REPORT

Experimental evidence that partner choice is a driving force in the payoff distribution among cooperators or mutualists: the cleaner fish case

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Abstract

Supply and demand largely determine the price of goods on human markets. It has been proposed that in animals, similar forces influence the payoff distribution between trading partners in sexual selection, intraspecific cooperation and interspecific mutualism. Here we present the first experimental evidence supporting biological market theory in a study on cleaner fish, *Labroides dimidiatus*. Cleaners interact with two classes of clients: choosy client species with access to several cleaners usually do not queue for service and do not return if ignored, while resident client species with access to only one cleaning station do queue or return. We used plexiglas plates with equal amounts of food to simulate these behaviours of the two client classes. Cleaners soon inspected 'choosy' plates before 'resident' plates. This supports previous field observations that suggest that client species with access to several cleaners exert choice to receive better (immediate) service.

INTRODUCTION

Many cases of sexual selection, intraspecific cooperation and interspecific mutualism have in common that interactions can be seen as a trade between two individuals belonging to two different classes of traders (Noë *et al.* 1991; Noë & Hammerstein 1994). For example, males may offer nuptial gifts to females in exchange for copulations (Thornhill 1976), territory owners allow unrelated helpers to stay within the territory in exchange for feeding their offspring (Reyer 1986), and lycaenid butterfly larvae provide a sugar rich solution for ants in exchange for protection against predators (Pierce 1987). All examples have in common that there is no apparent fixed exchange rate for the commodities. Instead, the size of nuptial gifts, the effort of helpers or the quantity of nectar solution correlate with the ratio of the two trader classes: the fewer females, territory owners or ants that are available, the higher is the offer of their respective partner traders (Noë *et al.* 1991; Noë 2001). The paradigm most used for the evolution of cooperation between unrelated individuals, the iterated prisoner's dilemma game (Axelrod & Hamilton 1981), does not account for a flexible payoff matrix. Therefore, Noë and colleagues (Noë 1990; Noë *et al.* 1991; Noë & Hammerstein 1994; see also Bull & Rice 1991; Wilkinson & Sherratt 2001)

proposed that basic human market theory can provide the general framework to predict payoff distributions among partners in all these cases. The basic features of a market are as follows (after Noë 2001). (1) The choice of a partner is based on expectations of a higher profit (fitness gain) compared to a choice of another partner. (2) There is competition among members of the more common (chosen) class over access to the rare class. This competition causes an increase in the value of the commodity offered. (3) Supply and demand for the commodities exchanged determine their value. (4) Commodities on offer can be advertised (list of features taken from Noë 2001). Thus, market theory may explain strong asymmetries in payoffs as long as one commodity that is short in supply and high in demand is traded against a commonly available commodity that is, therefore, in less demand.

Market theory qualitatively fits many examples of fluctuating payoffs (examples in Noë *et al.* 1991; Noë 2001). In addition, several recent studies on sexual selection, intraspecific cooperation and interspecific mutualism have used market theory to test predictions about payoff distributions and provided observational support for market theory (Barrett *et al.* 1999; Henzi & Barrett 1999; Pavlowsky & Dunbar 1999; Stopka & MacDonald 1999; Green *et al.* 2000; Bshary 2001; Bshary & Schäffer in press). However,

experimental evidence that it is the option to choose between potential partners that causes a shift in payoff distribution is still lacking.

Here, we present the first experiments designed to test predictions from market theory, using the cleaner fish *Labroides dimidiatus* as subjects. Cleaner fish remove parasites and other material from the surface, the gills and sometimes the mouth of 'client' reef fish, which visit them at their so called cleaning stations (recent reviews: Losey *et al.* 1999; Côté 2000). From a market point of view, client species can be categorized as either resident species with small territories or home ranges that usually allow them to access one cleaning station only, or as species with larger home ranges that cover several cleaning stations. As the latter can choose between different cleaners, we call them choosy clients. Cleaners compete among each other over access to choosy clients, while each cleaner has exclusive access to its resident clients. In market terms, cleaners have a 'veto position' (Kahan & Rapoport 1984) for interactions with residents: residents either visit them or are not inspected at all. Market theory therefore predicts that the service quality offered by cleaners should be relatively poor, i.e. just high enough that there remains a net benefit for the client so that it keeps visiting the cleaner. Choosy clients, however, are expected to use their choice options to try and play cleaners off against each other. They should visit cleaning stations where the service is better than average, inducing cleaners to raise their service quality to out-compete others. The cheaper it is for choosy clients to exert their choice, the more cleaners are expected to be pushed towards a service quality that leaves them just a net benefit.

