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Biological Markets

The Ubiquitous Influence of Partner Choice on the Dynamics of Cleaner Fish – Client Reef Fish Interactions

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ABSTRACT

The applicability of biological market theory with its emphasis on partner choice is explored using the interactions between the cleaner wrasse *Labroides dimidiatus* and its “client” reef fish as a model system of mutualism. Cleaners have small territories, which the majority of reef fish species actively visit to invite inspection of their surface, gills, and mouth. Clients benefit from the removal of parasites while cleaners benefit from the access to a food source. Some client species (choosy clients) have large home ranges that cover several cleaning stations, whereas other clients have small ranges and have access to one cleaning station only (resident clients). Field observations, field manipulations, and laboratory experiments revealed that whether or not a client has choice options influences several aspects of both cleaner and client behavior. Cleaners give choosy clients priority of access. Choosy clients switch partners if cheated by a cleaner (= cleaner feeds on mucus/scales), whereas resident clients punish cheats. Cleaners and resident clients, but not choosy clients, build up relationships before normal cleaning interactions take place. Cleaners are particularly cooperative if choosy clients are bystanders of an interaction but less so when resident clients are bystanders. When it comes to the frequency of cheating by cleaner fish, however, partner choice options are overrun by client control mechanisms: predatory clients are far less often cheated than nonpredatory clients, irrespective of choice options. Future research needs to focus more on empirical testing of game theory so that this new information can be used to formulate deductive models.

INTRODUCTION

On human markets, goods or services are traded against money or other goods. It is well established that changes in the ratio between the supply of a good/service

and the demand cause changes in its price. This is because when the supply is higher than the demand, potential buyers are able to compare prices and choose the cheapest offer. This choosiness of buyers is crucial, as it exerts pressure on sellers to outcompete each other with lower prices in order to sell their goods. These principles have recently been applied to cooperative (within species) and mutualistic (between species) interactions in animals (Noë et al. 1991; Noë and Hammerstein 1994, 1995; Noë 2001). The biological market approach has two major goals:

1. Explain adaptations that are the result of “market selection.” Market selection explains the evolution of mechanisms enabling partner choice as well as adaptations that increase the chances of being chosen in cooperative and mutualistic systems. There is an obvious overlap with the evolution of mate preference and the selection for secondary sexual characters driven by mate choice, but we propose to use the label “market selection” only in relation to cooperation outside the mating context. A crucial difference is that covariance between choice mechanisms and chosen traits typical for sexual selection (Fisher 1930) is unlikely to occur under market selection, notably when trading partners belong to different species.
2. Predict changes in exchange rates of commodities due to changes in the supply/demand ratio between these commodities.

Mechanisms, such as partner choice and outbidding competitors, are relevant in three major fields within behavioral ecology: sexual selection, intraspecific cooperation, and interspecific mutualism (see below). To date, surprisingly little attention has been paid to the selective force of partner choice outside the context of sexual selection. Similarly exchange ratios have been studied in the context of mating markets but not in the context of cooperation and mutualism. This is probably due to an obsession with partner control in the theoretical approaches to cooperation, as a result of a historically determined fascination with the evolution of altruism. Classical models of cooperation are usually based on an iterated version of the so-called Prisoner’s Dilemma (PD) game (Axelrod and Hamilton 1981). In short, a PD exists if two players, who can either cooperate or defect, receive a higher payoff from defection independently of the partner’s behavior; if both cooperate, however, they receive a higher payoff than if both defect. Because of the payoff structure, cooperation is highly unlikely in single-round PD games, but in iterated versions several strategies have been proposed that lead to evolutionarily stable cooperation (reviewed by Dugatkin 1997). In other words, once all individuals of a given population play certain cooperative strategies, the population cannot be invaded by individuals playing any defecting strategy. The cooperative strategists, on average, gain higher payoffs than the individuals playing a defective strategy.

At first glance, it appears that partner control models and biological market models address different problems invoked in cooperative interactions. “Traders” on biological markets may react to partners that do not yield enough

“profit” by terminating the cooperative relationship. The negative effects of this decision to the actor can be limited if he can switch to an alternative partner. The biological market paradigm explicitly excludes the use of force to extort commodities from partners in the same sense that mainstream economical models also ignore the possibility of theft and robbery. In partner control models, which usually focus on the interactions of two players only, all forms of defections and reactions to defections are considered, from simply terminating the cooperation to the use of force and other forms of coercion. Partner control models thus cover the whole spectrum of cooperative to exploitative interactions. In reality, there are obvious connections between partner choice and partner control issues. Ultimately, the two approaches have to be brought together. To keep things simple at first, however, it may be desirable to study partner choice and partner control separately.

In this chapter we use data on cleaner fish – client reef fish interactions to explore how market theory may explain (a) payoff asymmetries between cooperating partners, (b) differences in strategic options that are available to partners, (c) how partner choice interacts with partner control mechanisms, and (d) how incomplete control over the resources traded may lead to a shift from mutualism to parasitism.

BIOLOGICAL MARKETS IN NATURE: A SHORT OVERVIEW OF THE EVIDENCE

Noë and Hammerstein (1994, 1995) concentrated on cooperative and mutualistic systems in which two classes of traders can be distinguished that control different commodities. In such systems, “bartering” can take place through the mechanism of partner switching. Consistent partner choice over many generations can lead to the selection of specific adaptations comparable to secondary sexual characters, which evolve under selection through mate choice. Noë and Hammerstein (1994) used the example of delayed plumage maturation in purple martins based on data presented by Morton et al. (1990). Male purple martins may control several nest cavities, most of which are “martin houses” provided by humans in this day and age. The male can only use one cavity for breeding, since the species has obligatory biparental care. However, he can allow a pair consisting of a yearling male and his mate to breed in another cavity under his control. By copulating with the female of the subordinate pair, the dominant male gains some extra offspring that are cared for by another male. The subordinate males also gain, since they usually sire some chicks produced by their mate. Without access to this nesting opportunity, they would not have any offspring at all. Noë and Hammerstein (1994) proposed that the delayed plumage maturation in the purple martins is selected for through the choice made by the dominant males among the yearlings. By accepting only males that carry obvious signs of subordination as subletters they would lower the risk of

challenges to their own position. Females probably prefer males with a mature plumage and males with delayed plumage would not be able to hold a nest cavity for very long, since they would attract immediate attacks from other adult males.

