The costs and benefits of resource sharing: reciprocity requires resource heterogeneity

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Abstract

The evolution of resource sharing requires that the fitness benefits to the recipients be much higher than the costs to the giver, which requires heterogeneity among individuals in the fitness value of acquiring additional resources. We develop four models of the evolution of resource sharing by either direct or indirect reciprocity, with equal or unequal partners. Evolution of resource sharing by reciprocity requires differences between interacting individuals in the fitness value of the resource, and these differences must reverse although previous acts of giving are remembered and both participants survive. Moreover, inequality in the expected reproductive value of the interacting individuals makes reciprocity more difficult to evolve, but may still allow evolution of sharing by kin selection. These constraints suggest that resource sharing should evolve much more frequently by kin selection than by reciprocity, a prediction that is well supported by observations in the natural world.

Introduction

After successful foraging bouts, vampire bats sometimes share food by regurgitation with their less successful roost-mates (Wilkinson, 1984; also DeNault & McFarlane, 1995). They share with both kin and nonkin, as long as they have a long-standing social interaction. Wilkinson (1984, 1987) has shown that this sharing behaviour has likely evolved by both kin selection and reciprocity. This sharing of food is almost essential for the survival of vampire bats; they would starve to death after only about two unsuccessful nights without feeding (Wilkinson, 1984). The benefits of sharing food are immense, but what of the costs? Wilkinson (1984) has shown that the costs of giving some food away after a successful bout of foraging are much lower than the benefit, because the relationship between fitness (in this case, probability of starvation) and food level is not linear (McNab, 1973). A small amount of food matters more when a vampire bat is close to starvation than when it is

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sated. This asymmetry of value of a resource seems to be an essential element of the evolution of food sharing behaviour.

Cooperation is relatively common in the animal kingdom, yet resource sharing (without coercion or immediate payment) is very rare among unrelated individuals (Stevens & Gilby, 2004; see also our *Discussion*). Reciprocal altruism has been successfully applied to explain many behaviours related to grooming and defensive coalitions, so why is it so rarely responsible for the evolution of resource sharing? In this paper, we explore the situations in which resource sharing can evolve by reciprocity, and we show that the conditions for such reciprocity should rarely exist. Evolution of cooperation or altruism by reciprocity requires that the benefits of an act far outweigh its costs; resource sharing involves physical constraints that make it unlikely for these costs and benefits to differ sufficiently for sharing to increase the fitness of the giver.

An altruistic act, by Trivers' (1971) definition, gives benefits to its receiver and incurs direct costs to its performer (although the indirect effects of the act may be positive to the giver). In evolutionary terms, these costs and benefits are measured in terms of fitness. All else being equal, behaviours that lower fitness of their

carriers are not expected to increase by evolution, but of course various mechanisms can in principle allow for altruism to evolve. These mechanisms fall into at least two categories, which are not mutually exclusive: kin or group selection (Hamilton, 1964a,b; Maynard Smith, 1964; Wilson, 1975; Wilson & Sober, 1994) and reciprocal altruism (Trivers, 1971; Axelrod & Hamilton, 1981; Nowak & Sigmund, 1998).

The evolution of altruism by either of these mechanisms depends on three things: the cost (in fitness) to the giver of the altruistic act, the benefit to its recipient, and some measure of the relative probability that the act will eventually lead to a gain in fitness of either the giver or another individual that shares its alleles. This is most famously represented in Hamilton's Rule (Hamilton, 1964a,b), which describes the conditions under which altruism is expected to evolve by kin selection:

$$c/b < r$$

where c is the fitness cost to the individual performing the act of altruism, b is the benefit to the recipient and r is the genetic relatedness between the giver and the recipient. The conditions that allow the evolution of altruism by reciprocity among unrelated individuals sometimes can be expressed in a similar format (Nowak & Sigmund, 1998),

$$c/b < q$$

where q is the probability that, as a result of acting altruistically at one time, a giver may receive the benefit of the altruistic act in the future. The relatedness r and the probability q both describe the relative probability that an individual with the altruist's genotype will receive the benefits of an altruistic act. For a single act of giving, the meanings of c and b are the same in both equations. (If related individuals have repeated interactions, then the interpretation of b and c in Hamilton's rule must also include the indirect benefits of reciprocity.)

Since Trivers' original paper, altruism has been more widely defined as an act that reduces the fitness of the actor in the long term. If an act of giving on average increases the fitness of the actor over the long term, then in strict terms it is not altruistic (Hamilton, 1964a,b; Grafen, 1985; West *et al.*, 2007). Reciprocity will only evolve by natural selection if it increases the life-time fitness of individuals that give. Hence, we will use the term 'reciprocity' rather than 'reciprocal altruism' throughout this paper.

To understand the conditions under which giving may evolve, we need to know when the benefits and costs of actions are expected to fit the required criteria. Both r and q are usually expected to be much less than 1, meaning that the benefits must greatly exceed the costs in order for giving to evolve. This asymmetry between cost and benefit should often exist in the context of resource sharing. Individuals will vary in their resource supply, and they may vary in their ability to convert resource into fitness. Theoretical examinations of the relationship between fitness and resource status have often assumed it to be either convex or sigmoidal in shape because of diminishing fitness returns with increasing resource levels (Schaffer, 1978), based on the assumption that an individual should saturate in its ability to convert high levels of resources into reproductive success. The relationship between resource access and fitness has been the subject of some empirical work, and the results are mixed and incomplete. Although it is reasonable to assume that there is an upper bound to fitness as a function of resource status under ideal conditions, there may be cases where the natural range of available resources constrains the fitness/resource function to a region where it is linear, or nearly so (Thomas, 1983; Hutchings, 1991). Other studies have found that the shape of the curve may depend upon specific environmental conditions (Hirche *et al.*, 1997; Strohm & Linsenmair, 2000). However, empirical research has found broad support for convex curves among a diverse range of organisms from *Drosophila melanogaster* (Chiang & Hodson, 1950) to the bushcricket *Requena verticalis* (Gwynne, 1984) and the vampire bat, *Desmodus rodentus* (McNab, 1973; Wilkinson, 1984).

