

Biting cleaner fish use altruism to deceive image-scoring client reef fish

Redouan Bshary*

University of Cambridge, Department of Zoology, Downing Street, Cambridge CB2 3EJ, UK,
and Max-Planck-Institute for Behaviour and Physiology, Seewiesen, 82319 Starnberg, Germany

Humans are more likely to help those who they have observed helping others previously. Individuals may thus benefit from being altruistic without direct reciprocity of recipients but due to gains in 'image' and associated indirect reciprocity. I suggest, however, that image-scoring individuals may be exploitable by cheaters if pay-offs vary between interactions. I illustrate this point with data on cleaner-client reef fish interactions. I show the following: (i) there is strong variation between cleaners with respect to cheating of clients (i.e. feeding on client tissue instead of parasites); (ii) clients approach cleaners, that they observe cooperating with their current client and avoid cleaners that they observe cheating; (iii) cleaners that cheat frequently are avoided more frequently than more cooperative cleaners; (iv) cleaners that cheat frequently behave altruistically towards their smallest client species; (v) altruistic acts are followed by exploitative interactions. Thus, it appears that cleaners indeed have an image score, which selects for cooperative cleaners. However, cheating cleaners use altruism in potentially low-pay-off interactions to deceive and attract image-scoring clients that will be exploited.

Keywords: mutualism; indirect reciprocity; communication network; tactical deception;
Labroides dimidiatus

1. INTRODUCTION

Examples that humans help other humans in situations where it is unlikely that the recipient of an altruistic act will ever reciprocate in the future are common (Alexander 1987). Such behaviour could nevertheless be adaptive (Nowak & Sigmund 1998; Leimar & Hammerstein 2001) assuming that (i) bystanders observe the interaction, (ii) individuals attribute an image score to each group member, the value of each score depending on how often they observed a given member helping and how often they observed the same individual refusing help, and (iii) individuals receive help only if their image score is above a critical threshold. An experiment with first-year students that was based on these assumptions supported the adaptive value of image scoring: those who helped received more help from others than students who did not help and had earned more money at the end of the experiment (Wedekind & Milinski 2000). Note that indirect reciprocity based on image scoring converges with communication theory (McGregor 1993) that emphasizes that signalling takes place in a communication network. Bystanders may eavesdrop on interactions and consequently adapt their behaviour during future interactions with individuals they observed previously. That animals know about relationships between other individuals has been documented in a variety of species from monkeys to crabs (Cheney & Seyfarth 1990; Naguib & Todt 1997; Oliveira *et al.* 1998*a,b*). As a consequence of eavesdropping, one would expect so-called audience effects; the alteration of signals in the presence of bystanders (Dutreland *et al.* 2001; Johnstone 2001).

But why should a system, which is purely based on

altruistic actions evolve in the first place? Verbal arguments (Zahavi 1995; Roberts 1998) propose that the initial step towards 'give and you shall be given' was 'give and you shall be chosen for collaboration'. In this scenario, altruism is seen as a form of honest signal, a behavioural handicap that may advertise an individual's willingness to cooperate with potential partners in a repeated Prisoner's Dilemma situation (Axelrod & Hamilton 1981). The Prisoner's Dilemma emphasizes the problem that mutual cooperation yields higher pay-offs than does mutual defection, but defection yields a higher benefit than cooperation irrespective of what the partner does. In order to obtain the repeated benefits from cooperation, individuals should choose to collaborate with partners that they have observed to help others in the past. I suggest, however, that under certain circumstances, image scoring might lead to deception based on indirect reciprocity: an individual may behave altruistically to fool observers into an interaction during which they will be exploited. I illustrate this idea with field data on interactions between cleaner wrasses, *Labroides dimidiatus*, and their client reef fish, collected at Ras Mohammed National Park, Egypt.

Reef fish commonly seek cleaner fish at their small territories, so-called cleaning stations, to have their parasites and dead or infected tissue removed (recent reviews by Losey *et al.* 1999; Côté 2000). Classical cooperation theory has focused on the question why cleaners may enter the mouth of predators without being cheated and eaten (Trivers 1971). However, the most common conflict during cleaning interactions occurs when cleaners feed on client tissue (Randall 1958; Gorlick 1980; Grutter 1997). Experimental evidence (Bshary & Grutter 2002) indicates that feeding on client tissue is not a by-product of parasite removal, and hence can be called cheating. Cheating by cleaners becomes visible when clients make short jolts in response to cleaner bites (Bshary & Grutter 2002). While

*Address for correspondence: University of Cambridge, Department of Zoology, Downing Street, Cambridge CB2 3EJ, UK (rb286@cam.ac.uk).

predatory clients hardly ever jolt during interactions, non-predatory client species jolt about two to six times per 100 s interaction, often followed by immediate evasive action by the client (Bshary 2001). A cleaner that refrains from taking bites that result in client jolts can be said to behave altruistically compared with conspecifics, that take such bites more regularly (*sensu* the definition of altruistic behaviour by Bull & Rice (1991)). Non-predatory clients respond to cheating by cleaners in two different ways. Resident client species with access to only one cleaning station often chase the cleaner, while client species with access to several cleaning stations usually swim off and visit another cleaner station for their next inspection (Bshary & Grutter 2002; Bshary & Schäffer 2002).

