and the bad DISC will be in the role of recipient with an ALLC donor. As ALLC does not attend to image score, it will donate to either individual. The invasion criterion for DISC is given by

\[ cwz(1-z) > 0. \]  

(2)

So, if errors occur with any probability and interaction persists, DISC will invade.

Next, consider case in which DISC is common. Here, ALLC invades because it does not engage in costly punishment of defections from errors. When an ALLC finds itself in the role of donor with a recipient who had just committed an error, it donates and thus maintains its positive image score. When a DISC is in the role of donor to the same error-committing recipient, it does not donate and thus acquires a negative image score. Because DISC is common, in the subsequent round, both the good ALLC and the bad DISC will be in the role of recipient with a DISC donor. As such, the donor DISC will offer aid to the good ALLC and not to the bad DISC. In this model, discriminators are punished (i.e. they acquire a bad image score) whenever they perform their police work by withholding aid from individuals with bad image scores. ALLC is not punished in this way because it does not do any of the police work. The invasion criterion for ALLC against DISC is given by

\[ w > \frac{c}{b(1-z)}. \]  

(3)

Finally, we look at the invasion criteria for ALLD along the ALLC–DISC edge. When condition (3) holds, there exists an unstable equilibrium given by

\[ x_3 = \frac{c}{bw(1-z)}. \]  

(4)

Notice that Eq. (4) and Eq. (1) are identical. Thus, the dynamics of this system are as follows. If the initial frequency of DISC is below Eq. (4), ALLD goes to fixation. If the initial frequency of DISC is above Eq. (4), selection leads to the ALLC–DISC polymorphism given by Eq. (1). From here, any perturbation, such as drift, which momentarily decreases the frequency of DISC, allows ALLD to invade and then go to fixation.

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\(^{1}\)The derivation of fitness functions for each strategy and the subsequent evolutionary dynamics analyses are presented in the appendix.
Whereas cooperation through image scoring could persist indefinitely when errors are not considered, cooperation can no longer evolve when they are added.

In a world with errors and reputations of good or bad, it is no longer sufficient to know who donated and who did not. Individuals must be able to distinguish between those defections motivated by punishment and those defections motivated by selfishness. That is, strategies must parse defections into those which are justified and which are unjustified.

3. Indirect reciprocity based on standing strategies can be an ESS

Strategies based on image scoring are not evolutionarily stable because they treat all defections as negative, and as a result punish justified ones. It seems plausible that a strategy that attended to whether an observed defection is justified might be more successful.

One way to do this is to introduce the notion of “standing.” Everyone starts out in good standing. An individual falls into bad standing whenever he fails to cooperate with a good-standing partner (unjustified defection). A donor’s standing is unchanged if he fails to cooperate with a bad-standing partner (justified defection). Good standing can be regained whenever an individual cooperates, irrespective of the standing of the partner.

In this section, we test whether indirect reciprocity based on a standing strategy can evolve, looking at two variants: reputation discriminator (RDISC) and contrite tit-for-tat (CTFT). We find that indirect reciprocity based on either of these strategies can evolve. Further, these strategies are evolutionarily stable with large domains of attraction.

3.1. Reputation discrimination

The RDISC strategy cooperates with those in good standing and defects on those in bad standing. In this regard, RDISC is identical to Nowak and Sigmund’s DISC. The difference in the two strategies lies in reputation assignment. The RDISC strategy assigns good standing to all those that cooperated in the previous round. When observing defections, the RDISC strategy makes a distinction between justified and unjustified defections. That is, an individual that defects on a good-standing partner is assigned bad standing while the reputation of an individual that defects on a bad-standing partner is unaltered.

As before, individuals live in an infinite, unstructured population. Each round, every individual acts as a potential donor to a randomly chosen partner. An intended donation can go wrong due to error with probability \( x \). One round of social interaction always occurs. A subsequent round occurs with probability \( w \).