In Fig. 1, we draw two possible relationships between the supply of resource available to an individual and that individual's fitness, which can vary both within and between species. In order for the recipient's fitness gain (b) to exceed the fitness costs (c) accrued by the donor as a result of exchange of the gift between the actors, the gain on the resource/fitness function must be greater for the recipient than the donor at their current resource levels. (If the change in resource level is small relative to the second derivative of the resource/fitness function, this change is well approximated by the slope.) In Fig. 1a, with a linear relationship between resources and fitness, it is impossible for c/b to be less than 1, so we would not expect resource sharing to evolve, regardless of the value of other factors. In Fig. 1b the resource/fitness function is sigmoidal; consequently the change in fitness per unit of resource depends upon the resource level of the actors. With this function, an individual in high resource status can give resources at a lower cost than the benefits derived by the recipient with a lower resource status.

With linear and constant resource/fitness functions, reciprocal resource sharing should never evolve, because b cannot exceed c. With variation over time within individuals or variation among individuals in their resource status, the necessary asymmetry between costs and benefits may exist. For sharing to evolve by reciprocity, however, the benefits of sharing must exceed the costs for each individual, which implies that individuals must change over time with respect to their fitness value of resources. If the value of resources does not change over time for each individual, then at best a giver may recover what it has previously lost.
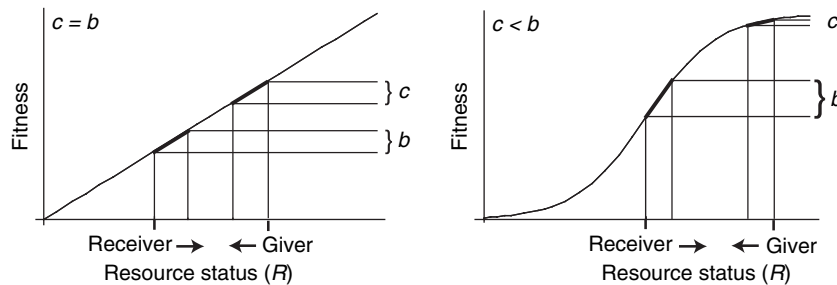
Fig. 1 Resource/fitness functions. The fitness costs or benefits of losing or gaining some amount of resource depend upon the slope of this function for the individuals involved. In the left panel, fitness is linearly associated with resources, and the costs to any giver are equal to the benefit to a receiver. In the right panel, the curvature of the resource/fitness function varies as a function of resource status. Because a potential giver (top right) has an amount of resources that puts it in a relatively flat area of this curve, the fitness costs of losing these resources is small. For the receiver in this case, however, the same amount of resource added to its value gives it a much larger increase in fitness, because its resource/fitness function is much steeper at that point. In this case the benefits greatly exceed the costs, but had the roles of giver and receiver been reversed the costs would have outweighed the benefits.

In this paper, we extend the theory of reciprocity to include the effects of asymmetries in the costs and benefits of donors and receivers, a feature that appears to have importance for the evolution of food sharing in the vampire bat, but which may be generally unlikely in nature. Reciprocal resource sharing requires that the giver and receiver value a resource differently, and that the values of the resource reverse before the reciprocal transaction. This change in the fitness value of resources must occur although the potential future giver still remembers the previous transaction and both parties survive and remain in proximity. The rate of uncorrelated change in resource status of interacting individuals sets the time scale for the memory required to maintain reciprocity. In this paper we quantify this logic, and we show that the conditions for the evolution of resource sharing by reciprocity will become extremely difficult to satisfy. In all but a few cases, resource sharing is unlikely to evolve by reciprocity, but sharing may evolve readily via kin selection.

Conditions for the evolution of resource sharing

We assume that the resource status of individuals can change over time, and as a result the fitness effects of giving or receiving resources also can change for an individual. For simplicity, we will allow any individual to be in one of only two possible states at a given time. We will assign the labels 'high' and 'low' status to these two states, but this is potentially misleading because what is important is that the 'high' status individuals have lower slopes to their resource/fitness functions than do individuals of 'low' status. (See Fig. 1.)

We will consider the case when possible episodes of resource sharing are discretely divided into episodes of possible interaction between individuals. We call these interactions 'rounds', but we do not mean to imply any

necessary regularity of these episodes. For example, in the case of vampire bats, the interactions following each night's foraging would constitute a round. In each round, individuals are paired with a single other individual, and these pairings are random with respect to the strategies employed by the partners. With direct reciprocity, individuals are paired at random for the first round, but then the pairings are continued until one of the two partners dies or leaves the immediate area. With the indirect reciprocity models, the pairs are formed at random and independently each round. Note that our derivations do not prohibit an individual from engaging in interactions with multiple individuals, as long as the rules for each pairing are the same. Multiple interactions, if distributed equally for each phenotype, will affect the magnitude of the effects of sharing, but not the relative ranks of the phenotypes.

Definitions

We imagine three possible strategies (corresponding to alleles at an unreasonably simplified locus): 'altruist' (A), 'cheater' (C), and 'discriminator' (D). We use these letters as subscript identifiers throughout; for example, the frequencies of these three strategies are defined to be p_A, p_C and p_D respectively. These strategies are modified from those used by Nowak & Sigmund (1998). The altruist strategy always gives when it is at high status and paired with a low status individual. The cheater individuals never give. Discriminators give when high status and paired to low status individuals, but only if they do not believe their partner to be a cheater.