The weak point in this account is that the situation is rather unnatural: the evolution of delayed plumage maturation over the period that humans provide grouped nest cavities in the form of martin houses is unlikely. However, Greene et al. (2000) recently provided a very similar example in another colorful North American bird, the lazuli bunting, observed in a natural setting. In this species, dominant males do not accept yearling males with delayed plumage maturation in adjacent cavities but in adjacent territories. Greene et al. carefully checked that the conditions for market selection were met.

Under market selection, the evolution of mechanisms for implementing choice can be expected in the choosing class. Bull and Rice (1991) hypothesized such a mechanism for the fig/fig-wasp system: the selective abortion of overexploited figs. Although this is probably not the mechanism that figs use to control overexploitation (Herre and West 1997), the abortion mechanism has been described for similar pollination mutualisms (e.g., Pellmyr and Huth 1994; Fleming and Holland 1998). Both sides in a market may evolve mechanisms that ensure that the partner (a) cannot rob a commodity and (b) has to pay a price as high as the law of supply and demand allows. Flowers may, for example, have structures that force pollinators to stay longer and take up more pollen, instead of offering more nectar.

Biological markets can be found throughout the living world. As long as there is a possibility to exchange commodities and at least one of the trading partners can exert choice, the market mechanism may influence the outcome of the interaction. One should not forget, however, that commodities from abiotic sources may play a role as well. Such resources can sometimes be in competition with commodities provided by one of the trader classes. This is, for example, the case in the biological markets involving mycorrhiza (Schwartz and Hoeksema 1998; Wilkinson 2001) and rhizobia (Simms and Taylor 2002), i.e., mutualisms in which plants exchange nutrients with fungi and bacteria, respectively. These markets can be strongly influenced by abiotic sources of these nutrients, including artificial fertilizers (West et al. 2002).

Exact quantitative predictions of exchange rates on the basis of supply/demand ratios are hard to make, both for human economic systems and for biological systems. It is easy, however, to predict in which direction the exchange rate will change when the supply/demand ratio shifts. The most straightforward and simple example published to date is probably by Henzi and Barrett (2002): Baboon females like to inspect and handle the infants of other females, but they are not allowed to do so without “paying” for it by grooming the mother first. Henzi and Barrett predicted that females would have to groom longer when there were fewer infants available in the group, a prediction that held both when mothers were dominant over the would-be handlers of their infant and when the mothers

were subordinate. There was a quantitative difference between the two cases: the use of force can alter or even overrule market effects (see below).

Together with further examples of biological markets given in Noë et al. (1991), Noë and Hammerstein (1994, 1995), and Noë (2001), these examples show that market theory provides a general framework to study payoff distributions among partners in sexual selection, cooperation, and mutualism. We will now explore the applicability of market theory and its current limits by providing a detailed overview on a field and experimental study on the mutualism between the cleaner wrasse *Labroides dimidiatus* and other reef fish species.

A CASE STUDY: MUTUALISM BETWEEN THE CLEANER WRASSE *L. DIMIDIATUS* AND CLIENT REEF FISH

In coral reefs from the Red Sea through the Indo-pacific to the Great Barrier Reef in Northeastern Australia, the best way to see a wide variety of fish species within a short time period is to locate a cleaner wrasse, *L. dimidiatus*. These fish are visited by the majority of other reef fish species who often “pose” for the cleaner by spreading their pectoral fins and stopping coordinated swimming, leading to “head up” or “head down” postures, depending on the species. Posing is a signal to the cleaner fish that the visitor seeks its service, which comprises the removal of ectoparasites and dead or infected tissue from the body surface, the gills, and sometimes even inside the mouth. The deal seems to be straightforward: the cleaner fish gets access to an easy meal and the so-called “client” gets cleaned. *L. dimidiatus* is just one of a large variety of cleaning organisms but it is probably the best studied (for reviews, see Losey et al. 1999; Côté 2000). The interaction between *L. dimidiatus* and its clients has attracted considerable attention, one reason being that it is particularly suited to test game theoretical models of cooperation among unrelated organisms. Individual *L. dimidiatus* may have more than 2000 interactions per day, eat about 1200 parasites per day, and may reduce the parasite density on clients by a factor of 4–5 (Grutter 1999). Most recently, it was found that clients without access to cleaner fish in their natural environment showed a higher stress response to capture than clients with access to cleaner fish (R. Bshary, R. Oliveira, and A. Canario, unpubl. data). The difference can be seen as a net difference between costs and benefits of cleaning interactions. There is thus little doubt that interactions between cleaner fish and clients are overall mutualistic, i.e., to the benefit of both partners.