We focused on one single aspect of service quality: whether or not clients are inspected immediately after they arrive at a cleaning station. Cleaners cannot always offer immediate service to all clients as sometimes two or more clients seek inspection simultaneously. Under such circumstances, the cleaner has to make a choice of which client to inspect first and which one it will let wait. Waiting at a cleaning station incurs some costs on the clients as it is often incompatible with other activities, such as foraging. According to market theory, choosy clients should have priority of access over residents because they would use their choice options otherwise and switch to another cleaner fish, while residents have to stick to their partner cleaner fish. Observations by Bshary (2001) revealed that choosy clients indeed have priority of access. In addition, Bshary & Schäffer (in press) found that if choosy clients are ignored they will switch to another cleaner, but if they are inspected they often return to the same cleaning station. These data make it likely that the clients' choosiness causes their priority of access over resident clients. The causal link between choosyness and priority of access, however, is missing. Therefore alternative explanations cannot be refuted. For example, cleaners interact longer and more frequently with parasitized rather than unparasitized clients (Gorlick 1984; Sikkel *et al.* 2000; Bshary & Grutter in press). Choosy clients could thus be a better food patch because they are often larger than resident clients (Bshary 2001), and fish size is often correlated with parasite load (Grutter 1995; Grutter & Poulin 1998). In addition, choosy clients might be more heavily infested independently of body size if they visit cleaners less frequently to optimize their own foraging, or covering larger areas increases infection rate. Thus, the cleaners' preference for client species with choice options might simply be explained by optimal foraging decisions (marginal value theorem, Charnov 1976; Parker & Stuart 1976) which do not account for client strategies.

To test whether or not there is a causal link between client choice options (and corresponding behaviour) and priority of access at cleaning stations, we designed experiments that controlled for food patch quality. We used two plexiglas plates attached to a lever construction (Fig. 1) to simulate the natural behaviour of choosy clients and resident clients. We assumed that under natural conditions, cleaners obtain information about which client is choosy and which client is a resident in two ways. (1) Choosy clients usually swim off if they are not inspected immediately, while resident clients tend to queue for service (Bshary 2001). (2) If ignored, choosy clients usually switch to another cleaning station (Bshary & Schäffer in press), while resident clients are likely to return as soon the cleaner is available again (R. Bshary, personal observation). We simulated these differences in two experiments. In Experiment 1, we retrieved the 'choosy plate' if the cleaner did not start foraging on it and left the 'resident plate' until it had been inspected by the cleaner. In Experiment 2, we always
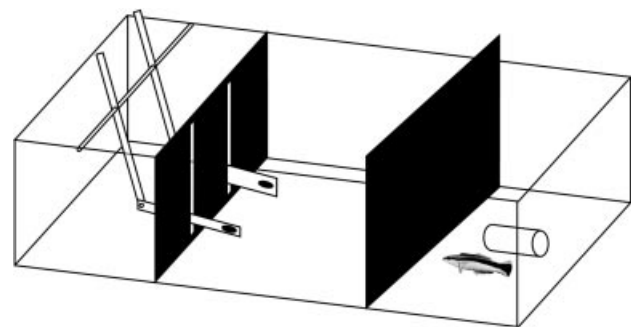

Figure 1 Experimental setup, showing the situation prior to the removal of the opaque barrier on the right that prevents the cleaner fish from accessing the two plexiglas plates that are slid into its compartment. The lever construction above the compartment, inaccessible (due to the second opaque barrier on the left) to the cleaner, allows retrieval of the plates without interfering directly with the cleaner. The black dots on the two plexiglas plates indicate the positions of the food items.

retrieved the plate that was at first neglected but we slid the resident plate back after the cleaner had finished with the choosy plate (which was then retrieved) while the choosy plate was only available in the next trial. The two plates were similar in colour and shape but one was double the height of the other one to allow cleaners to differentiate between them and to monitor the 'behaviour' of the two plates. Otherwise, the two plates had the same amount of food on them in each trial. The cleaners were challenged to maximize their food intake, which meant that they had to forage on the choosy plate first so that they could feed on both plates within each trial. According to marginal value theorem (Charnov 1976; Parker & Stuart 1976), both plates should be equally attractive as they offered the same amount of food. In contrast, market theory would predict that due to the differences in 'behaviour', cleaners should develop a preference for the choosy plate during a series of trials.