We assume that the players have no information about the number of rounds that will be played. Individuals have high status with probability η. The probability of moving from high state to low between successive rounds is π_{hl}, and the probability per round of changing from low to high status is π_{lh}. These transition probabilities are

unaffected by past resource sharing. Individuals have some chance of death or emigration between rounds; the probability that an individual remains alive and present is s for all individuals.

We use these assumptions and definitions to derive the conditions under which sharing might be stable. The notation is summarized in Table 1.

Direct reciprocity between individuals with the same resource/fitness function

Reciprocity, either direct or indirect, requires that the same individual who gives at some point has a high expectation of being a recipient in the future. In this model, a discriminator strategy gives when at high status to a partner of low status, but only if the partner has not refused giving in the previous round if the conditions were correct. In other words, the discriminator only punishes defection if in the previous round it was at low status, the partner was at high status, no gift was given, and if this defection is remembered with probability m. In all other cases the discriminator gives by the same rules as the altruist.

To investigate the fitness effects of these strategies, we consider the marginal effect on fitness over multiple potential rounds of sharing. Because the interacting individuals have no information about their partners in the first round, but subsequently they do, the expected fitness effects may differ between the first and all subsequent rounds. The marginal fitness effect of each strategy in a given round is labelled $\delta W_{i,t}$, where i indicates the strategy and t is the round. Total fitness effects are assume to be additive over all rounds. According to the rules we have laid out, individuals only incur the cost of giving or the benefit of receiving when

Table 1 Definitions of terms.

Variable	Meaning
c	Fitness cost of one act of giving
b	Fitness benefit of one act of giving
A	Altruist strategy – always gives
C	Cheater strategy – never gives
D	Discriminator strategy – gives to all but perceived cheaters
p_i	Phenotypic frequency of strategy i (where i is A, C, or D)
η	Probability of being in high status
π_{hl}	Probability that a high status individual changes to low status by the next round
m	Probability that a lack of giving in the previous round is remembered by the interacting partner
$\delta W_{i,t}$	Fitness effects on strategy i from round t
σ	Probability of survival between rounds
ζ	Probability that a low-high pair were both reversed in status in the previous round
J	Probability that a low status cheater revealed itself as cheater in the previous round
O, Y	Markers to indicate two different types of individuals with potentially different resource/fitness functions

one partner is high and another partner is low status; therefore the fitness differences between strategies are all proportional to the probability of a high status individual being paired with a low status individual, or $\eta(1-\eta)$. The fitness effects of the first round are:

$$\delta W_{A,1} = \eta(1-\eta)[-c + b(p_A + p_D)]$$
$$\delta W_{C,1} = \eta(1-\eta)[b(p_A + p_D)], \qquad (1)$$
$$\delta W_{D,1} = \eta(1-\eta)[-c + b(p_A + p_D)]$$

and for subsequent rounds, assuming persistence of both partners:

$$\delta W_{A,t>1} = \eta(1-\eta)[-c + b(p_A + p_D)]$$
$$\delta W_{C,t>1} = \eta(1-\eta)\{b[p_A + p_D(1 - \zeta m)]\}. \qquad (2)$$
$$\delta W_{D,t>1} = \eta(1-\eta)[-c(1 - p_C \zeta m) + b(p_A + p_D)]$$

The number of rounds that affect fitness depends on the survivorship (and residency) of both partners. The probability that a partnership persists t rounds after the first is s^{2t}. Thus the total expected fitness change because of resource sharing for discriminators will be

$$\delta W_D = \delta W_{D,1} + \sum_{t=1}^{\infty} s^{2t}\delta W_{D,t>1} = \delta W_{D,1} + \frac{s^2 \delta W_{D,t>1}}{1 + s^2}. \quad (3)$$

Similar equations describe the other strategies.

In eqn (2), ζ is the probability that a pair of individuals that are currently high and low status were in the previous round reversed: low and high. For the special case where changes in status are uncorrelated for members of a pair,

$$\zeta = \left(\frac{\eta \pi_{hl}}{\eta \pi_{hl} + (1-\eta)(1-\pi_{lh})}\right)\left(\frac{(1-\eta)\pi_{lh}}{\eta(1-\pi_{hl}) + (1-\eta)\pi_{lh}}\right). \quad (4)$$

This term ζ increases when both high and low status individuals are prone to change status between rounds. If either type does not change status frequently, ζ will be small.

It is convenient to look at the differences in fitness effects of the altruists and cheaters compared to the discriminators:

$$\delta W_D - \delta W_A = \frac{cm\zeta \, p_C s^2 \eta(1-\eta)}{1 - s^2} \qquad (5)$$

$$\delta W_D - \delta W_C = \frac{\eta(1-\eta)[b \, m\zeta p_D s^2 - c(1 - m \zeta p_C s^2)]}{1 - s^2}. \quad (6)$$

With these differences, the discriminator strategy is more fit than the altruist, provided that there are any cheaters in the population and that the direct effect of giving is reduced fitness ($c > 0$). Thus the pure altruist strategy will be at a low frequency except by drift and mutation, and we will ignore it hereafter. Thus, the discriminator strategy is most fit if $\delta W_D - \delta D_C > 0$, or if

$$\frac{c}{b} < \frac{s^2 p_D m \zeta}{1 - s^2 p_C m \zeta}. \qquad (7)$$

As the frequency of discriminators approaches zero, this condition cannot be met for costly gifts. At the other

extreme, a population of discriminators cannot be invaded deterministically by the cheater genotype if

$$\frac{c}{b} < s^2 m\, \zeta. \qquad (8)$$

(This is derived from assuming that the population is nearly fixed for the discriminator allele and that the cheater allele is introduced at a very low frequency; that is, in the limit as $p_C \rightarrow 0$.) Note that the right-hand side of this inequality is equivalent to the probability that an act of giving in one round is repaid in the following round.

