

KINDS OF SOCIAL INTERACTIONS

Contrasting nepotism, ecological mutualism, social reciprocity, and some other interactions that mimic social reciprocity

Nepotism refers to help to genetic relatives. It can be direct or indirect. **Direct nepotism** means passing benefits directly to genetic relatives (as from parents to offspring), evolved presumably because such behavior tended to increase the frequency of the genes leading to that kind of helping, through increases in the reproduction of the helped relative. **Indirect nepotism** refers to cases when help is given to someone who then gives it to a relative of the original helper; an example is any member of a bonded pair of parents helping the other member of the pair, who then passes the benefit one way or another to their genetically shared offspring. Nepotism yields a net phenotypic cost, but, presumably (if it is evolved and the environment is still "right") genotypically (or genetically) profitable (see Table 1, p. 40, DHA). The discussion of nepotism, or how "inclusive fitness" can be maximized through helping of relatives, begins on p. 43 of DHA.

To discuss mutualism and reciprocity adequately probably requires definitions of some other interactions: predation, parasitism, and commensalism (see the table on p. 5 of this handout). All three terms are typically used to refer to interactions between species. **Predators** and **parasites** exploit members of another species at the expense of those prey or hosts. Typically, predation is the term used when an animal catches and eats members of another species, often smaller than the predator -- as when a coyote catches and eats a jackrabbit. Parasitism is typically used when the exploiters are smaller than the exploited individuals, but wild dogs prey upon zebras (there is no hard and fast rule, and it may not be important to us here to worry about a fine distinction between these two terms). **Commensals** exploit members of another species, but it is difficult or impossible to identify any cost to the latter -- or any gain. So, theoretically, at least, commensalism refers to cases where the "exploited" animal gains or loses nothing. For example, many species of beetles, mites, and crickets live in ant nests, but for most of them no cost to the ants has been discovered, and the ants do not appear to behave toward such presumed commensals as if they were costly. In **ecological mutualism**, both parties benefit. Both parties benefit in **social reciprocity** too. Mutualism is believed to occur very widely in the animal and plant kingdoms, but social reciprocity (which, unlike mutualism, is probably restricted to within-species interactions) is believed to be highly restricted -- some people believe reciprocity may occur only in primates, and a few believe it has not been demonstrated unequivocally in any species but humans -- and perhaps chimpanzees and a few others. So we have a topic worth a little more attention, because every way that any organism acts that is costly to it -- and does not appear to be just an accident, an incidental effect of some other adaptation, or the result of a novelty in its environment to which it has not yet adjusted evolutionarily -- is important to anyone who assumes that natural selection is the central guiding force of evolution. It's also an important topic for students of human behavior because nepotism and social reciprocity are both complex and pervasive in human life. This topic, which entered biology in a serious way with Robert L. Trivers' 1971 paper on "reciprocal altruism," is important enough that three complete issues of the journal *Ethology and Sociobiology* was devoted to defining social reciprocity and discussing virtually all efforts to locate or assign it to any and all organisms (Volume 9, Numbers 2-4, July 1988, pp. 67-257). Reciprocity is an ancient term in literature and the social sciences, but before 1971 it had never been analyzed in terms of its effect on reproductive success.

Here are some thoughts: Contrasting ecological mutualism, nepotism, and social reciprocity would be easier if mutualism involved no investment prior to the interaction. But in the genetic and ontogenetic senses, it probably always does, when (1) the mutualism is evolved (as any particular case of mutualism likely is) and (2) the interaction is temporally limited, as when it starts partway through the life of one or both interactants (as with the mutualism between ants and acacias) or occurs and recurs (as with cleaner fish and their "cleanees," which Trivers thought was a case of reciprocal altruism) (Contrast these with termite-protozoan mutualism, which seems continually in

place). The acacia tree has evolved to invest in ants by producing Beltian bodies and nectar (food for ants), and hollow thorns (homes for ants); if ants don't show up, it loses (ants protect acacias from various insects that feed on them, which the ants use for food). The ants have surely evolved to locate and favor acacia trees, though their adaptations in this respect are not as obvious to us as those of the tree, and these investments would be costly if suitable acacias were not available. But failures by either party would hurt the failing party too, and that plus the fact that the accommodating traits are evolved, and cannot be turned on and off as quickly during the organism's life, represent insurance -- virtually guarantees -- against defection.