There are several forms of conflict in these interactions. One of the most well known involves the possibility of predatory clients defecting by eating the cleaner rather than letting it inspect — a problem that Trivers (1971) used to explain his concept of reciprocal altruism. He proposed that predators refrain from eating cleaners despite the energy gain being higher than the gain from the removal of parasites in one single interaction. Refraining from eating cleaners only becomes advantageous for the predator when the repeated removal of

parasites by a particular cleaner leads to a larger benefit than eating that cleaner. Trivers's idea has not yet been tested but there is some evidence that predators may eat cleaners under some circumstances (Côté 2000). In this chapter, we do not limit ourselves to the game between cleaners and predatory clients but rather focus on the strategies cleaner fish use when confronted with different types of clients and how these clients deal with them. It is important to note that the majority of client species feed on plankton or graze and are hence not potential predators of cleaners.

Recent experimental evidence suggests that cleaners regularly cheat clients by consuming client mucus and scales, as the consumption of these food items is not linked to the removal of ectoparasites (Bshary and Grutter 2002a). In addition, there might be conflicts between cleaners and clients over the timing and duration of interactions. This conflict is most obvious when two or more clients seek inspection from the same cleaner simultaneously so that the cleaner has to choose between them. As we shall see, the solutions to these conflicts are often, but not always, dependent on the ratio between supply and demand.

Methods

We refer to a single species of cleaner wrasse: *L. dimidiatus*. All reported field observations and field experiments were conducted at Ras Mohammed National Park, Egypt. Data were either collected while sitting 2–3 m in front of a cleaning station or by following individual clients. Interactions between cleaners and clients were first observed and then the key information was noted on a Plexiglas plate. Laboratory experiments were conducted at the Lizard Island Research Station, Great Barrier Reef, Australia. For methodological details, we refer to the respective publications of the original data.

Game Structure

For a thorough appreciation of what happens during interactions, it is important to outline the strategic options of cleaners and clients. Note that the game structure applies to *L. dimidiatus* but may be different for other cleaner fish species.

1. *Repeated game structure*: Individual clients seek inspection about 5–30 times per day, in extreme cases more than 100 times a day (Grutter 1995). Even clients with territories or home ranges that cover large reef areas may interact repeatedly with the same individual cleaner fish. Cleaners may have more than 2000 cleaning interactions per day (Grutter 1995). Cleaners are territorial and usually move within very confined areas of a few cubic meters, which led to the term “cleaning station.” Clients can tell individual cleaners apart through site recognition (unless there is a pair of cleaners at one station) and/or individual recognition. Experimental evidence indicates that cleaners can recognize individual clients (Tebbich et al. 2002), although it is hard to quantify how many they actually recognize under natural conditions.

2. *Choice options:* Due to the cleaners' site fidelity, a client decides whether or not to visit a cleaner and to seek an interaction; cleaners only have the option of ignoring a visiting client. Members of some client species (also called "residents") have small territories or home ranges, which allow them access to only one cleaning station. Cleaners, thus, have veto power (Noë 1990) in that they have exclusive access to these clients without competition from other cleaners. Cleaners are, therefore, expected to be in a strong position with respect to the service quality: they can cheat residents more often and let them wait longer than nonresident clients. Individuals of nonresident client species have home ranges that cover several cleaning stations (further called "choosy clients"). In these cases, cleaners compete among each other to attract these clients. As each cleaner remains at its respective cleaning station, competition can only take place through outbidding each other with better service quality, not through aggressive interference or actively approaching clients. Clients with the option to choose between cleaners are therefore expected to show preference for the cleaners that offer the best service.
3. *Asymmetry in possible sanctions:* About 15% of client species are predatory in the sense that they hunt fish that are the size of cleaners. In interactions between cleaners and predatory clients, both have symmetrical strategic options, i.e., each party can either cooperate or cheat. However, the effects of cheating on the partner are highly asymmetric: an exploited predator only loses a little bit of mucus, whereas an exploited cleaner loses its life. In interactions between cleaners and the 85% nonpredatory client species (grazers or plankton feeders), the strategic options are asymmetric: the cleaner can cooperate as well as cheat whereas the client has no option to exploit the cleaner to its own advantage. These clients can only control the duration of an interaction, i.e., by swimming off, they can terminate an interaction.

A PURE MARKET GAME DETERMINED BY SUPPLY AND DEMAND: CLIENT–CLIENT COMPETITION OVER PRIORITY OF ACCESS TO CLEANER FISH

Sometimes a client arrives at a cleaning station while the cleaner is inspecting another client; sometimes two or more clients seek the inspection of a cleaner fish simultaneously. In such cases, individual clients compete directly over access to the cleaner fish. This competition takes place only through inviting the cleaner for inspection, not through aggressive displacement (Bshary 2001). Market theory makes the following predictions for these situations:

1. Cleaners should give priority to choosy clients over resident clients. The reason is that choosy clients can visit another cleaning station rather than queuing for service. A cleaner that ignores a choosy client in favor of a resident client could lose access to a food source, and selection is

expected to work against that decision rule. Resident clients have no strategy available to push a cleaner into giving them priority of access. They have to come back at a time that is more convenient for the cleaner if they want to be inspected at all. A cleaner's access to this food source is thus just delayed if it ignores the resident's invitation for inspection in favor of another client.

2. The preference for choosy clients should be independent of the clients' quality as a food patch. Optimal foraging theory based on the marginal value theorem (Charnov 1976) would lead to an alternative prediction: as client size strongly correlates with parasite load (Grutter 1995), the decisions of the cleaner fish should be determined by the relative body sizes of clients that present themselves simultaneously.

Field observations were in line with predictions based on market theory. Cleaners switched from resident clients to choosy clients 51 times but only once the other way round; when a choosy client and a resident client invited inspection simultaneously, the cleaners inspected the choosy client in 65 out of 66 observations (Bshary 2001). These results were independent of the clients' relative body sizes, as the choosy clients were smaller than the residents in 12 (switching) and in 21 (queuing) occasions. Following individual long-nosed parrotfish, *Hipposcarus harid*, for up to 120 minutes, Bshary and Schäffer (2002) confirmed that choosy clients are indeed active players in the game. The probability of a client returning to the same cleaning station for its next inspection was high (median of 13 individuals: 60%) if it was inspected, but low (median: 0%, $n = 13$) if it had been ignored in favor of another (choosy) client.