Sharing by direct reciprocity is evolutionarily stable against invasion by a cheating strategy if the expected costs of each act of resource sharing are less than the expected benefits times the probability of receiving those benefits. Under these circumstances, this probability is determined by several factors, including the probability of a partner remembering previous interactions (m) and the probability that both individuals survive to subsequent rounds to give those benefits (s^2). Most pertinent to our current discussion, however, is that both individuals must change between rounds to different states (see eqn 4 for ζ). In order for the transaction to be mutually beneficial (and therefore stable against cheating), both parties must on average expect increased fitness. For individual A to give to individual B in round 1, A must have a lower slope to its resource/fitness function than individual B. But in order for this episode of sharing to be repaid, by the next round A and B must have both changed to a resource status such that the relative ranking of their slopes is reversed. Direct reciprocity requires that individuals change in their resource status often; moreover status cannot be highly positively correlated among partners.

This model makes several simplifying assumptions. However, the same general principles should apply to more generalized models; that change in the importance of resources is necessary over short time periods and that these changes must be different between the two interacting partners. What determines a 'short time scale' depends on the longevity of the individuals in their current resource state and their ability to remember the social status and past behaviour of the partner.

Direct reciprocity between individuals with different resource/fitness functions

Not all individuals need have the same resource/fitness function, particularly if these individuals vary in their reproductive value. Reproductive value was defined by Fisher (1930) to be the expected future contribution of an individual to the gene pool. (Although Fisher's mathematical formulation included only direct fitness effects, he recognized that the indirect fitness contributions of an individual should also be included.) An individual with high reproductive value has a higher

potential future fitness, by definition; therefore, all else being equal, its resource/fitness function will have higher slopes. The reproductive value of an individual provides a scale for its resource/fitness function; *all else being equal* the slope of this function at a given level of resources will be proportional to the individual's reproductive value. All resource/fitness functions are bounded at zero for essential resources; those with higher absolute values will therefore have higher slopes on average. In many species, reproductive value varies predictably as a function of age, social status, reproductive caste, etc. With variation in resource/fitness functions among individuals, some individuals will value resources more than others, but this variation is likely to persist through changes in resource status (Fig. 2).

In *Appendix A*, we extend the model developed in the last section to allow for the two interacting individuals to be drawn from separate categories that have different resource/fitness functions. For example, the two categories may be old and young, male and female, rich and poor, etc. We use the abbreviations 'O' and 'Y' to subscript the parameters to distinguish the two categories. To add generality, individuals from different categories may differ in their probability of being in a high resource state, their probabilities of transition between states, and perhaps most importantly, the possible costs and benefits of giving or receiving at those two states. (See Fig. 2 for an illustration.) Each individual may still vary between resource levels in this model.

In this section we only consider the fitness effects of interactions between individuals from different categories. We assume that, if an individual may belong to both categories during its life, that the strategies it follows during these two periods are genetically independent.
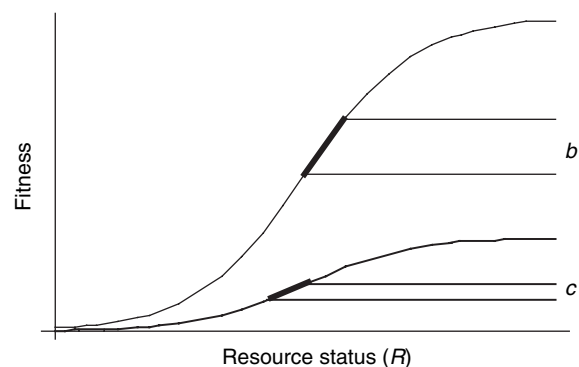
Fig. 2 Resource/fitness functions of two individuals that differ only in terms of reproductive value. The bottom curve corresponds to an individual with reproductive value 30% as great as the individual on the top graph. Even with similar amounts of resource, the costs and benefits of a gift can be greatly different. Individuals with lower reproductive values, all else being equal, will have lower costs and lower benefits of a gift compared with an individual with higher reproductive value.

Therefore the interactions between individuals of the same category are determined by the same processes described above. In this section, therefore, we only consider interactions between individuals of different categories.

As shown in *Appendix A*, discriminators cannot invade a cheating population, but a population fixed for the discriminator type will not be invaded deterministically if

$$\frac{c_Y}{b_Y} < \frac{s_Y s_O \zeta_{OY} m\, \eta_O (1 - \eta_Y)}{\eta_Y (1 - \eta_O)} \tag{9}$$

and

$$\frac{c_O}{b_O} < \frac{s_Y s_O \zeta_{YO} m\, \eta_Y (1 - \eta_O)}{\eta_O (1 - \eta_Y)}. \tag{10}$$

Thus the conditions for resource sharing to evolve are more difficult to satisfy: the discriminator allele frequencies for both 'O' discriminators and 'Y' discriminators must approach one, in spite of selection against both when rare. Discriminators must have reached high frequency, and two sets of conditions must be met. The more the two categories differ in their parameters, the more difficult it will be to satisfy the necessary conditions for both. Asymmetry in the probabilities of different classes being in different states will make reciprocity more difficult to evolve.