Parties in ecological mutualism come to depend on each other for the same reasons a parasite can afford (to specialize) to depend on a particular host, or any organism specializes to depend on a particular food source: it is reliably available and cannot change fast enough to thwart its use (and these things are true in such a way that failure to specialize represents an overall cost or a losing strategy within the exploiting species). In mutualism, because the "used" individual also gains rather than loses, it evolves to accept and facilitate and use the interaction rather than to escape it. This set of changes must come about, sometimes, because a prey organism finds a way to use or divert exploitation by another species (parasite, predator, or commensal), or because a parasite "inadvertently" (or accidentally, in evolutionary terms) evolves a convergence of interests with its host (the ultimate of which is to become an obligate parasite that is transmitted the same way the host's genetic materials are -- which results in a kind of "mutualism" of previously adversarial genetic materials and a muddling or loss of their separate identities). Investment that evolves through genetic changes and occurs in every individual as a result of normal ontogeny can be regarded as somatic effort of the organism. To invest in the ability to carry out actions advantageous to one's self (as does the individual actor in a case of ecological mutualism) is not the same as investing in the reproduction of another individual at cost to one's own somatic or reproductive effort, even if the cost is temporary (i.e., the investment of social reciprocity).

I speculate that ecological mutualism typically arises out of (+-) or (+0) situations (parasitism or commensalism: see table, p.4). I also speculate that social reciprocity never evolves out of such situations -- that its evolutionary antecedents are utterly different (see below). In other words, I think the apparent similarity between ecological mutualism and social reciprocity is an illusion.

Here are some of the ways I have thought about why "cheating" can occur in social reciprocity but not in ecological mutualism:

1. In social reciprocity there is virtually always a temporary (or sequential) unbalancing of benefit flows through temporary phenotypic or genotypic altruism. Thus, either individual potentially can gain by defecting after receiving beneficence. I say "virtually always" because it is possible to imagine simultaneous exchanges that probably qualify as social reciprocity. I can pay for a cheeseburger with one hand and receive it simultaneously with the other hand, even if this is not typical. Some authors in the 1988 journal mentioned above refuse to call it social reciprocity if the benefits are transferred in both directions simultaneously, but I don't think that's a useful argument: there is still risk in a simultaneous transfer that isn't present in a delayed exchange in mutualism. After all, I may be hiding the amount of money in my hand or the cheeseburger may not have any meat in it. The fact that we demand near simultaneity in some exchanges is evidence for the probability of cheating and an effort to reduce its likelihood, not evidence against any such probability.

It seems clear that in some reciprocity the individuals involved also sometimes deliberately *delay* the requirement of repayment, perhaps to test the integrity of the individual who is temporarily ahead; to appear beneficent or independent of immediate need; to allow one's interactant to repay at a time and in a way that is least expensive to him; to demonstrate a feeling of trust; or, on the other hand, to retain the ability to call in the debt when and how the beneficent individual feels like it, or when it will be most valuable to him (there are probably other reasons I haven't thought of; the point is that such cases do not cast doubt on the above argument about simultaneity).

2. Social reciprocity typically has a non-obligate nature that includes the facts that (a) defection will not necessarily destroy the defector, or even cause him a loss (sometimes); (b) there are often multiple "players" in the larger game of social reciprocity who can substitute for either party in an ongoing series of exchanges and even cause gain to a defector; and (c) investment in another under the above conditions is likely to render him a more desirable partner to someone else, who may then

actively woo him to defect.

3. Ongoing sequences of social reciprocity are usually easily divisible into large numbers of small, substitutable transactions, facilitating defection at many different points in the flow of transactions. I think this point and the last one together are very important for understanding social reciprocity. The presence of multiple players, and the ability of players to divide their transactions into countless units whose costs and benefits can be evaluated separately, together facilitate social shuffling (defections, switching of partners) that can lead to gains for the initiators of chances, including cheaters. Moral, ethical, and legal systems are instituted to prevent some of these kinds of defections, including defections by the makers of rules that permit defections by some but not by others.