A variety of studies indicate that these control mechanisms seem to work in that clients receive a net benefit from cleaning interactions (Grutter 1999, 2001; Sikkel *et al.* 2000). However, I will present evidence that a minority of cleaner fish, *L. dimidiatus*, cheat their clients much more frequently than most of their conspecifics do. These phenotypic defectors (*sensu* Sherratt & Roberts 2001) cheat in particular non-predatory client species with access to several cleaning stations and larger resident client species but not the smaller resident species. Thus, the aggression of larger residents and partner switching of choosy clients fail to control the behaviour of these cleaners. Clients should therefore try to avoid interactions with these 'biting' cleaners and visit 'normal' cleaners only. Rather than avoiding cleaners on the basis of personal negative experience, clients could use information from observed interactions and attribute an image to the cleaner. As cleaners have more than 2000 interactions per day (Grutter 1995), interactions indeed often take place in the presence of other clients. Note that image scoring is one sided as non-predatory clients have no means to cheat cleaners and cleaners therefore do not need to attribute an image to their clients (attributing an image score to predatory clients would be useful if the predator interacted in sight with another cleaner, which is an unlikely scenario). I observed the behaviour of clients arriving at a cleaning station in relation to what information they could gather about the cleaner's current interaction. Image-scoring theory (Nowak & Sigmund 1998; Leimar & Hammerstein 2001) would predict that arriving clients invite inspection if they see the cleaner cooperating with its client but avoid cleaners that they see cheating their client. In other words, the image score of a cleaner should be positive if the observed interaction ends without a conflict, and negative if the observed interaction ends with a conflict, i.e. the client darts off or chases the cleaner. As a consequence of image scoring by clients, one would predict that biting cleaners lose more potential clients for interactions than normal cleaners. I therefore analysed whether interactions of biting cleaners indeed end more often with conflicts than interactions of normal cleaners, and whether visiting clients more often evade approaching biting cleaners than normal cleaners.

Finally, I address the question of how image scoring may lead to deception. Game theoretic models (Nowak & Sigmund 1998; Leimar & Hammerstein 2001) predict that cheating can only spread in a population that contains indiscriminate altruists, while a population of image scorers is resistant against invasion of cheating individuals.

However, these models assume that all players are both potential helpers and potential receivers of altruistic acts. By contrast, only cleaner fish have an image score in cleaner fish–client interactions, and clients that invite inspection are not behaving altruistically but they expect a net benefit from the interaction. Under these circumstances, altruism could be used to attract image scorers who are then exploited. In this context, I describe a behavioural pattern of biting cleaners when interacting with small resident clients, which may function to improve their image score and attract clients. Cleaner fish often stimulate the dorsal area of their clients with their own pelvic and pectoral fins (Potts 1973), their mouth pointing away from the client. This behaviour is thus incompatible with foraging. Instead, it serves to manipulate clients that are unwilling to interact with a cleaner into staying for inspection and to reconcile with clients after a conflict due to cheating by the cleaner (Bshary & Würth 2001). While such tactile stimulation is usually just part of an interaction, I will show that biting cleaners often provide tactile stimulation during the entire interaction with small residents. From the cleaner's perspective, it is a clearly altruistic behaviour. If this altruism functions as a signal to attract image-scoring clients, I predicted that altruistic interactions are followed by exploitative interactions. Alternatively, the altruism of biting cleaners might be a non-adaptive redirection of reconciliation: in the absence of the cheated client, the nearest client, which usually is a small resident, receives the tactile stimulation. In that case, one would predict that altruistic interactions follow exploitative interactions.