There are three strategies: ALLC, ALLD, and RDISC, which have frequencies \( x_1, x_2 \), and \( x_4 \), respectively. As everyone starts out in good standing, the RDISC strategy always attempts to donate in the first round.\(^2\)

As in previous models, ALLD is an ESS (Fig. 2). Unlike DISC, the RDISC strategy is also evolutionarily stable. Indirect reciprocity can now evolve and persist because the Reputation Discriminator strategy parses defections into those that are justified and those that are unjustified. As such, good-standing individuals that withhold donation from bad-standing individuals are not subsequently punished. Compare this with the image-scoring strategy that punishes others for withholding donation from bad-standing individuals. Also, along the entire ALLC–RDISC edge, selection favors the RDISC strategy. Again this is due to the ability of RDISC to selectively withhold cooperation from error-committers. Finally, note that the domain of attraction for RDISC is extensive.

Along the ALLD–RDISC edge, there is an unstable equilibrium point given by

\[
x_4 = \frac{1 - w}{w} \frac{1}{b - c - 1 - x}
\]

\(^2\)Nowak and Sigmund (1998a) consider a DISC strategy that cooperates in the first round with probability \( p \). It is shown that if \( p \) is allowed to evolve, \( p = 1 \) is the stable equilibrium. A similar result holds for RDISC.
If the initial frequency of \( \text{RDISC} \) is above this threshold (5), then \( \text{RDISC} \) increases in frequency and drives \( \text{ALLD} \) to extinction. If, instead, the frequency of \( \text{RDISC} \) is below this threshold (5), then \( \text{ALLD} \) increases and dominates. As in other models of cooperation, there is a minimum initial frequency of cooperators necessary to drive the defectors to extinction.

It is not possible to derive a general expression that divides the phase space between the domains of attraction for \( \text{ALLD} \) and \( \text{RDISC} \). However, simulation results indicate that the separatrix can be approximated using the minimum initial threshold of \( \text{RDISC} \) (5). If the initial frequency of \( \text{RDISC} \) is above (5), then the cooperative ESS usually emerges. If, instead, the initial frequency of \( \text{RDISC} \) is below (5), then defection dominates.

### 3.2. Contrite tit-for-tat

In this section, we consider the ‘standing strategy’ (Sugden, 1986), also known as contrite tit-for-tat \( (\text{CTFT}) \) (Boyd, 1989). Using computer simulations, Leimar and Hammerstein (2001) have shown that indirect reciprocity based on this strategy can evolve. \( \text{CTFT} \), like \( \text{RDISC} \), distinguishes between justified and unjustified defections. \( \text{CTFT} \) and \( \text{RDISC} \) use identical rules in assigning reputation. However, the two differ in their behavioral decision rules. \( \text{RDISC} \) only attends to its partner’s standing, while \( \text{CTFT} \) attends to both its own standing and that of its partner. When in good standing, \( \text{CTFT} \) donates to those in good standing and refuses donation to those in bad standing. When in bad standing, \( \text{CTFT} \) always attempts to cooperate in order to regain its good standing. Otherwise, this model is identical with that presented in Section 3.1, with \( x_3 \) now denoting the frequency of \( \text{CTFT} \).

The dynamics for \( \text{RDISC} \) (Fig. 2) and \( \text{CTFT} \) (Fig. 3) are similar. This is not surprising as \( \text{RDISC} \) and \( \text{CTFT} \) are similar strategies. They differ in behavior only when in bad standing, which happens to \( \text{RDISC} \) with probability \( z \) (9) and to \( \text{CTFT} \) with probability \( z(1-x_2) \) (14). When error rates are low probabilities Eq. (9) and Eq. (14) are close to zero. As in Section 3.1, the domain of attraction for \( \text{CTFT} \) is extensive.

The unstable equilibrium between \( \text{ALLD} \) and \( \text{CTFT} \) along the \( \text{ALLD} \)-\( \text{CTFT} \) edge is given by

\[
x^3 + x^2w(1-x) - xw(1-x) = 0
\]

which cannot be easily solved for \( x_3 \).

As in Section 3.1, a general expression for the separatrix between the domains of attraction for \( \text{ALLD} \) and \( \text{CTFT} \) cannot be derived. As before, it can be approximated using the unstable equilibrium between \( \text{ALLD} \) and \( \text{CTFT} \) (6).
4. Information availability as the limiting factor

To investigate the effect of incomplete information, we now assume that an individual knows the standing of his current partner with probability \( q \), and with probability \( 1 - q \) he has no information about his partner’s reputation. When the partner’s reputation is known \( RDISC \) and \( CTFT \) use the same decision rules outlined in the previous section. When \( RDISC \) and \( CTFT \) meet an unknown partner, we assume that they attempt to donate. In the next section we show that such trusting behavior is evolutionarily stable under a broad set of conditions. The fixed \( ALLC \) and \( ALLD \) strategies are unaffected by this new parameter.