Indirect reciprocity among individuals with the same resource/fitness functions

With indirect reciprocity, an individual may create a positive reputation by giving to others, and as a result of that reputation the individual may increase its probability of receiving gifts in the future. The conditions for the evolution of sharing by indirect reciprocity are similar to those for direct reciprocity: the expected ratio of costs to benefits must be less than the probability of receiving additional gifts in the future.

In this section, we consider a similar model as before, but with indirect reciprocity. Individuals are paired at random with potentially different members of the population for each round of possible resource sharing. In this model, discriminators follow the same rules as the altruists, with the additional requirement that the potential recipient has a good reputation. All individuals start with a good reputation regardless of genotype, but if an individual with high status does not give when paired with an individual of low status, the high status individual loses its good reputation for the next round with probability m, reflecting a potentially faulty memory on the part of the discriminators (when $m < 1$).

Here we derive the total fitness effect of both rounds of potential resource sharing. By the conditions assumed here, the fitness effects of sharing are the same in the first round with indirect reciprocity as with the direct reciprocity model above:

$$\delta W_{A,1} = \eta(1 - \eta)[-c + b(p_A + p_D)]$$
$$\delta W_{C,1} = \eta(1 - \eta)[b(p_A + p_D)]. \tag{11}$$
$$\delta W_{D,1} = \eta(1 - \eta)[-c + b(p_A + p_D)]$$

In subsequent rounds, the fitness effects of the three strategies are

$$\delta W_{A,t>1} = \eta(1 - \eta)[-c + b(p_A + p_D)]$$
$$\delta W_{C,t>1} = \eta(1 - \eta)\{b[p_A + p_D\,(1 - J\,m)]\}, \tag{12}$$
$$\delta W_{D,t>1} = \eta(1 - \eta)[-c(1 - p_C\,J\,m) + b(p_A + p_D)]$$

where J is the probability that a low status cheater was previously high status and did not give when it was expected. This requires that it changed from high to low between rounds and that it was paired with a low status individual in the previous round. We can write

$$J = \frac{\eta \pi_{hl}}{\eta \pi_{hl} + (1 - \eta)(1 - \pi_{lh})}(1 - \eta). \tag{13}$$

J will be greater if low and high status individuals are nearly equally common and if transition from high to low state is common. The probability of an individual surviving t rounds after the first is s^t.

With these equations, we can calculate the conditions under which different strategies will succeed. First notice that the unconditional altruists are never favoured relative to discriminators; at best they have equal fitness to the discriminators (in the case when $p_c = 0$):

$$\delta W_D - \delta W_A = \frac{\eta(1 - \eta)s\,c\,p_C\,J\,m}{1 - s}. \tag{14}$$

Therefore the frequency of unconditional altruists should decline to zero (except when cheaters are absent, when altruists may enter the population through drift or mutation). We therefore focus on the relationship between cheaters and discriminators. The difference in fitness between these strategies is

$$\delta W_D - \delta W_C = \frac{\eta(1 - \eta)[-c(1 - sJ\,m\,p_C) + b\,J\,m\,p_D\,s]}{1 - s}. \tag{15}$$

This difference is positive (leading to increased frequency of discriminators) when

$$\frac{c}{b} < \frac{J\,m\,p_D\,s}{1 - sJ\,m\,p_C}. \tag{16}$$

When discriminators are rare, cheaters are favoured. Above a critical point, discriminators may be favoured. A pure discriminator population is stable to invasion from cheaters if

$$\frac{c}{b} < J\,m\,s. \tag{17}$$

However, similar to the case studied by Nowak & Sigmund (1998), a population completely composed of discriminators can be invaded by altruists via genetic drift. If the frequency of altruists gets sufficiently high then the cheater strategy can subsequently invade. Therefore a population of discriminators is not stable against invasion.

In condition (16), Jms is the probability that a discriminator will receive an increased amount of benefit in response to previous giving. This can be broken down as follows: the focal individual must survive to the next round to reap a benefit (probability s), it must remember the previous round in order to gain the benefits of discriminating (m), and in order for it to gain more benefit than cheaters the cheater must have revealed itself in the previous round (J).

By the rules of this game, gifts are only given from high status to low status individuals; so the cheater must be low status in the second round in order to gain any benefit. In order for a cheater to reveal itself in the first round, however, it must have been in high status and paired with a low status individual. So J depends critically on the transition probability from high to low status between rounds, just as in the case of direct reciprocity. If individuals retain resource state between rounds of interaction, the conditions cannot be easily met for sharing to evolve by reciprocation.

Indirect reciprocity among individuals with different resource/fitness functions

Appendix B gives the details of the derivation for this case. Similar to the case of direct reciprocity, resource sharing is even more difficult to evolve among individuals with different resource/fitness functions. In this case, in order for resource sharing to be stable from invasion by cheaters, both of the following conditions must be met:

$$\frac{c_Y}{b_Y} < \frac{s_Y J_O m\, \eta_O (1 - \eta_Y)}{\eta_Y (1 - \eta_O)} \qquad (18)$$

and

$$\frac{c_O}{b_O} < \frac{s_O J_Y m\, \eta_Y (1 - \eta_O)}{\eta_O (1 - \eta_Y)}. \qquad (19)$$

Kin selection

With kin selection, the conditions for evolution of resource sharing are simpler. Resource sharing via kin selection depends only on two conditions: (1) relatives encountering one another during a period when one is in a sufficiently high status state and the other is in a low status state and (2) that the degree of relatedness between individuals is known, either directly or indirectly. Unlike with reciprocity, evolution of resource sharing by kin selection does not depend on individuals surviving with memory to the next round, and it does not depend on the regime of change in resource status. The limiting condition for reciprocity is that individuals must commonly change their condition, but this is not required for kin selection to act. As such, we should expect to see the evolution of resource sharing among individuals of different classes (i.e. with very different resource/fitness functions) to evolve most often via kin selection.