It could have been that choosy clients are better food patches than residents, independent of size, because they might visit cleaning stations less frequently than residents to optimize foraging, or that choosy clients are generally more infected than residents because they traverse larger areas, which might make them more vulnerable to infestation. Therefore, Bshary and Grutter (2002b) experimentally removed food patch quality as a confounding variable. Cleaner fish were kept in aquaria that had a compartment inaccessible to the cleaner. A lever construction allowed two Plexiglas plates of similar shape and color, but of different sizes, to be moved in and out of the cleaners' compartment. On both plates, equal amounts of mashed shrimp meat were spread over an area of 4 cm². Cleaners could thus choose between two food patches of equal quality and, when the two plates were presented simultaneously, had to decide which one to inspect first. The lever construction was used to mimic differences in behaviors between resident clients and choosy clients. Two differences could potentially provide cleaners with clues about clients being either residents or choosy under natural conditions. First, residents are often willing to queue for inspection when the cleaner is busy with another client, but choosy clients swim off in such situations. Second, residents may revisit the cleaner shortly after being ignored, whereas choosy clients switch to another cleaning station. We mimicked these two cues in two experiments.

Experiment 1: The “resident plate” was left in the cleaners’ compartment until the cleaner finished foraging, whereas the “choosy plate” was retrieved immediately if the cleaner started eating from the other plate.

Experiment 2: The plate that was first ignored was invariably pulled back, but the resident plate was pushed in again as soon as the cleaner had finished foraging on the choosy plate; the choosy plate was not returned.

Cleaners were repeatedly confronted with these situations, and market theory predicted that the cleaners should develop a preference for the choosy plate despite a lack of difference between the two plates regarding patch quality. In both experiments, a significant proportion of cleaners soon fed from the “choosy” plate first (median values for trials 16–20 in Experiment 1 and trials 11–15 in Experiment 2: 80%). In combination with the field observations, these results provide strong support for the market theory. The partner choice options (and the use of them) of choosy clients select for cleaner fish that give them priority of access over residents.

A Limitation of Market Theory: Predicting Cheating Frequencies by Cleaner Fish

From a client’s perspective, a good cleaning service does not only include getting priority of access but also that the cleaner searches for parasites and refrains from eating healthy client tissue. From a cleaner’s perspective, however, searching for parasites is time consuming whereas client mucus is readily available. Therefore, a conflict between cleaner and client exists over the cleaner’s foraging behavior. Most client species do not win this conflict entirely (cf. below) and fortunately, defections by the cleaner become visible to the observer through short jolts performed by clients in response to cleaner fish mouth contact. There is experimental evidence that client jolts are not related to the removal of parasites; to the contrary, clients jolt more frequently the less parasite infested they are (Bshary and Grutter 2002a). Jolt rates are therefore a good correlate of cleaner fish cheating rates. (This does not exclude the possibility that a jolt may sometimes occur in response to the removal of a parasite.) In an experiment in which anaesthetized parasite-free client surgeon fish *Ctenochaetus striatus* were added to a cleaner fish in an aquarium, most cleaners scraped the surface of their clients rather than feeding on prawns that were provided as an alternative food source (Bshary and Grutter 2002a). It thus appears that when clients cannot control cleaner fish behavior, cleaners are likely to cheat. So how do clients control cheating frequencies of cleaners, and what factors may explain variation among different client species with regard to cleaner fish defection frequencies?

Market theory predicts that choosy clients use their option to play cleaners off against each other to control cheating partners. It is therefore predicted that choosy clients swim off when the cleaner bites them and visit a different cleaner for their next inspection (similar to situations where cleaners ignore them as discussed above). Resident clients, however, lack this option of switching partners.

Market theory therefore predicts that residents have to accept more frequent cheating by the cleaner than choosy clients.

Field observations revealed that choosy clients do indeed use their choice option to control defecting cleaners. Long-nosed parrotfish came back to the very same cleaning station for their next inspection if the previous one had ended without a conflict due to cheating by the cleaner in 65% of observations; they, however, switched to another cleaning station if the cleaner had bitten them in about 90% of observations (Bshary and Schäffer 2002). Partner choice is not the only option for clients to keep the cleaner in check. As suggested by Trivers (1971), predatory clients can eat the cleaner. All clients have the option to attack the cleaner and chase it around, a strategy which may represent “punishment” sensu Clutton-Brock and Parker (1995). A strategy based on punishment includes three steps:

1. An individual A performs an act that increases its own fitness at the expense of the fitness of another individual B.
2. In response, individual B performs an act that is temporarily spiteful as it reduces the fitness of both individuals.
3. As a consequence, individual A will change its behavior in a way that is costly for itself but increases the fitness of individual B.

Note this strategy does not imply any causal understanding by the players. This form of punishment is exactly what happens during interactions between cleaners and resident clients. Cheating by cleaners was often followed by the clients chasing the cleaners (> 60% of responses). As a result of chasing, the interaction terminated in 95% of observations ($n = 195$). During the next interaction between the cleaner and the same individual, which is usually delayed by a few minutes, the cleaner refrained from cheating (median value of jolt frequencies in 36 client species is 0/100 s in interactions following chasing, compared to ~5/100 s on average). In summary, there are three ways in which different client species may control cleaner fish defection: kill and eat (predators), partner switching (choosy clients), and punishment (resident clients).