Figs. 4 and 5 depict the separatrices between the domains of attraction for \( RDISC \) (Fig. 4) or \( CTFT \) (Fig. 5) and \( ALLD \) at fixed values of \( q \). Looking at Fig. 4, suppose that \( q \) is set at 0.6. Thus, an individual knows the standing of his partner with a 60% probability. If the initial frequency of \( RDISC \) is sufficiently high that the population begins in the region to the right of the \( q = 0.6 \) line, then cooperation evolves and \( RDISC \) dominates. If instead, the initial frequency of \( RDISC \) is such that the population begins in the region to the left of the \( q = 0.6 \) line, then defection is the outcome; \( ALLD \) dominates. Note, the dividing lines in Figs. 4 and 5 are approximate; exact solutions cannot be readily derived. The unstable equilibrium along either

\[ \begin{align*}
\text{ALLD} & \quad \text{CTFT} \\
q = 0.9 & \quad q = 0.6 \\
q = 0.4 &
\end{align*} \]

Fig. 4. Domains of attraction for \( ALLD \) and \( RDISC \) at fixed values of \( q \). The farthest region to the left depicts the domain of attraction for \( ALLD \) at \( q = 1 \) (complete information). The remainder of the triangle represents the domain of attraction for \( RDISC \) at \( q = 1 \). Each dividing line to the right represents a decrement of 0.1 for \( q \). The farthest region to the right depicts the domain of attraction for \( RDISC \) when \( q = 0.4 \). The parameter values for this figure are as follows: \( a = 0.05, w = 0.95, b = 0.01, c = 0.003 \). Note, as explained in the text, these dividing lines are approximations.

\[ \begin{align*}
\text{ALLC} & \\
q = 0.9 & \\
q = 0.6 & \\
q = 0.4 &
\end{align*} \]

Fig. 5. Domains of attraction for \( ALLD \) and \( CTFT \) at fixed values of \( q \). The parameter values for this figure are as follows: \( a = 0.05, w = 0.95, b = 0.01, c = 0.003 \). Note, as explained in the text, these dividing lines are approximations.

5. Dealing with strangers and the emergence of trust

In every round of social interaction, all group members have a standing in their community. However, any particular individual may not know the standing for all other group members. In the previous section, we assumed that the \( RDISC \) and \( CTFT \) strategies always try to help strangers. We test this assumption by allowing these ‘trusting’ strategies to compete against ‘suspicious’ variants. Suspiciousness is introduced with a new model parameter, \( \delta \). Strategies intend to cooperate with partners of unknown standing with probability \( 1 - \delta \). Thus, when \( \delta = 0 \) trust is complete, individuals always attempt to help strangers. We label strategies for which \( \delta > 0 \) as either suspicious reputation discriminator (\( sRDISC \)) or suspicious contrite tit-for-tat (\( sCTFT \)).

Figs. 6 and 7 show the conditions under which trust \( (\delta = 0) \) dominates suspicion in dealings with strangers. To derive these results, we first assume that cooperation
has evolved; the world is dominated by either RDISC or CTFT. Then, we allow suspicion to evolve by introducing sRDISC or sCTFT, setting $\delta = 0.01$. Under most conditions, trusting strategies resist invasion by suspicious ones. When the effectiveness of communication ($q$) is low and/or the cost of donating ($c$ relative to $b$) is high, it pays to be suspicious when interacting with strangers. However, under such conditions, indirect reciprocity itself rarely emerges; defection is the more likely outcome.