2. MATERIAL AND METHODS

(a) *Study site and study animals*

The study was conducted in May–July 1999 at Mersa Bareika, Ras Mohammed National Park, Egypt. In this sheltered bay, incoming sand through wadis (riverbeds) led to the formation of many patch reefs, small isolated coral heads, which are isolated from each other by sandy areas. There is also fringing reef, especially towards the opening of the bay into the Gulf of Aqaba. The cleaner wrasse *L. dimidiatus* is the main cleaner fish in the area. This species is a protogynous hermaphrodite (Robertson 1972), i.e. individuals start their reproductive career as females and eventually change sex into males. There is no sexual dimorphism in coloration but males are the larger individuals within a pair. All observed individuals, both biting and normal individuals, were small adults and therefore most likely to be females. Four out of five biting cleaners shared a cleaning station with a larger partner and were observed to spawn in the female role, 6 out of the 11 normal cleaners also shared a cleaning station with a larger individual. The other individuals were solitary.

(b) *Data collection on biting cleaners and normal cleaners*

To find biting cleaners, I observed a total of 47 adult cleaners for a period of 10 min. Based on the frequency with which choosy clients jolted during this observation period, five cleaners were categorized as biting and observed further. In addition, I observed 11 normal cleaners that were chosen on the basis of convenient access. Normal cleaners were observed for 4 h each, biting cleaners for 3 h each, each hour being on a different day and time of day, between 07.00 and 17.00. The total obser-

vation time was 59 h. I sat 2–3 m in front of the cleaning station on the sand and first observed an entire interaction and then noted the following information on a Plexiglas plate.

- (i) Client species, determined according to Randall (1983).
- (ii) Client length, including the caudal fin, was compared with a reference measuring stick and estimated to the nearest centimetre.
- (iii) Duration in seconds was measured with a stopwatch.
- (iv) Number of client jolts.
- (v) Tactile stimulation of the client's dorsal area.

For the present analysis, I only distinguished whether or not this behaviour occurred during the entire interaction.

(c) *Data collection on image-scoring behaviour of clients*

I observed a total of 28 cleaning stations for 1 h each, between 07.00 and 16.00. I noted for each client arriving at the cleaning station whether or not it invited inspection by spreading its pectoral fins and stopping coordinated swimming movements before the cleaner fish got into body contact with it. The time interval between the beginning of an interaction and the end of the previous interaction was measured with a stopwatch to the nearest second. In addition, I noted whether the previous interaction had ended positive or negative. The end was defined as negative if the client darted off or chased the cleaner immediately after performing a jolt in response to cleaner fish mouth contact. An interaction ended positive if the cleaner terminated the interaction while the client was standing still, or if the client swam off slowly with the cleaner not following.

(d) *Data analysis*

I distinguished four client categories, namely predatory client species, non-predatory client species with access to several cleaning stations ('choosy clients'), larger non-predatory resident client species and smaller non-predatory resident client species. The distinction between predators, non-predatory resident clients and non-predatory choosy clients is based on differences in the way that these clients control cheating by cleaners. Predators may reciprocate and eat cleaners, residents use punishment and choosy clients switch to another cleaner for their next inspection (Bshary & Grutter 2002). The distinction between larger and small client species lacks a theoretical basis but preliminary observations on one biting individual during the previous field trip indicated that this distinction is important (see § 3). Large resident species are on average more than or equal to 10 cm long (including the caudal fin), small resident species are less than 10 cm. All choosy client species are on average more than 10 cm long. Within client categories, I did not further distinguish between species. Client species, which do not fit clearly into one of these categories, like most butterflyfish, are omitted from the analyses. For each individual cleaner and client category, I calculated the mean frequency of client jolts, the percentage of interactions that consisted of tactile stimulation only, the percentage of interactions that ended with a conflict following a client jolt and the frequency of clients evading an approaching cleaner relative to interactions that take place. The values for the five biting cleaners were then compared with the values for the 11 normal cleaners. Of all cleaners, only one biting cleaner was visited by shoals of the client species sergeant major, *Abudefduf vaigiensis*, and lunar fusilier, *Caesio lunaris*, during observations. Individuals belonging to shoals tend to jolt much more

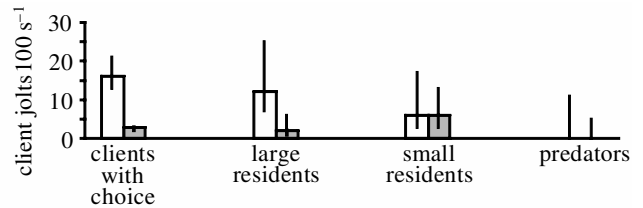


Figure 1. Jolt frequencies 100 s^{-1} interaction of four client categories as a correlate of cleaner fish cheating in interactions of five biting cleaners (open bars) and 11 normal cleaners (grey bars). Median and range of values for individual cleaners.

frequently than individuals that visit cleaners on their own (A. D'Souza and R. Bshary, unpublished data). Thus, including these data in the present analyses would have worked against the null hypothesis that cheating rates by cleaners are similar between individual cleaners. I therefore omitted the data on shoal visits from the analyses.