Predatory client species jolted less frequently than nonpredatory client species (Bshary 2001). Within the predator category, there was no significant difference between resident predators and choosy predators. Basically, predatory clients did not jolt (median values for both resident and choosy predatory species = 0/100 s interactions). Nonpredatory choosy clients, on average, jolted less frequently than nonpredatory resident clients. However, this result appeared to be confounded by size, in particular in resident species. There was a significant negative correlation between resident client size and jolt rates ($r_s = -0.51$, $n = 24$ species, $p < 0.01$). This correlation is not caused by larger resident clients being more likely to punish cleaners as there was no correlation between resident client size and probability of punishment (both small and large species punish > 60% of cleaner cheats). When only resident and choosy client species of similar size were considered, no significant difference in jolt rates between the two client categories were found ($p > 0.1$) (Bshary 2001). It thus appears that the

predators' option to kill the cleaner leads the cleaners to engage in an unconditional cooperative strategy during interactions with predators. In conclusion, being or not being able to choose among cleaners does not predict cleaner fish cheating rates. This is because the choice option of choosy clients is just one of several potential mechanisms, of which being able to retaliate cheating seems to be the most efficient. Predatory clients are cheated least frequently probably because they could eat cleaners; the punishment of cheating cleaners by resident clients is about as effective as the switching strategy of choosy clients. Nevertheless, the market situation still determines who has to invest in partner coercion in the form of "punishment" and who has not.

INTEGRATING MARKET THEORY INTO PARTNER CONTROL THEORY

Partner control theory in the context of cooperation is heavily biased toward the iterated PD game (IPD) (review in Dugatkin 1997). Since Axelrod and Hamilton (1981) used computer tournaments in the IPD and found that "Tit-for-Tat" (start cooperative and consequently play the strategy your partner played in the previous round) emerged as the superior strategy, many extensions have been explored (Dugatkin 1997). Recently, Roberts and Sherratt (1998) explored variable payoffs, and Nowak and Sigmund (1998) explored the evolution of altruistic behavior based on indirect reciprocity (help to receive future help from the observers rather than the recipient). However, most examples of intraspecific cooperation and interspecific mutualism do not seem to fit the models. Bshary and Grutter (2002a) argued that this is because the participants in most empirical examples have different strategic options and thus should be analyzed with the help of asymmetrical games. One class of traders usually lacks the option to gain anything from exploiting the partner, whereas the other class has the option to gain from cheating. A typical example is the cleaner fish – client mutualism explained above but there are plenty of others (Bshary and Grutter 2002a). For a further introduction into these systems, see Noë et al. (1991) and Noë (2001).

Because of the asymmetric structure of many cooperative and most mutualistic games, the IPD is not the appropriate framework to analyze which conditions lead to cooperative outcomes. In contrast, partner choice options will be of major importance in understanding the structure of the underlying game and the payoff configuration. As we argued above, partner choice can be a mechanism of partner control in asymmetric games. However, partner choice options (or the lack of them) may influence partner control games in other ways as well, as we illustrate below with further data on the cleaner fish – client mutualism.

Interaction between Partner Choice and the Need for Building up Relationships

Consider a model of reciprocal altruism where the investment of both partners can be variable. Roberts and Sherratt (1998) proposed that a strategy called

“raising the stakes” might prove to be an evolutionary stable solution to this game. Raising the stakes means that an individual will initially invest very little into its partner and will stepwise increase investment if the partner returns at least the same amount. If the investment is not met, the individual stops being altruistic. Thus, relationships are built up carefully and therefore no defecting strategy can yield large benefits, as only established relationships consist of partners trading large favors. Testing the predictions of the model within the asymmetric games between cleaners and clients by transferring cleaners, Bshary (2002b) found no support for a “raising the stakes” strategy. Introduction of a cleaner at a new locality affects its relationships with local residents and choosy clients differently. Interactions between transferred cleaners and residents were very different from established relationships. During observations that began two hours after transfer, cleaners refrained from cheating (median: 0/100 s interaction) and provided tactile stimulation to the dorsal area of the clients’ body during the entire interaction in about 80% of encounters. Tactile stimulation is a special treat that cleaners offer to their clients, usually to make clients that are unwilling to interact slow down for inspection or as a reconciliatory gesture after a conflict due to cleaner fish cheating (Bshary and Würth 2001). Tactile stimulation is incompatible with foraging and thus costly for the cleaner. Whether tactile stimulation yields any benefits to clients is currently unknown but clients readily accept this treat. Resident clients frequently fled from approaching transferred cleaners (median: 16% of all interactions) and often chased cleaners without apparent reason, i.e., without the cleaners trying to approach them (median: 26% of all interactions). After 24 hr, these behaviors of cleaners and clients were still significantly elevated compared with a control group in which cleaners were caught and released at their original cleaning station. (Fleeing and unprovoked aggression hardly ever occur when relationships are established.) Thus, cleaners and residents clearly build up relationships with transaction specific investments but opposite to the predictions of raising the stakes. Initial heavy investment by both partners is necessary to gain eventually the benefits of cleaning interactions between established partners. A likely explanation for this pattern is that residents seem to “expect” heavy cheating by the cleaner and show off their ability to punish first. Note that the behavior of residents toward immigrated cleaners restricts advantages that cleaners might gain from a roving strategy and works in favor of stationary cleaners.

Interactions between experimentally transferred cleaners and choosy clients were “normal” from the very beginning with respect to the parameters measured, i.e., duration of interactions, client jolt rate, and cleaners providing tactile stimulation. Cleaners were typically transferred over distances of 200–400 m coastline, which virtually excludes the possibility that the choosy clients already knew them from their previous station. This experiment again shows that market theory is essential to understand the strategies played by both cleaners and clients. It explains why relationships first go through a phase of investment in trust-building behavior when clients have no option to choose another partner

and have to rely on their ability to punish to control their partner. No such trust-building phase is necessary when the client can switch to another cleaner.