6. Invasion criteria for standing strategies

Previous results indicate that indirect reciprocity based on a standing-type strategy can be evolutionarily stable. However, defection is also an ESS. In order for indirect reciprocity to emerge from a world of defection, cooperative individuals must assort with one another in a non-random fashion. Axelrod and Hamilton (1981) show that kin selection and reciprocal altruism operate synergistically such that with a little relatedness and a low probability of future interaction, TFT can invade a population of ALLD. Here, we determine the degree of non-random assortment (kin selection) necessary to allow for the evolution of indirect reciprocity. Under invasion conditions, cooperative individuals (RDISC or CTFT) are rare while ALLD is common. Thus, on average, an ALLD individual never meets a cooperative individual. Instead he interacts solely with other ALLDs. The story is different for cooperative individuals. Assuming that organisms interact preferentially with kin, there is a probability that a cooperative individual interacts with another cooperative individual because of common ancestry of the cooperative gene. This probability is measured by the model parameter $r$. With probability $1 - r$, the partner of a cooperative individual does not have the cooperative gene and instead plays the ALLD strategy.

Figs. 8 and 9 depict the relatedness required to allow for the invasion of cooperative strategies for fixed values of $q$ and $w$. In order for cooperative strategies to increase when rare, there must be a high probability that individuals know the standing of one another (high values of $q$). The number of interactions does not appear to have a strong effect. This analysis indicates that indirect reciprocity can evolve only if social knowledge is nearly complete ($q \approx 1$). When information is complete ($q = 1$), the degrees of relatedness as a function of interaction lengths ($w$) necessary for cooperative strategies to increase when rare through indirect reciprocity are very close to the values found for TFT to increase
when rare through reciprocal altruism (as shown by Axelrod and Hamilton, 1981). However, as social knowledge tapers off (when $q \ll 1$), the conditions for the evolution of direct reciprocity and indirect reciprocity rapidly diverge.

7. RDISC vs. CTFT

In criticizing the image-scoring strategy of Nowak and Sigmund (1998b), Leimar and Hammerstein (2001) state that “image scoring strategies fail to represent the true strategic interests of an individual. Individuals cannot benefit by decisions based partly or wholly on the score of a potential recipient. The only influence of an individual’s current aid-giving decision on the probability of receiving aid in the future is due to the change in the individual’s own score. A rational individual in this setting should then use a strategy that takes his or her own score into account, but ignores the score of a potential recipient”. In this section, we test this assertion by comparing the fitness of the two standing-type strategies thus far analysed (RDISC and CTFT) when they interact with each other. By setting the frequencies of ALLD and ALLC to zero, we can now look at which standing strategy variant selection favors.
Under all parameter settings, CTFT has marginally higher fitness than RDISC. This slight fitness differential is attributed to the CTFT decision rule of cooperating when in bad standing. Recall, RDISC only cooperates when matched with a good-standing partner. Because this fitness differential is small, selection between the two strategies is essentially neutral. In such cases, other processes determine which strategy ultimately flourish.

First, perception errors have not been considered. The two strategies may respond differentially to these types of errors. Second, we have thus far stated that both RDISC and CTFT look favorably upon all cooperative acts. If the RDISC strategy were altered such that cooperation with bad standing individuals confers bad standing on the donor, CTFT would not be able to invade. This decision rule may approximate cultural norms that frown upon upstanding members of the community associating with known felons.

8. Discussion

To understand the evolution of human cooperation, new models are needed that move beyond reciprocal altruism. The model of indirect reciprocity presented by Nowak and Sigmund (1998a) represents an important step in this direction. Although dealing with an extreme and simplified case: a donation game with new partners every round, Nowak and Sigmund’s model touches upon unique aspects of human sociality that previous models were not able to capture such as trust, gossip, and reputation (for exceptions see Dugatkin and Wilson, 1991; Pollock and Dugatkin, 1992; Enquist and Leimar, 1993). However, as we demonstrate in this paper, if a process such as indirect reciprocity were to evolve and reputations were binary (either be good or bad), it could not be based on an image-scoring strategy (see also Leimar and Hammerstein, 2001). Image scoring requires only that agents be able to acquire information as to the actions of others. Those that cooperate are assigned positive image scores, while those that defect are assigned negative image scores. Our analysis shows that additional information is necessary to stabilize indirect reciprocity. Specifically, individuals must be able to infer motivations from observed defections, parsing them into those that are justified and those that are unjustified. Strategies that use standing have this property and are found to be evolutionarily stable.