Discussion

Reciprocal resource sharing by unrelated individuals is rare in the animal kingdom. In this paper, we have identified six conditions necessary for resource sharing by reciprocity to evolve and persist. These are listed in the following paragraphs, with the mathematical terms representing these in parentheses:

1 *Individuals must vary in their ability to translate resource into fitness (η).* For sharing to evolve, individuals must get more benefit from receiving resources than those resources cost to give. This variation must exist at a particular point in time; if all individuals are equal at any given time even if variable over time, the conditions for sharing will not exist. Seasonal change that affects all individuals similarly will not create the conditions for reciprocity to evolve.

2 *Individuals must switch frequently between states of excess and states of need (ζ or J).* With reciprocity, the asymmetry in the fitness value of resources must switch between two individuals over time. If only a single resource is involved, this asymmetry of costs and benefits can be true only if giving and receiving are separated in time and if the value of the resource to the individual changes over that time. For reciprocity, the models also require that the other participating individual also changes, but in the opposite direction. If changes rarely occur in the resource status of individuals, then cheater strategies can never be punished and the discriminating strategy is not stable to invasion.

3 *Both participants must expect to gain from the continued interaction.* We have explored the case when the benefits, costs, and changes in resource status may be different for the two participants in resource sharing. In order for reciprocity to evolve with unequal partners, both participants must on average increase in fitness by participation in sharing. With inequality between the partners, this becomes increasingly unlikely. Unequal participants add extra constraints to the evolution of reciprocity.

4 *Individuals must remember previous cheaters (m).* If a cheating individual's previous refusal to give is not remembered and punished by refusal of future gifts, then that cheater would gain benefit from future gifts as well as a sharer would. The cheater would thereby gain all the benefits without paying any of the costs of the discriminator. Therefore memory is critical to preserving a discriminating strategy from invasion by cheaters. Memory typically fails more with increasing time. If the resource states of individuals do not change within the time limits of memory, then reciprocity cannot evolve. The appropriate time scale for effective reciprocation may be quite short (Trivers, 1971; Axelrod & Hamilton, 1981; Mesterton-Gibbons & Dugatkin,

1992; Ramseyer *et al.*, 2006). The work presented here defines the critical period for memory; memory of the other individual's identity must persist long enough that both individuals change resource state.

In our models, we have only allowed memory of cheating to the next round, which makes reciprocity less advantageous. If memory of a cheating partner persisted for longer, then the potential benefit to discriminators over cheaters would increase. In any case, however, the proportional difference between the two strategies would depend on the probability of changing resource status within the time frame set by memory. If changing resource status is required to create the asymmetry between costs and benefits, then the advantage of reciprocity will depend on the rate of change in status.

5 *Individuals must survive to reap the benefits of present giving (s).* If a giving individual dies or disperses before the gift is repaid, then the gift is a net fitness loss to the individual. Only when gifts are repaid by future sharing from other individuals can reciprocity be favoured. With direct reciprocity, both individuals in a pair must survive to the next possible giving opportunity.

6 *Other discriminators must be present* (p_D). If no other discriminators are present, then there is no probability of being paid back for resource sharing.

Of these six conditions, the latter three have been well considered previously in the literature. In this paper we have explored the further limitations to the evolution of reciprocity caused by the need for rapid transitions in resource states of individuals, as complicated by the extra conditions requiring unequal partners. We should ask, under what circumstances will the required changes in resource status be common?

The evolution of altruistic resource sharing by kin selection does not suffer from the last five of these obstacles. Because no reciprocity is required, an altruistic act can be favoured by kin selection even without changes in the resource status of the participants over time and even without the survival of the donor. Givers are not required to remember cheaters, although they are required to identify kin, either directly or probabilistically by physical proximity. As long as there is a heritable component to altruism, other altruists are always likely to be present among the giver's kin. Finally, with kin selection the conditions for altruism do not depend on the benefits and costs of both participants, but just on the cost to the giver and the benefit to the recipient. As a result, kin selection may act under circumstances in which one participant predictably has a lower slope to its resource/fitness function than the recipient. We expect that these lower constraints explain the relative prevalence of sharing among relatives compared to sharing among nonkin.

Our analysis makes a clear prediction: if individuals differ in their reproductive value, resource sharing is unlikely to evolve by reciprocity. This prediction is consistent with what is known about reciprocal resource sharing in nature. Reciprocal resource sharing among nonrelatives is very rare in the animal kingdom. Adults often provide food for related young animals, but sharing between unrelated adults is quite rare, occurring in humans and other primates, vampire bats and few other taxa (Stevens & Gilby, 2004). A striking feature of the empirical literature on nonhuman resource sharing is the conspicuous absence of reciprocity as a well-supported explanation for observed behaviours (Stevens & Hauser, 2004). Chimpanzees have been observed to share both animal and plant foods under a range of conditions (Goodall, 1986; Mitani & Watts, 2001; Slocombe & Newton-Fisher, 2005; Gilby, 2006). Although reciprocal altruism has not been completely discounted as an explanation for chimp food sharing (Gilby, 2006), most authors have found much greater support for explanations involving kin selection (Mitani *et al.*, 2000), avoidance of the costs of repelling scroungers (Gilby, 2006), formation and maintenance of social bonds (Mitani & Watts, 2001; Slocombe & Newton-Fisher, 2005) and increased probability of successful mating (Teleki, 1973; Stanford *et al.*, 1994). Food sharing has also been studied extensively in Capuchin monkeys with similar explanations being offered (Perry & Rose, 1994; Rose, 1997) and with tentative support for 'attitudinal' reciprocity under laboratory conditions (de Waal, 2000). Food sharing between unrelated conspecifics is also seen in several species of birds, where it is often explained in terms of its effects on social status or the securing of a territory for breeding (reviewed in Kalishov *et al.*, 2005). Another type of resource sharing that is seen widely among many species of mammals is the nursing of other mothers' offspring. A recent review, however, found that all cases of this type of resource sharing could be explained by either kin selection, errors in the allotment of parental care, or byproduct mutualisms (Roulin, 2002), and that there was no conclusive support for reciprocal altruism. It would seem that the only well supported cases of reciprocal resource sharing in a nonhuman animal are the chimpanzee (de Waal, 1989) and the vampire bat, and kin selection provides part (but not all) of the evolutionary reason for the sharing in these species (Wilkinson, 1987).