Interaction between Partner Choice and Indirect Reciprocity

As in reciprocal altruism, an individual may help another improve his chances to receive help. In “indirect reciprocity,” however, the altruistic act improves an individual’s chances of obtaining help in return, not only from the recipient, but from bystanders who witnessed the altruistic act. By behaving altruistically, the altruist gains something like an “image score” or “social prestige” (Alexander 1987; Zahavi 1995), and individuals with a high score are the most likely ones to receive help by others or to be chosen as cooperation partners. This idea has been modeled by Nowak and Sigmund (1998) and by Leimar and Hammerstein (2001); Wedekind and Milinski (2000) provided experimental evidence for its adaptive value in humans. Transferring the logic of indirect reciprocity to the cleaner fish – client mutualism, it might pay for cleaners to refrain from cheating current clients if onlookers base their decision to invite inspection on what they witness: “Stay if you see a cooperative cleaner, flee if you witness a cheating cleaner.” (Remember that cheating is often followed by the client darting off or chasing the cleaner and that these behaviors probably provide an easily observable cue for bystanders as opposed to looking for client jolts.) The prediction based on image scoring is opposite to what is predicted by market theory. The market paradigm suggests that the cleaner can drop its service quality and hence cheat more frequently when there is a temporarily high demand for cleaning. Clients indeed seem to base their decision to seek inspection on what they witness: field observations revealed that if clients supposedly saw a positive interaction, they almost always invited inspection (median: 100%), and if they saw a negative interaction, they rarely invited inspection (median: 15%) (Bshary 2002a). Thus, cleaners have an image score that depends on how cooperatively they behave. In turn, cleaners cheated current clients less frequently in the presence of bystanders than in the absence of bystanders (A. D’Souza and R. Bshary, unpubl. data). Distinguishing between resident bystanders and choosy bystanders, the effect is significant only in the presence of choosy clients (negative correlation between current client jolt rate and number of choosy bystanders for 15 out of 16 species), not in the presence of resident clients (negative correlation between current client jolt rate and number of resident bystanders for 9 out of 14 species). This apparent differentiation by cleaners, which should be backed up with further data, makes sense in the light of market theory as only image scoring choosy clients may decide to visit another cleaner instead.

There is an interesting twist to the story: choosy client species that visit a cleaning station in large schools (*Abudefduf vaigiensis*, *Caesio lunaris*) jolt extremely frequently (about 20 jolts/100 s interactions), whereas jolt rates in interactions between cleaners and single-visiting individuals of the same species are “normal” compared to other client species (about 5 jolts/100 s interactions) (A.

D'Souza and R. Bshary, unpubl. data). A possible explanation is that individuals in schools are not moving independently of the other school members and therefore stay around at the station as long as the school does, even if the cleaner cheats. School cohesion might thus offset image scoring, and in its absence, the market effect of a temporarily high demand for cleaning service leads to low service quality by cleaners.

CONCLUSIONS AND OUTLOOK

We believe that market theory, with its emphasis on partner choice, provides a useful framework to study payoff distributions and strategy sets of collaborators in intraspecific cooperation and interspecific mutualism. In particular, market theory generates testable predictions about exchange rates that may result in payoff asymmetries between partners, whereas partner control models based on the IPD do not. As partner choice occurs to some extent in most natural systems, partner choice by the limiting class of traders can be a powerful control mechanism to control defection by members of the common class of traders. Therefore, future partner control models must have partner choice options incorporated into their assumptions to become more realistic. Until now, the incorporation of partner choice within the framework of the IPD has focused on defectors being able to rove (see references in Dugatkin 1997) and has concluded that partner switching may hinder the evolution of cooperation. Other recent models, however, suggest that partner choice may enhance cooperation (Ferriere and Michod 1995).

Pure free markets will probably turn out to be very rare in nature. The form and outcome of most cases of cooperation and mutualism will be determined by more than partner choice and outbidding alone. The market effect is but one of several sources of leverage cooperating individuals have over each other. Other sources are:

- The option of simply terminating the relationship.
- The option to switch from a cooperative to an exploitative strategy, described as “defection” in IPD models.
- The use of force to influence the outcome of current or future interactions. This is the sort of leverage described in models of dominance, in models of conflict, and in punishment models.
- The possibility to steal desired commodities, as in parasitic relationships.
- The possibility to influence interactions of the partner with third parties, as described in models that take “image scoring” into consideration.

Such sources of leverage contribute to what is known as the “power” one individual or group has over another in the economic, political, and sociological literature (Bowles and Hammerstein, this volume; Lewis 2002). Some or all of these sources of power may influence a single mutualistic relationship simultaneously. To keep things traceable, we need to understand fully the interactions with one or two sources of sole power. Ultimately, all six, and perhaps more,

building blocks should be integrated in what can be called “power models” of cooperation. It seems to us that the most promising way forward is to use well-understood empirical examples to guide the building of more complex models, in order to avoid the sterile theorizing of the recent past. Our remarks below are intended to guide the further development of market models.