In this paper, we analyse two standing strategy variants (RDISC and CTFT) to show that it is not crucial that individuals attend to their own standing when deciding upon a course of action. However, it is crucial that individuals are able to discern motivation from observed defection. The question then becomes how individuals make this distinction. In systems of reciprocal altruism, organisms can track the actions of their partners through direct observation. When one partner defects out of turn, the other can take appropriate action. In a system of indirect reciprocity, where individuals are constantly paired with new exchange partners, what does an individual make of a partner who defected on his previous partner? Was the defection retaliatory or selfish? If group size is small, perhaps individuals can monitor the goings on of all others and thus properly attribute standing to a partner observed defecting on another. As group size increases, however, this assumption seems implausible. Language seems to offer individuals access to information about others that were not able to observe directly. Integrating this hearsay with personally observed information, individuals may be able to accurately track the standings of other group members. This argument is parsimonious with the observation that something like indirect reciprocity seems to be extremely rare in nature with the notable exception of humans. Without effective communication, reputations may only exist in the context of a stable dyad. Once communication is possible, an individual’s reputation takes on more global characteristics.

Recent experiments investigate the propensity of subjects to cooperate when there is no expectation of reciprocation from current partners. Wedekind and Milinski (2000) find that individuals playing a donation game are more likely to donate to those that had previously donated. However, as Leimar and Hammerstein (2001) have noted, these experiments do not allow for a standing strategy to be implemented. It is unclear whether potential donors would respond differentially to observed justified and unjustified defections. To test this, Milinski et al. (2001) add second-order information with the hypothesis that image-scoring strategists would not use this second-order information whereas standing strategists would. The authors find that subjects are as likely to withhold donation from justified defectors as they are from unjustified defectors, which is indicative of an image-scoring strategy. This interpretation is misleading because it fails to capture how the standing strategy works in practice. The model presented by Milinski et al. (2001) assumes that the standing strategy uses entire action-histories for all other group members to infer motivation from recently observed actions. The authors ignore language, the crucial adaptation that makes indirect reciprocity possible. Rather than encoding action-histories, individuals encode standings (in this case a state variable with a value good or bad) for other group members, engage in social interaction, communicate with one another, and then update standings. An experiment that incorporates this would allow one to accurately distinguish between an image-scoring strategy and a standing strategy.
It is interesting to note that Nowak and Sigmund (1998a) mention the standing strategy as possibly a better candidate for explaining indirect reciprocity. They did not model the strategy stating that it would be susceptible to errors in perception. Including such errors adds sufficiently complexity to render analytic techniques intractable. However, Leimar and Hammerstein (2001) subjected the standing strategy to errors in perception in their computer simulations. So long as errors in perception are sufficiently low relative to errors in implementation, the standing strategy is an ESS. Preliminary work by one of the present authors (Panchanathan) suggests that when agents are embedded in social networks, this restriction is lifted; cooperation based on a standing strategy can be sustained in the face of high rates of perception error.

Appendix A. Image scoring fails when errors occur

In this section we generalize the model of indirect reciprocity presented by Nowak and Sigmund (1998a) by including errors. The error-rate is denoted by the parameter $\alpha$. Two simplifying assumptions are made. First, only one-way errors can occur (intended cooperation leading to accidental defection). Second, errors are assumed to be sufficiently rare that the possibility of simultaneous errors can be ignored.

The frequencies of the strategies $ALLC$, $ALLD$, and $DISC$ are denoted by $x_1$, $x_2$, and $x_3$, respectively. The parameter $w$ measures the probability of an additional round of social interaction. The parameter $b$ measures the incremental benefit to fitness received by an individual when his partner cooperates. Likewise, $c$ measures the incremental cost borne by the actor when he cooperates.