Richard Connor (1991 U-M doctoral graduate), in a 1992 paper in the *Journal of Evolutionary Biology* (5:523-528), titled "Egg-trading in simultaneous hermaphrodites: an alternative to Tit-for-Tat," suggests that traded benefits can be divided into parcels so small that the expense of transferring to a different partner after receiving a parcel of benefit at the cost of the partner is greater than the benefit to be gained by cheating, through taking the benefit and leaving. "**Parcelling**" benefits to avoid being cheated (or to avoid being cheated "big") surely occurs in complex social reciprocity of the sort practiced by humans, and is subject there to the kinds of complex responses suggested by Trivers (1971, The evolution of reciprocal altruism. *Quart. Rev. Biol.* 46:35-57.). But Connor's idea is that parcelling can be carried to an extreme that actually prevents cheating, so may be involved in many social interactions outside the realm of social reciprocity in any sense that might require large, complex brains. Parcelling can be understood by considering simultaneous mutual grooming by organisms. Thus, horses and other ungulates sometimes stand facing in opposite directions and nibble or bite or "groom" each other on the neck or shoulders or on the top of the rump. In some organisms, such as impala, the argument has been made that ticks or other parasites are being removed, but for horses and most other cases no one knows what benefits might be accruing as a result of being so groomed. During the summer of 1992, my assistant, Rebecca Scherdt, and I attempted to discover the size of a parcel of withers-nibbling in horses by initiating it in one horse facing another's withers by scratching the first horse on the withers and then, eventually, stopping abruptly. In 30 trials we found that the scratched horse gave 0-3 nibbles after "nibbles" on itself terminated, with an average of 0.75 nibbles. That's a pretty small parcel.

This is a good place to identify another kind of interaction that has confused people for a long time, which Richard Connor (1986: Pseudo-reciprocity: investing in mutualism. *Animal Behaviour* 34:1562-1566) called "**pseudo-reciprocity.**" If a male bird feeds a female while courting her, and she later allows him to mate with her, it was thought by many that social reciprocity had taken place. The female was paying the male for his earlier investment. Connor noted that the female might be merely doing that thing most beneficial for her at the time, and that the male had merely shown her that he was the best possible mate. In such case, the female does not ever suffer a phenotypic cost, so there is no phenotypic altruism for her. The male is engaging in reproductive effort, which always involves risks and delays in return. There is no way for either male or female to cheat. If the male only partially feeds, it is not cheating but taking a special risk; if the female does not choose the feeding male as a mate, she is presumably making the best (on the basis of her evolved responses to the relevant cues) "decision" (i.e., the most reproductive one).

I regard Connor's arguments with respect to pseudo-reciprocity and parcelling as extremely important, for they show us how we can regard the big complex sort of brain that humans have as having evolved as a social tool without being confused about social interactions in organisms without big, complex brains which resemble social reciprocity. Connor has recently tackled another set of such interactions and has chosen to call them (in a manuscript) "**inveigling.**" He is referring to a tendency in some species, such as starlings, for individuals to mimic relatives by helping (e.g., feeding) juveniles, thereby confusing the juveniles about who are their relatives. Because social learning is (evidently) the mechanism of kin recognition, whoever feeds a juvenile may become, in its eyes, a close genetic relative. Subsequently, then, the helped individual may help the nonrelatives that confused them by feeding them, or the offspring of the inveiglers. In other words, the original helper, by helping a non-relative and thereby exploiting a kin recognition device, thwarts that helped individual's ability to use its own capabilities to maximize its inclusive fitness via appropriate

distribution of its resources among its genetic relatives. This interaction, too, a type seen in a number of bird species (probably in many parental forms that live in groups), may seem superficially to have the complex consequences of the human kind of complex social reciprocity.

For three reasons, I favor the hypothesis (see the diagram) that social reciprocity arose out of nepotistic interactions rather than from, say, mutualism or pseudo-reciprocity:

1. Nepotistic interactions involve phenotypic investments (costs), and willingness to "give" without phenotypic returns. The returns in nepotism are genetic. The willing nepotist, primed to give without necessarily expecting any phenotypic returns, is thus primed to become an investor in social reciprocity.

2. Ongoing nepotistic interactions take on the aspect of social reciprocity if there is an alternation of relative needs and relative abilities of the two participants to supply the other's needs.

3. Spousal interactions, especially when parental care is extensive, may be an important precursor because they show all of the above features; they are indirectly nepotistic, since one invests in a spouse because of increased reproductive opportunities for one's (a) gametes (courtship) or (b) zygotes (parental investment).