For the analysis of the image-scoring behaviour of clients, I ranked the rates with which each client species was inviting for inspection in four different situations (to calculate Friedman tests with n as the number of species). The previous interaction had ended either short ($\leq 5 \text{ s}$) or long ($> 5 \text{ s}$) ago, in combination with either a positive or a negative end. Based on preliminary observations, I assumed that 5 s would be the critical time interval that would allow clients arriving at the station to have gathered information about the end of the previous interaction if the time interval was 5 s or shorter but not if it was longer. Time intervals less than or equal to 5 s between subsequent interactions were found when clients had to queue (remaining at the station after spreading the fins as an invitation for inspection failed to attract the cleaner) at the station while the cleaner still interacted with another client, and when approaching clients were within a 0–2 m distance from the cleaner when the previous interaction ended. Note that any inaccuracy in the criterion would be in favour of the null hypothesis that image scoring does not take place. Cleaners are usually found at exposed positions on the reef and interactions can therefore be observed by humans and thus probably also by arriving clients from several metres distance away.

(e) *Statistics*

Data were processed with the computer program SPSS-X. All tests are non-parametric and two-tailed. Friedman tests with subsequent multiple comparisons were calculated according to Conover (1980).

3. RESULTS

(a) *Jolt frequencies of the different client categories when interacting with normal and biting cleaners*

Non-predatory client species with access to several cleaning stations jolted about five times more frequently when they interacted with biting cleaners than with normal cleaners (Mann–Whitney U -test, $m = 11$, $n = 5$, $U = 0$, $p = 0.002$; figure 1). Confidence intervals (99%) for each individual cleaner overlapped within the categories of biting and normal cleaners, while there was no overlap in the confidence intervals between cleaner categories, with only one exception (table 1). Remember that the distinc-

Table 1. Observed frequencies and 99% confidence intervals of jolts 100 s^{-1} of choosy clients and of the larger resident species, and of interactions between cleaners and small residents that consisted of tactile stimulation only. (Bold values indicate outliers from the general picture.)

cleaner fish	choosy clients' jolts 100 s^{-1}	large residents' jolts 100 s^{-1}	small residents tactile stimulation
biting 1	8.3–13–19.1	11.5–16–21.5	4.8 –18–39.1
biting 2	10.9–16–22.4	8.6–13–18.7	37.2–55–72.0
biting 3	11.0–16–22.2	5.1–8–11.9	37.4–58–82.1
biting 4	15.5–21–27.4	16.0–27–40.6	30.3–45–60.36
biting 5	10.0–13–16.6	4.8–18–39.1	36.6–64–86.0
normal 1	1.9–3–4.6	0.6–2–5.3	0.0–5–28.8
normal 2	1.6–3–5.3	1.6–3–5.3	2.7–8–17.9
normal 3	1.9–3–4.6	2.6–6–11.5	1.5–9–23.7
normal 4	1.8–3–4.9	0.8–3–7.5	1.8–10–27.3
normal 5	1.8–3–4.8	0.5–5–14.0	0.0–6– 33.6
normal 6	1.1–2–3.4	0.1–1–3.8	5.4–20– 44.3
normal 7	1.9–3–4.6	0.1–1–4.7	0.6–12– 43.0
normal 8	1.9–3–4.6	3.6–7–12.1	3.3–18– 46.1
normal 9	0.7–3– 10.6	0.3–2–6.7	0.9–4–10.7
normal 10	1.8–3–4.8	2.7–7–14.3	2.2–9–23.1
normal 11	0.8–2–4.7	2.2–4–6.7	0.0–5–30.2

tion between biting and normal cleaners was based on a 10 min observation period prior to data collection. The bimodal distribution of the data justifies the distinction between 'normal' cleaners and 'biting' cleaners. In addition, larger non-predatory resident species jolted more frequently when interacting with biting cleaners rather than normal cleaners (Mann–Whitney U -test, $n = 11$, $m = 5$, $U = 0$, $p = 0.002$; figure 1), although the difference was less pronounced and confidence intervals of biting frequencies tended to overlap between cleaner categories (table 1). There was no significant difference with regard to jolt frequencies of smaller residents (Mann–Whitney U -test, $n = 11$, $m = 5$, $U = 25$, $p = 0.78$; figure 1). To make sure that the results were not due to biting cleaners interacting with different client species than normal cleaners, I made separate analyses for the most common client species of each client category. Both longnose parrotfish (*Hippocampus harid*, choosy client) and lined bristletooth (*Ctenochaetus striatus*, large resident) jolted more frequently when interacting with biting cleaners than with normal cleaners (Mann–Whitney U -tests, *H. harid*: $n = 11$, $m = 3$, $U = 2$, $p = 0.02$; *C. striatus*: $n = 7$, $m = 4$, $U = 2$, $p = 0.016$). By contrast, no such significant differences were found for the small resident black and white chromis, *Chromis dimidiatus* (Mann–Whitney U -test, $n = 11$, $m = 5$, $U = 22$, $p = 0.53$).