Modeling Market Theory

Earlier, we stated that market models might (a) help explain the evolution of traits beneficial to the partner but detrimental to its bearer as well as (b) provide quantitative predictions about exchange rates of commodities based on supply/demand ratios. Noë and Hammerstein (1994, 1995; see also Noë 2001) have taken initial steps toward solving the first problem, but the second issue has barely been addressed, apart from the obvious prediction that exchange rates should shift in favor of a trader class whose commodity becomes in short supply. The second problem has been totally ignored in cooperation theory until now. This has partly been due to historically determined blindness, but also because it may prove to be a more difficult issue to resolve. In sexual selection theory, this problem has not been ignored and several models have been proposed to explain, for example, the relationship between the operational sex ratio and parental investment. The same problem exists in cooperative and mutualistic interactions. Flowering plants, lycaenid butterfly larvae, and aphids have to decide how many units of sugar they offer to pollinators or ants. Similarly, helpers have to “decide” how much food they provide to the territory owners’ offspring, and cleaners have to decide how often they cheat their clients.

Incomplete Control over Trading and a Shift from Mutualism to Parasitism

To explore the effects of partner choice, it is best to assume that each trading partner has complete control over the resource or commodity it offers. In reality, however, forceful exchange of goods or robbery may occur frequently. In particular, in situations where one partner cannot control whether an interaction takes place or when it ends, the other partner may be more likely to cheat. Based on cleaner fish – client data, Johnstone and Bshary (2002) developed a model with the following properties.

1. One class of traders in a potentially mutualistic interaction has the option to vary the degree to which it exploits its partner, assuming that exploitation yields a higher payoff than cooperation.
2. The potential victim has variable degree of control over the duration of an interaction.

It turned out that as long as the potential victim has sufficient control of the duration, interactions were mutualistic for both participants. With decreasing control and increasing temptation to defect, the outcome of interactions became more and more parasitic. The model yields three important implications: First,

cooperation may be stable when only one partner has the option to cheat. Second, despite the temptation to cheat, cooperation may evolve in one-round interactions. Finally, two figurative screws, namely the temptation to cheat and the degree of control by the potential victim, can be turned to explain interactions shifting between mutualism and parasitism. As it stands, the model is very simple in its assumptions. Incorporating the possibility for the potential victim to switch partners would probably make the mutualism more stable. In general, we predict that combining the market effect with any other source of leverage may offer a powerful approach to explain transitions from mutualism to parasitism.

Statements and Open Questions

- Partner choice should be recognized as one of several sources of leverage cooperating organisms have over each other. Other such sources are the option to refuse interactions, to switch from cooperation to exploitation, the use of force, the possibility to steal commodities, and the effect on the “image score” of the partner.
- Partner choice options, influenced by the costs of choosing and by supply and demand are major predictors of payoff distributions among cooperators and mutualists. Future research must take the step from qualitative predictions in payoff shifts to quantitative predictions of “exchange rates.”
- Participants in cooperation and mutualism typically have different options, which means that asymmetric games are the appropriate paradigms. Although these asymmetries do not affect market theory, it is clear that IPD models are useless to explain or predict the evolution or the strategies played in these systems. To understand the evolution of cooperation between unrelated individuals, we need asymmetric strategy sets.
- As it stands, the emphasis of future research should be on collecting quantitative data that allow the development of deductive models as a basis for new empirical research. A lack of empirical studies that confirm the predictions of available partner control models, most of which were developed unconstrained by facts, may reflect the lack of realism of these models.
- Restricted market games in which individuals may have incomplete control, either over the recourse they trade or over the course of interactions, are most likely to yield a framework that may help to understand under which circumstances symbioses may be commensalistic or parasitic rather than mutualistic.
- Cooperation and defection are often seen as a hallmark of Machiavellian intelligence, the idea that primates have their large neocortex to cope with a complex social environment (Byrne and Whiten 1988). Nowak and Sigmund (1998) proposed that indirect reciprocity based on image scoring may have been crucial for the evolution of human societies. As it stands, these phenomena may well occur in a wide variety of taxa. We therefore wonder how cognitive abilities or constraints influence game structures and how one could potentially distinguish “complex” cooperation from “brainless” cooperation.

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REFERENCES

- Alexander, R.D. 1987. *The Biology of Moral Systems*. New York: Aldine de Gruyter.
- Axelrod, R., and W.D. Hamilton. 1981. On the evolution of co-operation. *Science* **211**:1390–1396.
- Bshary, R. 2001. The cleaner fish market. In: *Economics in Nature*, ed. R. Noë, J.A.R.A. van Hooff, and P. Hammerstein, pp. 146–172. Cambridge: Cambridge Univ. Press.
- Bshary, R. 2002a. Biting cleaner fish use altruism to deceive image scoring clients. *Proc. Roy. Soc. Lond. B* **269**:2087–2093.
- Bshary, R. 2002b. Building up relationships in asymmetric cooperative interaction between cleaner fish and client reef fish. *Behav. Ecol. Sociobiol.* **5**:365–371.
- Bshary, R., and A.S. Grutter. 2002a. Asymmetric cheating opportunities and partner control in a cleaner fish mutualism. *Anim. Behav.* **63**:547–555.
- Bshary, R., and A.S. Grutter. 2002b. Experimental evidence that partner choice is the driving force in the payoff distribution among cooperators or mutualists: The cleaner fish case. *Ecol. Lett.* **5**:130–136.
- Bshary, R., and D. Schäffer. 2002. Choosy reef fish select cleaner fish that provide high service quality. *Anim. Behav.* **63**:557–564.
- Bshary, R., and M. Würth. 2001. Cleaner fish *Labroides dimidiatus* manipulate client reef fish by providing tactile stimulation. *Proc. Roy. Soc. Lond. B* **268**:1495–1501.
- Bull, J.J., and W.R. Rice. 1991. Distinguishing mechanisms for the evolution of cooperation. *J. Theor. Biol.* **149**:63–74.
- Byrne, R.W., and A. Whiten, eds. 1988. *Machiavellian Intelligence*. Oxford: Clarendon Press.
- Charnov, E.L. 1976. Optimal foraging, the marginal value theorem. *Theor. Popul. Biol.* **9**:129–136.
- Clutton-Brock, T.H., and G.A. Parker. 1995. Punishment in animal societies. *Nature* **373**:209–215.
- Côté, I.M. 2000. Evolution and ecology of cleaning symbioses in the sea. *Oceanogr. Mar. Biol. Ann. Rev.* **38**:311–355.
- Dugatkin, L.A. 1997. *Cooperation among Animals: An Evolutionary Perspective*. Oxford: Oxford Univ. Press.
- Ferriere, R., and R.E. Michod. 1995. Invading wave of cooperation in a spatially iterated prisoner's dilemma. *Proc. Roy. Soc. Lond. B* **259**:77–83.
- Fisher, R.A. 1930. *The Genetical Theory of Selection*. Oxford: Clarendon.
- Fleming, T.H., and J.N. Holland. 1998. The evolution of obligate pollination mutualisms: *Senita* cactus and *senita* moth. *Oecologia* **114**:368–375.
- Greene, E., B.E. Lyon, V.R. Muehler et al. 2000. Disruptive sexual selection for plumage coloration in a passerine bird. *Nature* **407**:1000–1003.
- Grutter, A.S. 1995. Relationship between cleaning rates and ectoparasite loads in coral reef fishes. *Mar. Ecol. Prog. Ser.* **118**:51–58.
- Grutter, A.S. 1999. Cleaner fish really do clean. *Nature* **398**:672–673.
- Henzi, S.P., and L. Barrett. 2002. Infants as a commodity in a baboon market. *Anim. Behav.* **63**:915–921.