METHODS

Study site and subjects

The experiments were conducted in June/July 2000 at Lizard Island Research Station, Lizard Island, Great Barrier Reef, Australia. Using barrier nets, we caught 12 adult cleaner fish, *Labroides dimidiatus*, from the nearby lagoon. *Labroides dimidiatus* is one of the main cleaning organisms and interacts with more than 2000 clients per day in this area (Grutter 1996).

Holding conditions

Cleaners were initially held pair-wise in aquaria of a minimum size of $50 \times 20 \times 20$ cm, with a constant flow of fresh sea water. Small polyvinyl pipes (15 cm long) were added for shelter. The fish were held in captivity for at least 25 days before being tested in the experiments. Their diet consisted of shrimps mashed onto plexiglas plates of variable size (from 7×10 cm to 10×20 cm). Cleaners became used to this feeding method within 1 week and after a maximum of 2 weeks would begin to feed while we placed the plates in the aquaria. Successively, each pair of cleaners was tested simultaneously in two experimental aquaria, which were $100 \times 25 \times 25$ cm in size, consisting of two compartments. The compartment with the cleaner fish was 75 cm long and had sand on the bottom. The polyvinyl pipe for shelter was placed centrally into the compartment in a way that its opening faced the opaque plexiglas wall (Fig. 1). Each cleaner spent one night in the experimental tank before it was tested in Experiment 1 the next morning. Experiment 1 lasted 2 days for each cleaner. After a 2-day recovery period in their original holding tank, cleaners were again moved into the experimental tank where they were

held for one night and tested in Experiment 2 the next morning. Experiment 2 lasted 1 day for each cleaner. After the experiments were finished, all fish were released at the site of their capture.

General methods of experiments

Food units of prawn were measured with a high precision scale. In each trial, one food unit (0.001 g $\pm$ 0.0003) was placed on each of the two plexiglas plates within a 2×2 cm^2 area. The food was spread out so that 4–5 small food items were on each plate. The food was on the outer sides of the two plates, facing the aquarium walls (Fig. 1), so that cleaners could not rapidly switch between feeding on either plate. One plate was 14×5 cm in size, the other one was 14×10 cm in size. Each plate was connected to a lever above the compartment which enabled us to push the plates through the gaps into the cleaners' compartment, and to retrieve them whenever we wanted them out of reach of the cleaner (Fig. 1). The order in which each plate was presented either through the left or the right gap during successive trials was predetermined with coin tossing. We did not use random sequences that dictated the same pattern in more than 3 successive trials to reduce the risk that cleaners might develop a side preference. Before the two plates were slid into the cleaner's compartment, the cleaner was confined to the opposite side of its compartment by placing an opaque white plastic wall in the middle of the compartment. The white plastic wall was slightly wider than the aquarium to provide a good seal, so it was not at a right angle to the aquarium sides (Fig. 1). The two plates were pushed for an equal distance through the gaps. Because of the opaque plastic, the cleaner could not get any information on where the choosy plate and where the resident plate was. In addition, the observer did not know where the cleaner fish was at any time. The white plastic was lifted after 6–10 s. While lifting the white plastic, the observer twisted it slightly so that its two sides would constantly touch the aquarium walls to prevent the plastic from causing unwanted water circulation and then placed it on top of the aquarium. By the time the plastic was out of the water, the cleaners had often already begun to forage on one of the two plates. The plate where the cleaner fed on first as determined by direct observation was scored as the one it preferred.

Experiment 1: does the behaviour 'one plate remains until inspected while the other one does not' induce a cleaner preference for the latter?