While there is a fundamental difference in game structure between resident clients and choosy clients with respect to interaction with cleaners (residents punish cheats by cleaners while choosy clients swim off; Bshary & Grutter 2002), the data shown above indicate that the size of clients is a better predictor of the behaviour of biting cleaners than the strategies played by their clients. In fact, if one looks at large residents and choosy client species of similar size (10–20 cm body length), there is no significant difference with respect to client jolt rates (Mann–Whitney U -test, $m = 17$ choosy client species, $n = 8$ resident species, $U = 67$, $p = 0.97$).

Predatory clients hardly ever jolted at all, no matter what class of cleaners they interacted with (Mann–Whit-

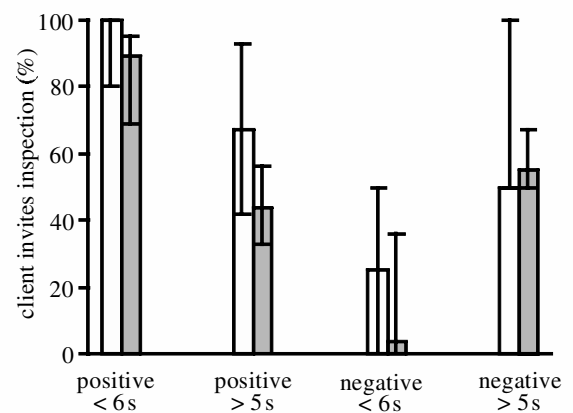


Figure 2. Matched data of frequencies of resident client species (open bars) and client species with choice options (grey bars) (median and interquartiles of all species values) arriving at a cleaning station invite (i.e. stop swimming before) inspection in four different situations. The previous interaction ended either short ($\leq 5\text{ s}$) or long ($> 5\text{ s}$) ago and either positive (without conflict) or negative (with conflict).

ney U -test, $n = 11$, $m = 4$, $U = 20$, $p = 0.77$; figure 1). I further investigate interactions between cleaners and non-predatory client species only.

(b) Image-scoring behaviour of clients arriving at a cleaning station

There were significant differences between the four situations distinguished with respect to the probability that arriving resident or choosy clients invite for inspection (Friedman tests, all resident non-predatory species combined: $\chi^2_3 = 11.5$, $n = 9$ client species, $p < 0.01$; non-predatory client species with choice options: $\chi^2_3 = 18.4$, $n = 10$ client species, $p < 0.001$; figure 2). Multiple comparisons revealed that the probability of both resident and choosy clients stopping to invite for inspection after a positive interaction had just finished was significantly higher than in the other three situations. If a negative interaction had

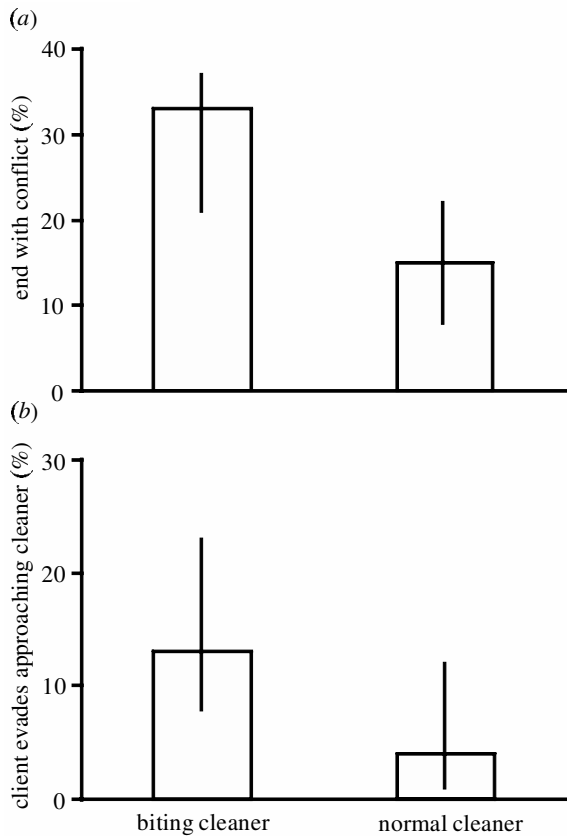


Figure 3. Frequencies (median and range) of interactions of 11 normal cleaners and five biting cleaners, which ended with a conflict ((a) client darting off or aggressive following a jolt) and frequencies (median and range) of how often interactions did not take place because a client evaded from the approaching cleaner (b).

just finished, the probability of inviting was significantly lower than in the other three situations. If the previous interaction was longer ago, the probability of inviting for inspection was intermediate and not affected by the actual outcome of the previous interaction. Crucial values for the multiple comparisons are as follows—resident client species: $T_2 = 6.87$, $T_3 = 12.47$, the critical rank sum difference between samples for $p < 0.05$ was 7.00; client species with choice options: $T_2 = 15.52$, $T_3 = 18.99$, the critical rank sum difference was 6.18.