- Herre, E.A., and S.A. West. 1997. Conflict of interest in a mutualism: Documenting the elusive fig wasp–seed trade-off. *Proc. Roy. Soc. Lond. B* **264**:1501–1507.
- Johnstone, R.A., and R. Bshary. 2002. From parasitism to mutualism: Partner control in asymmetric interactions. *Ecol. Lett.* **5**:634–639.
- Leimar, O., and P. Hammerstein. 2001. Evolution of cooperation through indirect reciprocity. *Proc. Roy. Soc. Lond. B* **268**:745–753.
- Lewis, R.J. 2002. Beyond dominance: The importance of leverage. *Qtlly. Rev. Biol.* **77**:149–164.
- Losey, G.C., A.S. Grutter, G. Rosenquist et al. 1999. Cleaning symbiosis: A review. In: *Behaviour and Conservation of Littoral Fishes*, ed. V.C. Almada, R.F. Oliveira, and E.J. Goncalves, pp. 379–395. Lisbon: Instituto Superior de Psicologia Aplicada.
- Morton, E.S., L. Forman, and M. Braun. 1990. Extrapair fertilizations and the evolution of colonial breeding in purple martins. *Auk* **107**:275–283.
- Noë, R. 1990. A veto game played by baboons: A challenge to the use of the Prisoner's Dilemma as a paradigm for reciprocity and cooperation. *Anim. Behav.* **39**:78–90.
- Noë, R. 2001. Biological markets: Partner choice as the driving force behind the evolution of cooperation. In: *Economics in Nature: Social Dilemmas, Mate Choice and Biological Markets*, ed. R. Noë, J.A.R.A.M. van Hooff, and P. Hammerstein, pp. 92–118. Cambridge: Cambridge Univ. Press.
- Noë, R., and P. Hammerstein. 1994. Biological markets: Supply and demand determine the effect of partner choice in cooperation, mutualism and mating. *Behav. Ecol. Sociobiol.* **35**:1–11.
- Noë, R., and P. Hammerstein. 1995. Biological markets. *Trends Ecol. Evol.* **10**:336–339.
- Noë, R., C.P. van Schaik, and J.A.R.A.M. van Hooff. 1991. The market effect: An explanation for pay-off asymmetries among collaborating animals. *Ethology* **87**:97–118.
- Nowak, M.A., and K. Sigmund. 1998. Evolution of indirect reciprocity by image scoring. *Nature* **393**:573–577.
- Pellmyr, O., and C.J. Huth. 1994. Evolutionary stability of mutualism between yuccas and yucca moths. *Nature* **372**:257–260.
- Roberts, G., and T.N. Sherratt. 1998. Development of cooperative relationships through increasing investment. *Nature* **394**:175–179.
- Schwartz, M.W., and J.D. Hoeksema. 1998. Specialization and resource trade: Biological markets as a model of mutualisms. *Ecology* **79**:1029–1038.
- Simms, E.L., and D.L. Taylor. 2002. Partner choice in nitrogen-fixation mutualisms of legumes and rhizobia. *Integ. Comp. Biol.* (formerly: *Am. Zool.*) **42**:369–380.
- Tebich, S., R. Bshary, and A.S. Grutter. 2002. Cleaner fish, *Labroides dimidiatus*, recognise familiar clients. *Anim. Cogn.* **5**:139–145.
- Trivers, R.L. 1971. The evolution of reciprocal altruism. *Qtlly. Rev. Biol.* **46**:35–57.
- Wedekind, C., and M. Milinski. 2000. Cooperation through image scoring in humans. *Science* **288**:850–852.
- West, S.A., E.T. Kiers, E.L. Simms, and R.F. Denison. 2002. Sanctions and mutualism stability: Why do rhizobia fix nitrogen? *Proc. Roy. Soc. Lond. B* **269**:685–694.
- Wilkinson, D.M. 2001. Mycorrhizal evolution. *Trends. Ecol. Evol.* **16**:64–65.
- Zahavi, A. 1995. Altruism as a handicap: The limitations of kin selection and reciprocity. *J. Avian Biol.* **26**:1–3.