Evidence for reciprocal altruism has been found in many other forms of cooperative behaviour such as grooming and alliance forming in vervet monkeys (Seyfarth & Cheney, 1984, but see Hemelrijk & Ek, 1991), grooming in chimpanzees (Hemelrijk & Ek, 1991), nongrooming-based coalition forming in olive baboons (Packer, 1977), 'dear enemies' (Fisher, 1954) and defensive coalitions in hooded warblers (Goddard, 1993), allogrooming in impala (Hart & Hart, 1992; Mooring & Hart, 1992), egg-trading in polychaete worms (Sella, 1985). The rarity of food sharing by reciprocity stands in stark contrast.

The conditions for resource sharing by kin selection are much less stringent than those for reciprocity. Most known examples of kin selected altruism involve individuals of different age or different reproductive status. For example, post-reproductive individuals with flat resource/fitness functions often give to younger individuals with steeper slopes (Sear *et al.*, 2000; Lee, 2003) and individuals belonging to sterile castes often give resources to reproductive castes (Crespi & Yanega, 1995). Resource sharing interactions between individuals with very different reproductive value appear to be much more likely to evolve by kin selection than by reciprocity (Roulin, 2002). The additional constraints on reciprocity created by the need for changes in resource status over short time periods predict that food-sharing could be common among relatives, as observed, but rare among nonkin.

If access to food is variable over space and time, then some individuals may encounter amounts of food in excess of their current needs whereas others find none. If the finding of food is relatively equally common among interacting individuals, then this heterogeneity of availability could select for reciprocity. Heterogeneity in food availability selects for mechanisms that buffer day-to-day food availability, and reciprocity may offer a mechanism for such buffering. However, other mechanisms are potentially available to some species, such as storage (either externally in caches or internally as fat). On the other hand, if food resources are obtained more steadily and not as feast or famine, then the value of additional resources available to different individuals is likely to be roughly equivalent, and the circumstances promoting reciprocity will not occur. Thus we should expect that food sharing by reciprocity, if ever it appears, should be associated with resources that are available heterogeneously with great variation among individuals.

In this paper, we have explicitly dealt with sharing of a single resource, but if more than one resource can be shared it may become easier for the conditions for the evolution of reciprocity to be met. Of course, for many organisms there are multiple resources that have different, nonoverlapping values, for example foods that supply different nutrient needs. In these cases, if individuals vary in which resources they hold, then this may create the essential asymmetry among individuals to allow reciprocity to evolve. Individuals need not change in their resource status in order for them to both be in high-status when giving and low status when receiving, when the status is determined for different resources. Of course, this sort of reciprocation encourages the evolution of division of labour in the right social contexts. Moreover, reciprocity in which food sharing is repaid by nonfood gifts remains possible, because the values of the actions to giver and receiver may be asymmetric.

The failure to find many examples of resource sharing via reciprocity may result from the many constraints on the evolution of reciprocity. In particular, we offer the hypothesis that the requirement for changes in needs among interacting individuals, over the short time scale set by survivorship and memory, greatly constrains the biologically plausible opportunities of the evolution of reciprocity.

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Appendix A

Direct reciprocity between individuals from different classes

As in the model described in the text, fitness differences between genotypes only arise when in one round a high status individual is paired with a low status individual. The rules followed by discriminators are defined in the same way as in the text.

First we will consider the fitness of the Y individuals. (The fitness of the O individuals can be determined from these same equations but with the O and Y subscripts reversed.)

Let ζ_{YO} be the probability that a pair of individuals that are currently young-high/old-low were young-low/old-high in the previous round. In other words, the probability that both individuals have swapped their resource status is:

$$\zeta_{YO} = \frac{(1-\eta_Y)\pi_{lhY}}{(1-\eta_Y)\pi_{lhY} + \eta_Y(1-\pi_{hlY})} \times \frac{\eta_0\pi_{hlO}}{\eta_0\pi_{hlO} + (1-\eta_0)(1-\pi_{lhO})} \tag{A1}$$

The term ζ_{OY} is defined as above but with the roles of O and Y reversed. Using this and terms defined in the same way as in the text, we can find the marginal effects on fitness in the first round:

$$\delta W_{A,Y,1} = \eta_Y(1-\eta_O)(-c_Y) + \eta_O(1-\eta_Y)b_Y(p_{A,O}+p_{D,O})$$
$$\delta W_{C,Y,1} = \eta_O(1-\eta_Y)\left[b_Y(p_{A,O}+p_{D,O})\right],$$
$$\delta W_{D,Y,1} = \eta_Y(1-\eta_O)(-c_Y) + \eta_O(1-\eta_Y)b_Y(p_{A,O}+p_{D,O}) \tag{A2}$$

and in subsequent rounds:

$$\delta W_{A,Y,t>1} = \left(\eta_Y(1-\eta_O)(-c_Y) + \eta_O(1-\eta_Y)b_Y(p_{A,O}+p_{D,O})\right)$$
$$\delta W_{C,Y,t>1} = \eta_O(1-\eta_Y)\left\{b_Y\left[p_{A,O}+p_{D,O}(1-\zeta_{OY}m)\right]\right\}.$$
$$\delta W_{D,Y,t>1} = \eta_Y(1-\eta_O)\left[-c_Y(1-p_{C,O}\zeta_{YO}m)\right]$$
$$\qquad\qquad + \eta_O(1-\eta_Y)b_Y(p_{A,O}+p_{D,O}) \tag{A3}$$