(c) Consequences of cheating and image scoring on the frequencies of negative ends and on the frequencies of clients evading approaching cleaners

As expected, interactions between clients and biting cleaners ended more frequently with the clients taking evasive action than interactions between clients and normal cleaners (Mann–Whitney U -test, $m = 11$, $n = 5$, $U = 2.5$, $p = 0.004$; figure 3a). As predicted according to the clients' image-scoring behaviour, clients indeed avoided biting cleaners more often than normal cleaners (Mann–Whitney U -test, $m = 11$, $n = 5$, $U = 2.5$, $p = 0.004$; figure 3b).

(d) Tactile stimulation of clients

About 50% of interactions between biting cleaners and smaller residents consisted purely of tactile stimulation,

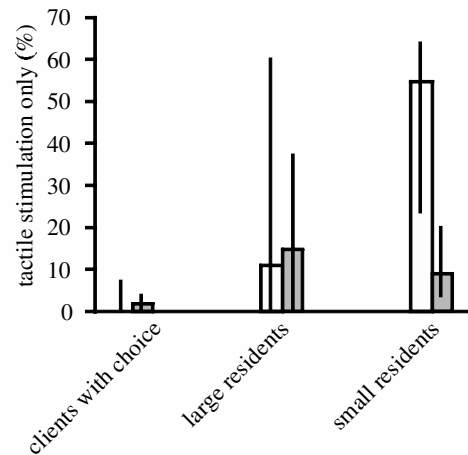


Figure 4. Frequencies (%) of interactions (median and range of individual cleaners) during which five biting cleaners (open bars) and 11 normal cleaners (grey bars) provided tactile stimulation of the client's dorsal area during the entire duration of the interaction.

significantly more frequently than in interactions between normal cleaners and small residents (Mann–Whitney U -test, $m = 11$, $n = 5$, $U = 0$, $p = 0.002$; figure 4). Confidence intervals (99%) for the observed frequencies mostly did not overlap between cleaner fish classes (table 1). No significant differences were found for large residents (Mann–Whitney U -test, $n = 11$, $m = 5$, $U = 24$, $p = 0.7$; figure 4) or for non-predatory choosy clients (Mann–Whitney U -test, $n = 11$, $m = 5$, $U = 25.5$, $p = 0.8$; figure 4). Again, these results are not due to biting cleaners interacting with different client species than normal cleaners. *Chromis dimidiatus* received more tactile stimulation from biting cleaners than from normal cleaners (Mann–Whitney U -test, $n = 11$, $m = 5$, $U = 2$, $p = 0.004$), while there was no significant difference for *H. harid* (Mann–Whitney U -test, $n = 11$, $m = 3$, $U = 15$, $p = 0.60$), and the opposite effect was found for *C. striatus* (Mann–Whitney U -test, $n = 7$, $m = 4$, $U = 3$, $p = 0.036$).

Tactile stimulation of one client was followed by an interaction that terminated after a client jolted more often than expected. I found the same tendency in all five biting cleaners (Sign test, $n = 5$, $x = 0$, $p = 0.064$) and a binomial test of the pooled data was highly significant ($n = 87$, observed frequency of cheating following tactile stimulation = 0.70, expected frequency = 0.55, $p = 0.0056$). By contrast, interactions that ended after a jolt were not followed by interactions consisting of tactile stimulation more often than expected (Sign test, $n = 5$, $x = 2$, n.s., binomial test on pooled data: $n = 115$, observed frequency of tactile stimulation following cheating = 0.46, expected frequency = 0.45, $p = 0.89$).

4. DISCUSSION

I provided a description of behavioural patterns in biting and normal cleaner fish and how clients base their decision on whether or not to invite inspection by cleaners on information about the cleaner's previous interaction. Due to the observational nature of the data and a lack of theoretical framework, the results have to be interpreted with care and possible explanations of the results are partly *post hoc*.

Still, the results provide new ideas for a variety of topics, with plenty of gaps yet to be filled.

