

Report of the 90<sup>th</sup> Dahlem Workshop on  
*Genetic and Cultural Evolution of Cooperation*  
Berlin, June 23–28, 2002

Held and published on behalf of the  
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# Genetic and Cultural Evolution of Cooperation

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The MIT Press  
Cambridge, Massachusetts  
London, England

in cooperation with Dahlem University Press

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## 5

## Why Is Reciprocity So Rare in Social Animals?

### A Protestant Appeal

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#### ABSTRACT

After three decades of worldwide research on reciprocal altruism and related phenomena, no more than a modest number of animal examples have been identified. Even in primates, evidence for reciprocity is surprisingly scarce. In contrast to the shortage of support, reciprocal altruism and Tit-for-Tat-like behavior have been used as the prime explanation for cooperation among nonkin. From models based on this line of reasoning, one easily gets the impression that reciprocity should be widespread among social animals. Why is there such a discrepancy between theory and facts? A look at the best-known examples of reciprocity shows that simple models of repeated games do not properly reflect the natural circumstances under which evolution takes place. Most repeated animal interactions do not even correspond to repeated games. Partner switching and mobility often counteract the evolutionary stability of reciprocal altruism. Moreover, if learning is involved in mental implementation, then the timescale in which reciprocity can occur is often dramatically shortened. In the few known examples, quick reciprocation seems to be the rule, yet standard game theory fails to account for this empirical finding. More generally, it must be emphasized that mental mechanisms shape the evolution of reciprocity. An impressive mental machinery is required for nontrivial examples of reciprocity, as illustrated by the attribution problem (i.e., the problem of classifying other individuals' actions as cooperative, intentionally uncooperative, or unintentionally uncooperative). Emotions may play a role in the machinery underlying cooperation, but current game theory is conceptually not designed to account for the role emotions play. Collectively, this shows that many obstacles can impede the evolution of reciprocity and that evolutionary game theory needs new conceptual tools to understand these obstacles adequately.

## THESES

Some theoretical ideas appear to be so compelling that the lack of supporting evidence is indulged by major parts of the scientific community. This criticism applies to current thought in evolutionary biology regarding cooperation in repeated interactions. Thus, to provoke a change, I am "tacking up" some theses for public display. My aim is not to create an entirely new theory but rather to steer its course closer toward reality. It is in this light that I ask the reader to approach the following discourse.

In its simplest form the biological theory of reciprocity aims to explain apparently altruistic behavior by revealing its nonaltruistic nature. It strongly resembles the theory of repeated games. A repeated game, or supergame, consists of a series of interactions between the same two (or more) players. In each interaction, they play the same game. This game forms the building block upon which the supergame is built. After each round, the game is repeated with some probability so that the decision about continuation is externalized. Long before evolutionary game theory was born, it has been known (Luce and Raiffa 1957) that more cooperation is possible in a repeated game scenario than in a one-shot encounter.

The so-called folk theorems capture this popular wisdom in a mathematically rigorous way (e.g., Fudenberg and Tirole 1991). In essence, they state that if any one-shot game has a solution (Nash equilibrium) that does not fully exploit the scope for cooperation, then higher degrees of cooperation can be observed in appropriate solutions of the supergame, provided the expected number of future interactions is sufficiently large. The idea of supergame cooperation thus applies to a wide range of very different scenarios, and it helps to understand problems far beyond reciprocity, altruism, and the Prisoner's Dilemma. In this generality lies the temptation to overestimate the explanatory power of repeated games.

The drawback is that the theory of supergame cooperation is based on a very narrow picture of the long-term interaction pattern. Strategy spaces of repeated games do not include the option to end the sequence of interactions. Therefore, the decision to leave a partner and interact instead with other individuals is not permitted in the formal structure of a repeated game. As has been pointed out by Friedman and Hammerstein (1991), biological examples of reciprocity require different modeling approaches, and biologists often talk about something fundamentally different from repeated games when they discuss reciprocity (see also Connor 1992). Let us sum this up in a thesis.

### **Thesis 1: The assumption of forced interactions severely limits the applicability of repeated games.**

*The theory of repeated games applies to a large class of games and is therefore broad. Concurrently, it is very narrow in that players are treated as if they were attached to each other by some "magic glue."*

There are, of course, examples of animal and especially human interaction patterns (see also Hagen, this volume) for which it seems reasonable to idealize them as supergames. For example, two human neighbors in a residential area or two neighboring territory owners of an animal species may have to deal with each other for quite some time due to the transaction cost associated with moving to another house or territory.