Persistence of the pair to the next round occurs with probability s_O s_Y. Finding the differences in fitness between strategies:

$$\delta W_{D,Y} - \delta W_{A,Y} = \frac{c_Y\, m\, \zeta_{YO}\, p_{C,O}\, s_O s_Y \eta_Y\, (1 - \eta_O)}{1 - s_O s_Y} \quad \text{(A4)}$$

$$\delta W_{D,Y} - \delta W_{C,Y} = \frac{\eta_O\, (1 - \eta_Y)\left[b_Y\, m\, \zeta_{OY}\, p_{D,O} s_O s_Y\right] + \eta_Y\, (1 - \eta_O)\left[-c_Y\left(1 - s_O s_Y m\, \zeta_{YO}\, p_{C,O}\right)\right]}{1 - s_O s_Y}. \quad \text{(A5)}$$

The discriminator allele for Y individuals is always favoured over the Y altruist allele, so long as the frequency of O cheaters is > 0. The discriminator allele is favoured over the cheater allele if $\delta W_{DY} - \delta W_{CY} > 0$, which occurs when

$$\frac{c_Y}{b_Y} < \frac{s_Y s_O \zeta_{OY} m\, p_{D,O} \eta_O (1 - \eta_Y)}{(1 - s_O s_Y m\, p_{CO} \zeta_{YO}) \eta_Y (1 - \eta_O)}. \quad \text{(A6)}$$

Discriminators cannot invade a pure cheater population deterministically under any modelled circumstance, but discriminators cannot be invaded by cheaters if

$$\frac{c_Y}{b_Y} < \frac{s_Y s_O \zeta_{OY} m\, \eta_O (1 - \eta_Y)}{\eta_Y (1 - \eta_O)}. \quad \text{(A7)}$$

Similar conditions hold for the strategies in the O category individuals.

Appendix B

Indirect reciprocity between individual from different classes

Here s_Y is the probability to surviving until the next interaction of this type.

partners are otherwise randomly chosen each round. All terms have the same meaning as elsewhere in the paper, but the two different types of individuals may differ in all of the parameters, as marked with the subscripts. The fitness effects for the two rounds are

$$\delta W_{A,Y,1} = \eta_Y(1 - \eta_O)(-c_Y) + \eta_O(1 - \eta_Y)b_Y(p_{A,O} + p_{D,O})$$
$$\delta W_{C,Y,1} = \eta_O(1 - \eta_Y)\left[b_Y(p_{A,O} + p_{D,O})\right]$$
$$\delta W_{D,Y,1} = \eta_Y(1 - \eta_O)(-c_Y) + \eta_O(1 - \eta_Y)b_Y(p_{A,O} + p_{D,O})$$
$$\text{(B1)}$$

and

$$\delta W_{A,Y,t>1} = \eta_Y(1 - \eta_O)(-c_Y) + \eta_O(1 - \eta_Y)b_Y(p_{A,O} + p_{D,O})$$
$$\delta W_{C,Y,t>1} = \eta_O(1 - \eta_Y)\left\{b_Y\left[p_{A,O} + p_{D,O}(1 - J_O m)\right]\right\},$$
$$\delta W_{D,Y,t>1} = \eta_Y(1 - \eta_O)\left[-c_Y\left(1 - p_{C,O} J_O m\right)\right].$$
$$+ \eta_O(1 - \eta_Y)b_Y(p_{A,O} + p_{D,O})$$
$$\text{(B2)}$$

where

$$J_O = (1 - \eta_Y)\frac{\eta_O \pi_{hlO}}{\eta_O \pi_{hlO} + (1 - \eta_O)(1 - \pi_{hlO})}. \quad \text{(B3)}$$

With these fitness effects, we can find the difference in the fitness of the strategies as

$$\delta W_{D,Y} - \delta W_{A,Y} = \frac{c_Y\, m\, J_Y\, p_{C,O}\, s_Y \eta_Y\, (1 - \eta_O)}{1 - s_Y}, \quad \text{(B4)}$$

and

$$\delta W_{D,Y} - \delta W_{C,Y} = \frac{\eta_O\, (1 - \eta_Y)\left[b_Y\, m\, J_O\, p_{D,O} s_Y\right] + \eta_Y\, (1 - \eta_O)\left[-c_Y\left(1 + s_Y\left(1 - m\, J_O\, p_{C,O}\right)\right)\right]}{1 - s_Y}. \quad \text{(B5)}$$

In this appendix, we derive the fitness effects of an individual participating in a game with other individuals with a different resource/fitness function. As in the case with direct reciprocity in the *Appendix A*, we use the subscripts O and Y to mark which individuals have a O-type or Y-type resource/fitness function. In this model, individuals have the same resource/fitness function for all rounds. Each individual is always paired with an individual of the other type in all rounds, but the

Similar equations hold when the arbitrary subscripts O and Y are switched. Altruists of one type are never favoured over discriminators if there are any cheaters of the other type; at best the fitnesses of the discriminators and altruists are equal in the absence of cheaters. Conditions for discriminators having higher fitness than cheaters, according to eqn B5, are given in the text.