The data indicate that cleaner fish can be separated in two distinct classes, one that bites larger clients rarely, and one that bites larger clients frequently. This difference was particularly established with respect to (large) choosy clients as confidence intervals between cleaner classes did not overlap, with one exception. I found the same patterns for the single most common client species of each category and for the pooled data of all client species within each category, which justifies the use of the pooled data for greater statistical power. In relation to the differences in behaviour between individual cleaners, the following results need an explanation.

- (i) Clients make their decision to interact dependent on cleaner fish behaviour towards its previous client.
- (ii) Cleaners that bite (cheat) frequently are avoided more often than cleaners that mainly cooperate.
- (iii) Biting cleaners frequently behave altruistically towards small residents.
- (iv) Such altruistic interactions are frequently followed by exploitative interactions.

The first two results indicate that cleaner fish indeed have something that can be called ‘image’ (Nowak & Sigmund 1998) or ‘prestige’ (Zahavi 1995). As cooperative behaviour of cleaners towards current clients increases the probability of access to future clients, there is a component of indirect reciprocity present in cleaner–client interactions. The behaviour of clients arriving at a cleaning station selects for cleaners that refrain from cheating. Hence, current clients may receive a good service not just because otherwise they might switch to another cleaner or chase the cleaner but in addition because the cooperative behaviour of the cleaner attracts observing clients.

While the importance of indirect reciprocity for the behaviour of normal cleaners still has to be explored, it seems to be a major component of the biting cleaners’ strategy. The smaller residents did not reciprocate the tactile stimulation of biting cleaners in any obvious way. Both client parasite load and mucus load correlate positively with client size (Gorlick 1980; Grutter 1995), hence small clients offer the least attractive food patches of all clients. As bystanding clients decide whether or not to interact with a cleaner based on how it treats its current client, it seems plausible that the function of the altruistic acts is to attract larger resident and choosy clients to the cleaning station. The benefits of the biting cleaners’ service to small residents thus appear to be indirect. The observation that apparent cheating of partners often immediately followed interactions consisting of tactile stimulation is clearly in line with the indirect reciprocity concept. The results have important implications for theoretical approaches to indirect reciprocity. Existing models predict that image scoring drives altruistic behaviour towards fixation (Nowak & Sigmund 1998; Leimar & Hammerstein 2001). Cheating individuals can only re-invade an image-scoring population after genetic drift has led to an increase in non-discriminatory altruists (Nowak & Sigmund 1998). In the cleaner fish system, cheating individuals use one class of clients for altruistic behaviour to produce a signal that allows them to exploit another class of clients not despite

but because of image scoring. I suggest that biting cleaners make use of variation in pay-offs between interactions. They might behave altruistically in low pay-off interactions (smaller clients) and exploitatively in high pay-off interactions where mucus is easily accessible (larger clients). In particular, targeting non-predatory choosy clients for cheating seems plausible, as these clients do not inflict immediate cost on cheating cleaners but swim off (Bshary & Schäffer 2002). By contrast, the cheating of larger residents is more difficult to understand as residents often chase cleaners after a cheat (Bshary & Grutter 2002). Future research needs to establish whether the biting cleaners’ strategy yields (at least temporarily) higher pay-offs than cooperative cleaning, or whether biting and cleaning represent two alternative strategies, or whether biting cleaners make the best out of a bad job (Krebs & Davies 1993). There is some indication that cheating by cleaners is condition dependent (R. Bshary, unpublished data) but this link has to be further investigated.

The tactile stimulation of small residents by biting cleaners is exciting both because of the obvious costly nature of this behaviour (as it is incompatible with foraging) and because of its potential function. It remains an open question whether tactile stimulation is really altruistic in that it yields any fitness benefits to clients, for example via stress reduction, and if not why small residents still interact with biting cleaners. With respect to the function of tactile stimulation, the data suggest that biting cleaners use this behaviour as a signal out of context: it is not directed towards the current client but towards observers. As observers that approach are readily exploited, the altruism of biting cleaner fish seems to function as tactical deception of image-scoring clients. Tactical deception is the use of a signal from the normal repertoire out of context, so that it induces the usual response in receivers, to the signaller’s advantage and to their own disadvantage (Hauser 1998). Note that the definition is purely functional and does not assume specific cognitive abilities. Biting cleaners thus seem to exploit the eavesdropping of observing clients to their own advantage. Tactical deception is often seen as a hallmark of ‘machiavellian intelligence’, the notion that the high cognitive abilities of primates have evolved to cope with a complex social environment (Byrne & Whiten 1988; Whiten & Byrne 1998). However, Heyes (1998) has cautioned that the occurrence of tactical deception does not imply high cognitive abilities, i.e. the ability to read each other’s mind (Premack & Woodruff 1978). Instead, simple conditioning processes may be enough to associate the production of a signal out of context with reward, thereby increasing the probability that the rewarded individual will repeatedly produce the signal under similar circumstances. Cleaner fish are in an ideal situation to connect own behaviour with reward or punishment, as they have more than 2000 interactions per day (Grutter 1995). But one should expect that tactical deception is a general component of communication networks. Tactical deception should occur if it pays to alter the optimal behaviour in a situation to induce responses in bystanders, which will produce benefits during future interactions with these bystanders that exceed the momentary costs. How frequently wrong signals can be produced so that they still fool observers has to be evaluated. While verbal arguments predicted low frequencies (Dawkins & Krebs 1978), game