In contrast, car drivers are not attached to their gas stations. If it saves them money, many will switch from one station to another. This creates a market which is crucial for the understanding of why drivers shop at a particular place. To some extent, the car driver logic seems to apply to the mutualistic relationship between a cleaner fish and its clients. As Bshary and Noë discuss in this volume, clients that come from a long distance to the "cleaning station" seem to have a tendency to switch stations (cleaners) according to their offer. Even with such a mechanism at work, one may observe repeated visits of the same station. These repeats are driven by partner choice, however, and not by the magic glue of a repeated game. This leads to Thesis 2.

### **Thesis 2: Repeated interactions, as such, are not evidence for repeated games.**

*Repeated interactions alone are not sufficient evidence for a repeated game. Repetition can and will almost always result from strategic benefits that interacting animals incur by deliberately continuing to interact with their partners. When casting biological examples into the form of a repeated game, one excludes a potential incentive for noncooperative behavior from the analysis. This incentive is to take benefits and then leave the partner behind without giving anything in return. If one aims at explaining cooperation, it is necessary to understand why the scope for such exploitation is limited.*

To illustrate this thesis, consider the famous egg-trading procedure in a fish called the black Hamlet (*Hypoplectrus nigricans*). This fish is a simultaneous hermaphrodite, i.e., it produces both eggs and sperm. According to Fischer (1980, 1981), the black Hamlet typically has more sperm than needed to fertilize all the eggs of a mating partner. Eggs are, therefore, a precious commodity at the mating site where fish congregate that are ready to spawn during a given afternoon. In principle, it would be beneficial for an individual to fertilize the eggs of more than one partner. In practice, however, this is difficult to achieve, because eggs are "parceled" so that individuals cannot fertilize all the eggs of a mate at once. Egg parcels are never exchanged simultaneously and, to a large extent, mating takes place in an alternating sequence of giving (eggs) and taking (fertilizing). Fischer interpreted this as a Tit-for-Tat strategy in a repeated game. However, in a repeated game, two partners are forced to stay together and there would be no incentive for defection for the following reason: both partners need their eggs to be fertilized before nightfall and both gain a benefit from fertilizing the other's eggs. Partner control in a Tit-for-Tat-like fashion would seem

unnecessary in this particular model<sup>1</sup> (which, of course, does not capture what Fischer really had in mind).

The Hamlet egg-trading problem, in other words, does not meet the assumptions of a formal repeated game. Instead, it may better be considered in the context of markets. The Hamlet spawning ground shares an interesting feature with illegal drug markets. When two dealers are about to trade a large amount of heroin for a large amount of money, the one with the heroin may abscond with the money before handing over the heroin. The following strategic offer from the buyer, however, can create an incentive to participate *deliberately* in a repetitive interaction: "Give me the first portion of your heroin and I will pay for it; give me the next portion, and I will pay again, etc." Once the dealers enter this interaction sequence with heroin parceling, a cheater cannot run away with more than one unpaid portion of heroin. Now, if the cost of switching trading partners is high enough, then cheating would not be worth the free portion.

In the drug market, partner switching is costly because police are watching and violence is involved. Although the Hamlet fish have no guns and do not have to contend with authority, switching may nevertheless be costly. The cost can be estimated from how long it takes to find a new partner, at what time the mating market will close in the evening, how many eggs will be traded with the new partner, etc. Using Fischer's data, Friedman and Hammerstein (1991) made an attempt to show in a model that there is no incentive for cheating given the observed practice of parceling. After a spawning bout, a mate still possesses enough eggs to remain the preferred trading partner. This keeps the interaction going and we see how market arguments, rather than thoughts about repeated games, can enlighten the study of reciprocity. This leads me, therefore, to state the following thesis.

**Thesis 3: Partner switching and partner markets are important but often neglected issues in the study of reciprocity.**

*A vital strategic element in maintaining cooperation is to make it unprofitable for a social partner to switch. Therefore, the investigation of cooperation typically requires consideration of partner markets.*

In opposition to Thesis 3, one might be tempted to negate it on the premise that switching is rare or seldom observed in a number of animal examples. However, this would be a mistake since even then the unprofitability of switching is one of the main keys to the understanding of cooperation. Friedman and Hammerstein (1991) demonstrated this in their model for the egg-trading of the Hamlet fish. Conversely, Enquist and Leimar (1993) emphasized the profitability of switching and made the general point that mobility seriously restricts the evolution of cooperation in many animals. They argued, however, that the effect of mobility

<sup>1</sup> In general, partner control is an important issue even in market theory.

might be counteracted to some extent by behavioral propensities, such as suspiciousness toward strangers and gossiping. Vehrencamp (1983) expressed the idea that dominant animals in nonegalitarian animal groups cannot "exploit" other group members to extremes because this would create an incentive for subordinates to migrate and search for a group in which exploitation is less severe. In her theory of reproductive skew, Vehrencamp made an important conceptual step toward thinking about the role of partner markets in cooperation.