Male-female interactions may be an especially good case to use in trying to compare mutualism, pseudo-reciprocity, and reciprocity because they appear to include all three interactions. The overall male-female interaction -- that occurring between males, collectively, and females, collectively -- appears to be mutualistic; neither sex can get along without the other, each gains by the presence of the other, the situation is evolved, in most species neither sex can revert to the other (or it is difficult and expensive to do so) and so forth. The individual interactions of males and females, on the other hand, can take the form of pseudo-reciprocity, indirect nepotism (I have already described examples of such cases), or social reciprocity. When two parents are extensively parental and invest in offspring they have produced jointly, then, when they help each other alternately, the interaction can take the form of reciprocity in the same way that a reciprocal overlap can appear in long-term nepotistic interactions in which the partners keep changing places with respect to need and ability to give benefits. As already mentioned, the male-female interaction is a system of indirect nepotism when each partner invests in his own offspring by helping the mate who will use the benefits to invest in their joint offspring. It is interesting that Trivers did not mention male-female interactions in his original paper on reciprocity, although he later discussed them extensively in his 1972 paper on parental investment.

Although the conditions of ecological mutualism may be met often in within-species interactions, I suggest that ecological mutualism has little chance of graduating into social reciprocity when the interaction is interspecific, and that no cases of interspecific social reciprocity are known. Among the most interesting cases to analyze in this context would be those between humans and their most or longest domesticated pets, such as dogs and cats (Darwin remarked that man has selected his dogs to repay his kindnesses with interest).

To me, the exciting thing about understanding how social reciprocity works -- given that it is continuously and complexly present in elaborate networks among humans and rare or absent in virtually every other species (except, possibly, chimpanzees) -- is that the possibility of cheating (of gaining in more than one way, and sometimes massively) sets into motion an elaboration of (1) safeguards against cheating and (2) increasingly effective and complex ways of cheating. Now, just think about the human psyche (intellect, consciousness, purpose, conscience, foresight, planning, logic, reason, linguistic wability, morality, cleverness, deliberate deceit, self-deception, moralizing, self-righteousness, the subconscious, repression, humor, and all the rest). Think about the uniqueness of this set of attributes in humans. Think about facial expressions, blushing, lie detectors, guilt, and confessions (see the ms. on morality). And think about human social structure and the directions and kinds of changes in social structure and culture (mores, ethics, law, and the concepts of justice, right and wrong, social hustling, retribution, revenge, spite, and all the rest). Think about the stream of human social activities and the extent of individual recognition. And theatre and scenario-bulding. And so on.

Some hypotheses about different kinds of interactions between organisms

Kind of interaction (arrows indicate probable evolutionary sequences)	Parties interacting			Some comments about probable mechanisms
	1	2	3	
Predation	+	-		The investments here are genetic and developmental. They tend to be irreversible because the return is guaranteed if the other party is present. There are fewer correctable errors from which to gain by altering course by activities like learning.
Parasitism	+	-		
Commensalism	+	0		
	0	0		
Mutualism	- +	- +		Down to somewhere about here, I believe, you can keep on winning without learning much about the other party (except in pseudo-reciprocity you might have to now and then . . .)
	(guaranteed if other party is present; no learning required)			
Pseudo-reciprocity	- →	+		
	+ ←	+		
Indirect nepotism	- →	+		(Some kinds of nepotism do not require learning)
	+ ←	- →	+	
	(genetic returns)			
Direct nepotism	- →	+		Below here you cannot keep on winning without a lot of complex social learning. Below here, I believe, you cannot keep on winning without consciousness and self-awareness, which I think will become involved in a runaway evolutionary (intellectual) race in an ecologically dominant species like ourselves.
	+ ←	+	(genetic return)	
Direct reciprocity	- →	+		
	+ ←	-		
Indirect reciprocity	- →	+		(etc.)
	+ ←	-		
		- →	+	

Note: The word "learning" as used on this diagram refers not to learning in any and every context but explicitly to learning about the other organism and about the interaction. I am a little fuzzy on this, but consider the proposition that "quick changes" of strategy, social cheating, and such like probably are not possible except below that line on the right that suggests where it becomes impossible to keep on winning without a lot of complex learning.