Employing similar methods to Nowak and Sigmund (1998a), the following fitness functions can be derived:

\begin{align*}
W(ALLC) &= \frac{1 - z}{1 - w} [b x_1 + b x_3 (1 - w x) - c], \\
W(ALLD) &= \frac{1 - z}{1 - w} b x_1 + (1 - z) b x_3, \\
W(DISC) &= \frac{[b - c (1 - x) - b x_3 w (1 - x)] [1 - w + w x_3 (1 - x)]}{(1 - w) (1 - w x_3 (1 - x))} - b [x_2 + x (x_1 + x_3)].
\end{align*}

From these fitness functions, the derivations of Eqs. (1)–(4) are straightforward. To find the equilibrium between $ALLC$ and $DISC$ (1), simply find the value of $x_3$ when $W(ALLC) = W(DISC)$, setting $x_1 = 1 - x_3$ and $x_2 = 0$. For the invasion criterion of $DISC$ against $ALLC$ (2), set $x_3 = x_2 = 0$ and $x_1 = 1$, finding the condition under which $W(DISC) > W(ALLC)$. For the invasion criterion of $ALLC$ against $DISC$ (3), set $x_1 = x_2 = 0$ and $x_3 = 1$, finding the condition under which $W(ALLC) > W(DISC)$. Finally, for the invasion criterion of $ALLD$ against a population comprised of $ALLC$ and $DISC$ (4), we find when $W(ALLD) > x_1 W(ALLC) + x_3 W(DISC)$ given $x_1 = 1 - x_3$ and $x_2 = 0$. When condition (3) holds, the unstable equilibrium (4) is the only one in the interval of $[0, 1]$. When (3) does not hold, the shadow of the future is not sufficiently large; $ALLD$ is the only ESS.

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parameter \( q \), which measures the probability that an individual knows the standing of his current partner.

### A.2. Reputation discrimination

The frequencies for \( ALLC \), \( ALLD \), and \( RDISC \) are given by \( x_1 \), \( x_2 \), and \( x_4 \), respectively. It is also necessary to track the frequency of individuals for a given strategy in good standing in any particular round. We denote these frequencies with \( g_n(ALLC) \), \( g_n(ALLD) \), and \( g_n(RDISC) \), which refer to the frequency of good standing individuals in round \( n \) for \( ALLC \), \( ALLD \), and \( RDISC \), respectively. Additionally, we denote the frequency of good-standing individuals among the whole population as \( g_n \). In round 1, as no interactions have yet taken place, we assume all individuals are in good standing.

Thus in round \( n \), where \( n > 1 \),

\[
g_n(ALLC) = g_{n-1}(ALLC)(1 - g_{n-1}x_2) + (1 - g_{n-1}ALLC) \times (1 - g_{n-1}ALLC) = 0, \]

\[
g_n(RDISC) = g_{n-1}(RD\text{ISC})(1 - g_{n-1}x_2) + (1 - g_{n-1}(RDISC)) \times k(1 - g_{n-1}(RDISC)) \]

\[
g_n = x_1g_n(ALLC) + x_4g_n(RDISC). \tag{8} \]

As these recursions cannot be solved, we cannot compute fitness functions directly. However, simulation results indicate that these recursions rapidly converge. Therefore, to derive the fitness functions, we add the first round payoffs to the payoffs in round \( n \), by which the recursions in Eq. (8) have converged, weighted by \( w/1-w \). This last term reflects the weighting given to all rounds after the first. Simulation analysis reveals that little is lost using this approach.

Before computing fitnesses, we derive the equilibria for the recursions in Eq. (8).

\[
g_n(ALLC) \rightarrow 1 - z(1 - x_2), \]

\[
g_n(RDISC) \rightarrow 1 - \frac{z(1 - x_2)}{1 - qx_2}. \tag{9} \]

To find these equilibria, we make the following approximations. At equilibrium, these frequencies are close to 1. Thus all terms such as \((1 - g_n(ALLC))^2 \), \( z(1 - g_n(ALLC)) \), and \( x_1^2 \) tend to zero. The same holds true for \( RDISC \).