Whereas Vehrencamp focused her attention on the partner choice exerted by subordinate animals, Noë and Hammerstein (1994) showed that social partner choice exerted by dominant individuals can increase "exploitation" of subordinates by forcing them to be more cooperative than they would be in the absence of this choice. The degree of the subordinate's cooperation then depends on the "animal labor market" (see also Bowles and Hammerstein, this volume).

At this point it must be emphasized that we would "throw the baby out with the bathwater" if we claimed that functional analysis of reciprocity pertains only to partner choice and switching. Partners, even preferred ones, may have to be checked. So, why is some partner control necessary even when both partners know that in principle they are a perfect match? To answer this question, let us return to the gas station example. We approach our preferred station with good reason to believe that someone will sell us gas. Occasionally, we encounter a defective pump and have not been forewarned through a sign. When this happens, would we stand at the pump and wait forever? Fortunately, routine processes protect us from pursuing such unsolvable tasks for too long. It is very likely that these processes are not special adaptations to cheating in social interactions, since the propensity to change goals when tasks are unsolvable is crucial to the management of many problems an animal faces. Returning to the Hamlet example, if a fish fails to receive eggs from a partner for a long time, this resembles the situation where the pump is out of order, and a similar logic can be applied. This leads us to the next thesis.

**Thesis 4: Partner control can result from general mental processes that are not specific tools against cheating in social interactions.**

*Animals cannot waste their time on unsolvable tasks. If a partner fails to provide an expected "commodity," routine task switching may cause the animal either to search elsewhere for this commodity or to end the search. This kind of task control is likely to be a rather general feature of the mental machinery — one that protects the animal against locking itself into endless waiting states. Therefore, the behavioral contingency in reciprocal cooperation may not be a specific adaptation to cheating.*

Thesis 4 implies that general mental processes can be seen as preadaptations to reciprocal altruism. An animal that does not reciprocate would risk losing a

cooperating partner due to that partner's task control. To obtain reciprocity, however, much more needs to be implemented.

If learning is at least partially involved in the mental implementation of reciprocal altruism, then the following kind of problem arises. We learn to associate a stomach problem with the fish that we ate just prior to the onset of this problem but not with the steak that we ate a week ago. In a similar spirit, it seems plausible that learning would not allow animals to develop reciprocity when there is a significant temporal or contextual gap between the situations for giving and taking, or when rewards from cooperation are delayed relative to the rewards from noncooperation. This is nicely illustrated by the following experiments.

Clements and Stephens (1995) exposed captive blue jays to the repeated Prisoner's Dilemma. In their experimental setup the birds obtained immediate rewards from noncooperative behavior, whereas the rewards from cooperative action were slightly delayed. The authors reported that the jays were unable to learn sustained cooperation. Stephens et al. (2002) repeated this experiment using a modified setup where rewards were not directly given to the birds but accumulated in a transparent plastic box. Here, the jays could see their food gains but not consume them until a flap was finally opened. In this experiment, there was no delay between the rewards from cooperative and noncooperative action. The birds actually did learn sustained cooperation. Taken together, the two experiments demonstrate nicely that timescale considerations are important in explaining the facts, which brings us to the next thesis.

**Thesis 5: There is surprisingly little evidence for reciprocity in nonhuman animals, and the known examples seem to be largely restricted to reciprocation on short timescales.**

*Ever since Trivers (1971) wrote his seminal paper on reciprocal altruism, models of cooperation in repeated games have preoccupied and entertained the scientific community. However, as far as convincing data are concerned, the harvest has been very modest. There are few animal examples outside the primate world. Even in primates, the evidence for reciprocity is scarce (see Silk, this volume). The most typical form of reciprocity is the reciprocal grooming found in ungulates and some primates. Here, the effort is often parceled like in the egg trading of the Hamlet fish. The reward for a grooming act is often instantaneous. As explained above, the quick succession of giving and taking facilitates the implementation of reciprocity by learning.*

To challenge the message of Thesis 5, let us look at an example in which the timescale for reciprocation is not short. Wilkinson (1984) conducted a fascinating empirical study in which he describes blood donations among female vampire bats. The females roost in groups. Every day they fly out in search of blood. If a female fails to obtain a blood meal for two days in succession, her risk of starvation becomes very high. When females return from an unsuccessful

foraging excursion, they solicit a blood donation from other females. In an experiment with genetically unrelated individuals, Wilkinson demonstrated that if a donation takes place, the donator is more likely to be a female that has already received a donation from the soliciting bat than a female that had not been a beneficiary of her help.