On day 1, cleaners were exposed to two sessions consisting of 5 trials each. Time intervals between trials were 30 min, and between sessions they were 60 min. Two cleaners were

tested simultaneously every day, one with the small plate simulating the unwillingness of choosy clients to queue and one with the large plate simulating the very same thing. Cleaners could feed on the choosy plate only if they started to forage on it before they went foraging on the resident plate. Otherwise, the choosy plate was withdrawn while the cleaner was foraging on the resident plate, just as choosy clients leave if they are not inspected immediately. In contrast, the resident plate always stayed in the cleaner's compartment until the cleaner had stopped foraging on it, just as resident clients often queue for service if the cleaner inspects another client. For each session, we scored a cleaner's preference for the choosy plate if it had foraged first on that plate at least three times out of five trials. Otherwise, we scored a cleaner preference for the resident plate. On the second day, we reversed the client behaviour each plate simulated. So if the small plate had simulated a choosy client on the first day, it simulated a resident client on the second day, and vice versa. As on day 1, we had two sessions consisting of five trials each, and we scored cleaner preference as we did for the first day. We used Sign-Tests to determine whether a significant majority of cleaners had a preference for the choosy plate in any of the total four sessions.

Experiment 2: does the behaviour 'resident plate comes back soon after being ignored while the choosy plate does not' induce a cleaner preference for the latter?

Experiment 2 lasted 1 day, consisting of three sessions of five trials each. Time intervals between consecutive trials within sessions were 20 min, and between sessions they were 40 min. The same cleaners as in Experiment 1 were used. The major difference to Experiment 1 was that we always first pulled back the plate on which the cleaner did not feed immediately. As choosy clients usually switch to another cleaning station if they are not inspected immediately, the choosy plate would not be slid back until the next trial. In contrast, the resident plate was pushed in again as soon as the cleaner had stopped foraging on the choosy plate (which was then removed), just as resident clients usually come back to the cleaner soon after being ignored. The behaviour the two plates simulated was not reversed. Instead, we tried to test cleaners against their overall preference in Experiment 1. Thus, the cleaner out of each pair that had shown the overall stronger preference for the small plate in Experiment 1 was tested with the large plate simulating the behaviour of clients with choice options, while the small plate simulated the same behaviour for the second cleaner. Using this approach, we could not test all cleaners against their overall preference in Experiment 1, as a significant majority of them had fed first from the small plate more often than from the large plate (Sign-Test,

$N = 12$, $x = 1$, $P < 0.01$). As in Experiment 1, we determined cleaner preferences in each session and used Sign-Tests to determine whether a significant majority of cleaners had a preference for the choosy plate in any of the three sessions.

RESULTS

Experiment 1: does the behaviour 'one plate remains until inspected while the other one does not' induce a cleaner preference for the latter?

A significant majority of cleaners interacted more often with the choosy plate first during the second session (Sign-Test, $N = 12$, $x = 2$, $P < 0.05$) and, after the behaviour the two plates simulated was reversed, again during the fourth session (Sign-Test, $n = 12$, $x = 1$, $P < 0.01$, Fig. 2). During sessions 1 and 3, when the situation was new to the cleaners, there was no significant preference for the choosy plate (Sign-Tests, session 1: $n = 12$, $x = 5$, not significant (n.s.); session 4, $n = 12$, $x = 6$, n.s., Fig. 2). A trial by trial analysis indicates that cleaners carried over their built up preference for the choosy plate to the next day, leading initially to relatively many 'mistakes' as the behaviour that the plates simulated was now reversed (Fig. 3).

Experiment 2: does the behaviour 'resident plate comes back soon after being ignored while the choosy plate does not' induce a cleaner preference for the latter?

A significant majority of cleaners interacted more often with the choosy plate first during the second and third sessions (Sign-Tests, session 2: $N = 12$, $x = 1$, $P < 0.01$; session 4, $N = 12$, $x = 1$, $P < 0.01$, Fig. 4). During sessions 1, there was no significant preference for the choosy plate (Sign-Test, session 1: $N = 12$, $x = 5$, n.s., Fig. 5). As intended by us, a trial-by-trial analysis indicated that cleaners may indeed have carried over their preferences from Experiment 1 into Experiment 2. They began with a relatively low success rate but improved strongly during the first session (χ^2-test, trials $1 + 2$ against trials $4 + 5$, $\chi_1^2 = 5.4$, $N = 24$, $P < 0.05$, Fig. 5).