To compute fitness functions, we derive both round 1 payoffs and the payoffs in round \( n \), where condition (8) has been reached.

\[
W_1(ALLC) = (1 - z)[b(x_1 + b(1 - q)] - c],
\]

\[
W_1(ALLD) = (1 - z)[b(x_1 + b_3)],
\]

\[
W_1(RDISC) = (1 - z)[b(x_1 + b_4)] - c. \tag{10} \]

Summing up:

\[
W(ALLC) = \frac{1 - z}{1 - w}[b(x_1 + b_4)(1 - wq(1 - g_n(ALLC)) - c], \tag{11}
\]

\[
W(ALLD) = \frac{1 - z}{1 - w}[b(x_1 + b_4)(1 - w)], \tag{12}
\]

\[
W(RDISC) = \frac{1 - z}{1 - w}[b(x_1 + b_4)[1 - wq(1 - q)]] + \frac{1 - z}{1 - w} x_2[1 - wq(1 - g_n(RDISC))]. \tag{13}
\]

To find the unstable equilibrium between \( RDISC \) and \( ALLD \) (5), set \( W(ALLD) = W(RDISC) \), \( x_2 = 1 - x_4 \), and \( q = 1 \).

### A.3. Comtrite tit-for-tat

The frequencies for \( ALLC \), \( ALLD \), and \( CTFT \) are given by \( x_1 \), \( x_2 \), and \( x_3 \), respectively. As before, we track the frequency of individuals for a given strategy in good standing in any particular round. These frequencies are denoted by \( g_n(ALLC) \), \( g_n(ALLD) \), and \( g_n(CTFT) \), which refer to the frequency of good standing individuals in round \( n \) for \( ALLC \), \( ALLD \), and \( CTFT \), respectively. Additionally, we denote the frequency of good-standing individuals among the whole population as \( g_n \).

\[
g_n(ALLC) = g_{n-1}(ALLC)(1 - g_{n-1}x_2) + (1 - g_{n-1}(ALLC)) = 0, \tag{14}
\]

\[
g_n(CTFT) = g_{n-1}(CTFT)(1 - g_{n-1}x_2) + (1 - g_{n-1}(CTFT))(1 - x_2), \tag{15}
\]

Using similar approximations as before, we find the equilibria for these recursions.

\[
g_n(ALLC) \rightarrow 1 - z(1 - x_2), \tag{16}
\]

\[
g_n(CTFT) \rightarrow 1 - z(1 - x_2). \tag{17}
\]

As before, we find the payoffs in round 1.

\[
W_1(ALLC) = (1 - z)[b(x_1 + x_3) - c], \tag{18}
\]

\[
W_1(ALLD) = (1 - z)[b(x_1 + x_3)], \tag{19}
\]

\[
W_1(CTFT) = (1 - z)[b(x_1 + x_3) - c]. \tag{20}
\]

In round \( n \) we have

\[
W_n(ALLC) = \frac{1 - z}{1 - w}[b(x_1 + b_4) - c], \tag{21}
\]

\[
W_n(ALLD) = \frac{1 - z}{1 - w}[b(x_1 + b_4)], \tag{22}
\]

\[
W_n(RDISC) = \frac{1 - z}{1 - w}[b(x_1 + b_4) - c]. \tag{23}
\]
\[ W_{n}(ALLC) = (1 - \beta) [b x_1 + b x_3 (g_n(CTFT)) + (1 - q)] \]
\[ + (1 - g_n(CTFT)) - c], \]
\[ W_{n}(ALLD) = (1 - \beta) [b x_1 + b x_2 (g_n(CTFT)) (1 - q) + (1 - q)] \]
\[ + (1 - g_n(CTFT))), \]
\[ W_{n}(CTFT) = (1 - \beta) [b x_1 + b x_3 (g_n(CTFT)) (q g_n(CTFT) + (1 - q)] \]
\[ + (1 - g_n(CTFT))], \]
\[ W(ALLC) = \frac{1 - \frac{q}{1 - w}}{1 - w} [b x_1 + b x_3 (1 - w q g_n(CTFT)) \]
\[ (1 - g_n(ALLC)) - c], \]
\[ W(ALLD) = \frac{1 - \frac{q}{1 - w}}{1 - w} [b x_1 + b x_3 (1 - w q g_n(CTFT))], \]
\[ W(CTFT) = \frac{1 - \frac{q}{1 - w}}{1 - w} [b x_1 + b x_3 \]
\[ (1 - w q g_n(CTFT)) (1 - g_n(CTFT)) - c] - c]. \]

To find the unstable equilibrium between CTFT and ALLD (6), set \( W(ALLD) = W(CTFT) \), \( x_2 = 1 - x_3 \) and \( q = 1 \).

References