Admittedly, the bat example looks very much like a repeated game, and it has a strong flavor of reciprocity. But, Wilkinson did not expose the bats to the crucial contingency test. From his experiment, we cannot conclude that a female bat would be less inclined to cooperate in the future if another female refused to donate blood to her. Wilkinson's data could, for example, result from a tendency of the bats to like some females more than others on the basis of characteristics such as smell. This idea is not far-fetched because under natural circumstances the communally roosting females are actually kin groups. The explanation behind the blood donations may ultimately lie in the genetic relatedness of helpers and receivers, despite the fact that Wilkinson used unrelated individuals in his experiment. The reason is that kin selection may produce mechanisms that appear like reciprocity in the experiment with unrelated individuals: a kin recognition mechanism may be operating that needs calibration based on the concrete group in which it is used. Such a mechanism could produce friendly affinities in groups of unrelated individuals.

The more convincing examples of reciprocal altruism are indeed characterized by short timescales on which reciprocation occurs. Quick exchanges of altruistic acts are typical for reciprocal grooming, as it occurs in ungulates. Impala serve as an impressive example. They possess teeth that are adapted to grooming, often referred to as the "antelope comb." This comb is used to remove ectoparasites such as ticks. Much of the removal is done by self-grooming but, for obvious reasons, this does not include the head and neck. Females and nonterritorial males engage in interaction sequences where partners alternate in grooming one another. Newborn impala develop this capability during the first weeks of their life after which they groom with adults other than their mother and with other lambs (Mooring 1999). Adult grooming is not restricted to relatives. The amount of this activity that is given in an interaction sequence matches approximately the amount received (Hart and Hart 1992). Grooming is costly and the benefits from tick removal are substantial. Connor (1995) compares the impala system with the egg parceling found in the Hamlet fish. According to Connor, partner switching is not difficult given the impala's gregariousness but switching seems to be sufficiently costly because the initiator of an interaction has to groom first.

Now, if most reciprocity occurs on short timescales, this poses a serious problem to evolutionary game theory since standard models from game theory are "blind" to this restriction and would not predict it. Any passionate game theorist, like myself, should consider this as an alarm signaling the need for conceptual change.

**Thesis 6: Models from standard game theory fail to explain the short timescales on which animal reciprocity takes place.**

*Typical reciprocity models from evolutionary game theory are designed in such a way that they predict reciprocal altruism regardless of whether the time distance between giving and taking is short or long.*

Thesis 6 is not meant to convey the notion that just by introducing time into the models, one can achieve progress in understanding cooperation based on reciprocity. The crux of the issue is to invoke the actual mechanisms upon which evolution operates.

**Thesis 7: Mechanisms shape the evolution of cooperation.**

*The evolution of cooperation in repeated interactions depends strongly on assumptions about how much simple learning is involved in decision making as opposed to higher forms of cognition and hard-wired strategies. It is thus impossible to disentangle causal and functional analysis in this field of research.*

To illustrate this claim, let us take a short detour and consider an experiment conducted by Selten and Stoecker (1986) in their laboratory of behavioral economics. Randomly paired subjects played a fixed number of rounds of the repeated Prisoner's Dilemma. After this, partners were exchanged and the same repeated game was played with other randomly chosen partners. Many such exchanges took place in succession. The experiment, therefore, simulated the process of social learning without free partner choice in a finite population.

Game theorists would maintain that rational players should never cooperate in the repeated Prisoner's Dilemma of Selten and Stoecker's experiment, since the end of the imposed interaction sequence is fixed. Rational players then have to treat the last round as if they were operating in a one-shot game. Therefore, it pays to defect in the last round. Using the cognitive tool of backward induction, a similar argument can be made for all rounds, leading to all-out defection. Evolution acting on hard-wired strategies for this game would mimic the backward induction, provided there is enough genetic variation. Furthermore, it is possible to describe learning rules that would equally please the classical game theorist. With these parallels between advanced cognition, evolution, and simple learning in mind, one might wish to dismiss Thesis 7. The facts, however, teach us another lesson: real learning in humans produces a qualitatively different outcome, as we will now see.

In the series of encounters, subjects first developed or were predisposed with a cooperative attitude. Subsequently they discovered the benefit from defecting toward the end, the so-called *end effect*. However, the learning population did *not* mimic much of the backward induction. After many repeated games had been played in the population of subjects, the typical onset of defection failed to take place anywhere near the first round, and a lot of cooperation still occurred.