DISCUSSION

We used plexiglas plates to simulate the natural behaviour of two different client categories, namely resident clients with access to one cleaning station only, and choosy clients with access to several cleaning stations. Like choosy clients, the choosy plate was accessible to cleaners only if they started to feed on it immediately. In contrast, cleaners had always access to the resident plate, simulating their veto-position (Kahan & Rapoport 1984) towards resident clients in the
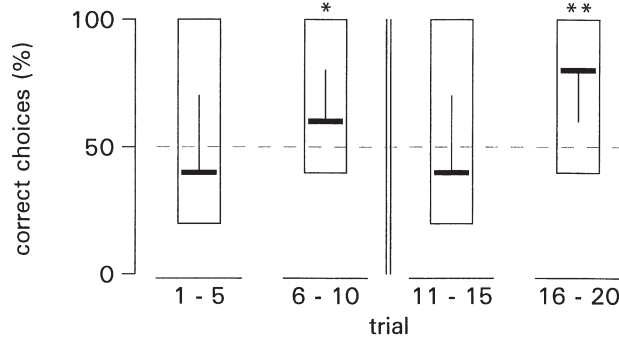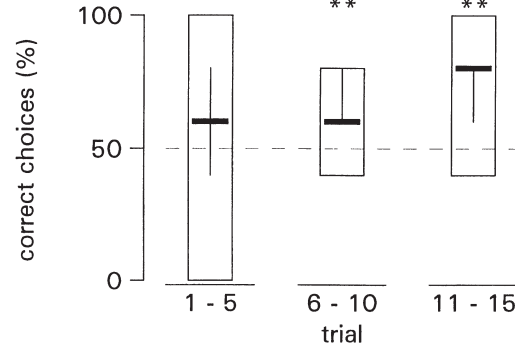
Figure 2 Experiment 1: median, interquartiles and range of percentage correct choices (to optimize food intake by foraging first on the choosy plate) of 12 cleaner fish in four experimental sessions in which the resident plate (but not the choosy plate) was left in the cleaners' compartment until the cleaners had finished inspection. Between session 2 and session 3, the correct choice for optimizing the food intake was reversed as indicated by the vertical barrier. *$P < 0.05$; **$P < 0.01$.

Figure 4 Experiment 2: median, interquartiles and range of percentage correct choices (optimize food intake by foraging first on choosy plate) of 12 cleaner fish in three experimental sessions. The plate that was initially ignored was retrieved and only the resident plate (but not the choosy plate) was pushed back into the cleaners' compartment after the cleaners had finished inspection of the first plate. **$P < 0.01$.

wild. The cleaners were challenged to maximize their food intake. This meant that they had to forage on the choosy plate first so that they could feed on both plates within each trial. Overall, the cleaners were able to solve this problem and developed a preference for the choosy plate.

Our experiment was abstract in several ways. First, the two plates did not resemble any client fish species in both shape and thickness. Second, our choosy plate did not visit another cleaner if it was not serviced immediately as natural clients would do (Bshary & Schäffer in press). However, we offered the cleaners the very same clues that they could potentially rely on in the wild to distinguish between choosy client species and resident client species. From a cleaner's
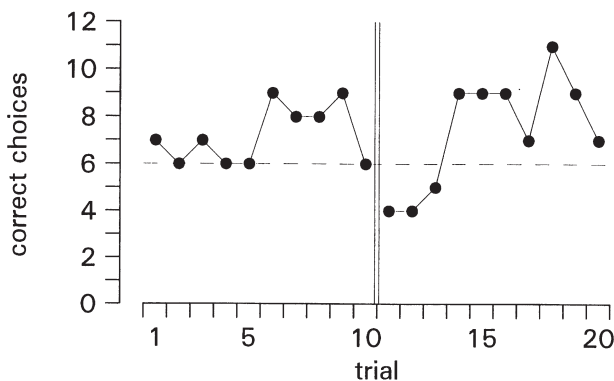

Figure 3 Experiment 1: trial-by-trial analysis of the number of cleaners (out of 12) that made the correct choice (optimize food intake by foraging first on the choosy plate). After 10 trials, the correct choice was reversed. The dashed line represents the expected value if cleaners chose randomly.

perspective, our experiments thus simulated a problem that they have to solve frequently under natural conditions, whenever a choosy client and a resident seek their service simultaneously. Field observations have shown that cleaners indeed give choosy clients priority of access over resident clients (Bshary 2001). In addition, it has been shown that choosy clients make use of their choice options and visit another cleaning station if they are ignored (Bshary & Schäffer in press). Our results controlled for patch quality and we found that the choosy plate had priority of access over the resident plate, and that the cleaners' preference could be reversed if the behaviour of the two plates was reversed. Note that the cleaners' decision rule in the experiments could be very simple and within the framework of optimality approaches, i.e. when you start foraging avoid the patch you have depleted last. In combination with the evidence on client behaviour under natural conditions, however, the experimental results clearly support the game theoretic approach to cleaning symbiosis based on market theory (Noë *et al.* 1991) and not the classical marginal value approach (Charnov 1976; Parker & Stuart 1976).

Cleaners used information on both 'plate behaviours' and differentiated between the two client categories the two plates simulated. The plate that simulated the behaviour of resident clients, i.e. remaining available until inspected or trying again shortly after being ignored, was soon approached only after inspection of the choosy plate was complete. This makes it plausible that cleaners use the same clues also in the wild to differentiate between residents and choosy clients. At the very least, our results show that cleaners can learn to use such clues relatively fast in an experimental situation.
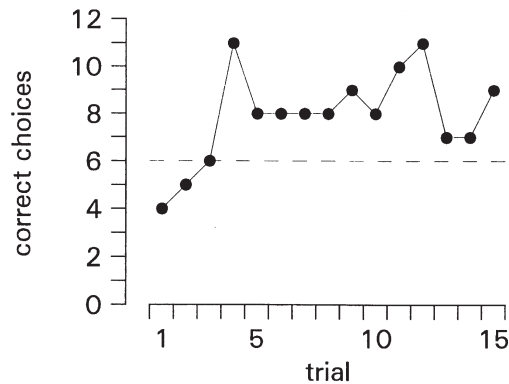
Figure 5 Experiment 2: trial-by-trial analysis of the number of cleaners (out of 12) that made the correct choice and foraged first on the choosy plate. The dashed line represents the expected value if cleaners chose randomly.

In conclusion, the experimental data support previous field observations that suggest that choosy clients have priority of access over resident clients (Bshary 2001) *because* they would otherwise switch to another cleaner for their next inspection (Bshary & Schäffer in press). Choosy clients thus receive a better payoff out of cleaning interactions than resident clients as they avoid the costs of waiting. While our experiments dealt with one aspect of partner choice, access to several cleaning stations instead of only one might influence other aspects of cleaner–client interactions. One of these has to do with the way clients react to cheating by cleaners. Cheating refers to the removal of healthy client tissue rather than parasites by the cleaner (Bshary & Grutter in press). Choosy clients mainly react to cheating by cleaners with swimming off and visiting another cleaner for the next inspection (Bshary & Schäffer in press). Resident clients, in contrast, do not have this option and therefore have to expend energy to punish cheating cleaners by chasing them around (Bshary & Grutter in press). These two different control mechanisms (partner switching and punishment) do not seem to lead to different cleaner cheating frequencies (Bshary 2001), but the responses of different client species to cleaner fish cheating are best understood within the framework of market theory.

Market theory with its emphasis on partner choice options (Noë & Hammerstein 1995; Noë 2001) thus provides a major framework to predict shifts in payoff distributions and partner control mechanisms in the cleaner fish mutualism. For the future, it will be particularly interesting to (1) develop and test quantitative predictions (see Hoeksema & Bruna 2000), and (2) integrate market theory with partner control theory, i.e. how partners prevent each other from cheating in potentially cooperative inter-actions. The paradigm for partner control theory, the iterated prisoner's dilemma game (Axelrod & Hamilton 1981) does not allow the option to switch partners. Extensions of the model have mainly dealt with the option for cheaters to rove and switch partners to avoid retaliation (Dugatkin & Wilson 1991; Enquist & Leimar 1993; but see Ferriere & Michod 1995). In the mutualism between *L. dimidiatus* and its clients, however, this is reversed as cleaners are stationary and it is up to the clients to choose their cleaner. For the sake of realism, game theoretic models should thus explicitly allow cheated individuals to switch partners.

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