Selten and Stoecker tried to interpret this empirical finding as follows. After gaining some initial experience with the game, a learning process guides an

individual's behavior. The subjects are prepared to cooperate first, but switch to noncooperation if either the partner has started to defect or a personal limit, say round  $r$ , is reached. If the current opponent switches to defection in a round earlier than  $r$ , an individual will have a tendency to move the switching threshold down in the next repeated game with a new opponent. Conversely, if the current opponent is still cooperating in round  $r$ ; the opposite tendency will occur, namely to shift  $r$  to a higher value. Simulations of this population learning process showed that the onset of defection moves a little from the end to earlier periods of the game but does not move all the way down to zero. A lot of cooperation is maintained.

Without taking this proximate learning mechanism<sup>2</sup> and its structural properties into account, it would have been difficult to understand the experimental findings under discussion. The learning mechanism as such was probably favored by natural selection because it is a *robust* method of dealing with a variety of problems. Evolution does not design a new mental tool for every problem that animals face, and it always operates by *modification of existing mechanisms*, not by selecting a strategy from an abstract strategy space. This explains why mechanisms can shape the evolution of cooperation, as expressed in Thesis 7.

Let us now move to another aspect of proximate causation, namely the mental bookkeeping involved in partner control. We have already seen that the necessity of this bookkeeping may have been overestimated in models that ignore the partner market. Still, we expect it to play some role in many social interactions. For a *long* time experimentalists have been challenged to demonstrate this bookkeeping. Seyfarth and Cheney (1984), for example, succeeded in providing some evidence for bookkeeping in vervet monkeys, but the interpretation of their well-known empirical results is difficult (Hammerstein 2001).

Silk (this volume) reviews the psychological literature and concludes that certain rigid forms of bookkeeping, like "I gave you this much, you owe me that much," seem to be counterproductive for the maintenance of human friendships. Beyond the primate world, our knowledge of bookkeeping is still extremely limited (see McElreath et al. [this volume] for a discussion of the stickleback predator inspection trips described by Milinski [1987]; see also Dugatkin [1997]).

The issue of mental bookkeeping becomes particularly interesting if one studies indirect forms of reciprocity. In indirect reciprocity (Alexander 1979, 1987; Sugden 1986), the return from a social investment is expected from someone other than the beneficiary of aid. The investment increases the investor's *reputation* in the social group where others have a propensity to help those with a good reputation. This idea raises the empirical and theoretical concern of how updating of reputation can be organized and what role strategic gossiping plays in this context. Some basic problems with the updating of reputation are discussed by Leimar and Hammerstein (2001) and McElreath et al. (this volume).

<sup>2</sup> Since Selten and Stoecker's experiment, economists (including Selten) have elaborated on the process by which human subjects adjust their behavior and beliefs.

**Thesis 8: Constraints on basic mental abilities of animals restrict considerably the evolution of reciprocity.**

When strategies such as Tit-for-Tat and reciprocal altruism are discussed, it is often said that they require very little mental machinery because all the animal has to do is to remember what happened during the last round of an interaction. Such statements reflect the simplicity of models rather than account for the problems real animals would face if they engaged in reciprocal altruism beyond grooming.

Mental machinery has to perform complex tasks in order to achieve subtle reciprocity based on partner control. If the partner, for example, fails to exhibit a cooperative act, this poses the attribution problem to determine whether the observed behavior really belongs to the class of noncooperative moves. The mental updating machinery must solve this problem. Routine learning may interfere with its information processing, which may be costly and error prone. Following Fessler and Haley (this volume), emotions probably play an important role and thus should be reflected in the model. This would require a radical change from the Bayesian approach that governs thinking and modeling in classical game theory. By assumption, a Bayesian decision maker is forced to use all available information for updating his decisions. In contrast, a strategic aspect of emotions may consist in shutting off or distorting input channels. To give an example, one cannot easily argue with an angry person; the door for communication is temporarily closed. This strategic stubbornness may add credibility to the threat that defection from cooperation would have negative consequences.

\* \* \*

Whether or not these theses will spur the hoped-for reformation remains to be seen. Most certainly, if we invested the same amount of energy in the resolution of all problems raised in this discourse, as we do in the publishing of toy models with limited applicability, we would be further along in our understanding of cooperation. No protest(ant) would then be necessary.

### ACKNOWLEDGMENTS

I wish to thank Ed Hagen, Joan Silk, Rob Boyd, Ernst Fehr, and Jack Werren for their ecumenical advice.

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