theoretic models indicate that that is not necessarily the case (Johnstone & Grafen 1993; Szamado 2000). In conclusion, communication network theory and the concept of indirect reciprocity provide an ideal functional framework to predict the occurrence of apparently altruistic behaviour and the occurrence of tactical deception, without having to worry too much about the cognitive abilities of the species involved.

I thank the EEAA in Cairo for permits and A. de Grissac, the Park rangers and I. Riepl for support. I also thank N. Davies, R. Johnstone, B. Knauer, A. Roulin, A. Russell, J. Schneider, W. Wickler and two anonymous referees for comments and support. Financial support came from the German Science Foundation (DFG) and a Marie Curie Fellowship of the EU.

REFERENCES

- Alexander, R. D. 1987 *The biology of moral systems*. New York: Aldine de Gruiter.
- Axelrod, R. & Hamilton, W. D. 1981 On the evolution of cooperation. *Science* **211**, 1390–1396.
- Bshary, R. 2001 The cleaner fish market. In *Economics in nature* (ed. R. Noë, J. A. R. A. M. van Hoof & P. Hammerstein), pp. 146–172. Cambridge University Press.
- Bshary, R. & Grutter, A. S. 2002 Asymmetric cheating opportunities and partner control in a cleaner fish mutualism. *Anim. Behav.* **63**, 547–555.
- Bshary, R. & Schäffer, D. 2002 Choosy reef fish select cleaner fish that provide high service quality. *Anim. Behav.* **63**, 557–564.
- Bshary, R. & Würth, M. 2001 Cleaner fish *Labroides dimidiatus* manipulate client reef fish by providing tactile stimulation. *Proc. R. Soc. Lond. B* **268**, 1495–1501. (DOI 10.1098/rspb.2001.1701.)
- Bull, J. J. & Rice, W. R. 1991 Distinguishing mechanisms for the evolution of cooperation. *J. Theor. Biol.* **149**, 63–74.
- Byrne, R. W. & Whiten, A. (eds) 1988 *Machiavellian intelligence*. Oxford: Clarendon Press.
- Cheney, D. L. & Seyfarth, R. M. 1990 *How monkeys see the world*. University of Chicago Press.
- Conover, W. J. 1980 *Practical non parametric statistics*, 2nd edn. New York: Wiley.
- Côté, I. M. 2000 Evolution and ecology of cleaning symbioses in the sea. *Oceanogr. Mar. Biol. A. Rev.* **38**, 311–355.
- Dawkins, R. & Krebs, J. R. 1978 Animal signals: information or manipulation? In *Behavioural ecology: an evolutionary approach* (ed. J. R. Krebs & N. B. Davies), pp. 282–309. Oxford: Blackwell Scientific.
- Dutreland, C., McGregor, P. K. & Oliveira, R. F. 2001 The effect of an audience on intrasexual communication in male Siamese fighting fish, *Betta splendens*. *Behav. Ecol.* **12**, 283–286.
- Gorlick, D. L. 1980 Ingestion of host fish surface mucus by the Hawaiian cleaning wrasse, *Labroides phthirophagus* Labridae, and its effect on host species preference. *Copeia*, 863–868.
- 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. 1997 Spatio-temporal variation and feeding selectivity in the diet of the cleaner fish *Labroides dimidiatus*. *Copeia*, 346–355.
- Grutter, A. S. 1999 Cleaner fish really do clean. *Nature* **398**, 672–673.
- Grutter, A. S. 2001 Parasite infection rather than tactile stimulation is the proximate cause of cleaning behaviour in reef fish. *Proc. R. Soc. Lond. B* **268**, 1361–1366. (DOI 10.1098/rspb.2001.1658.)
- Hauser, M. D. 1998 Minding the behaviour of deception. In *Machiavellian intelligence*, vol. 2 (ed. A. Whiten & R. W. Byrne), pp. 112–143. Cambridge University Press.
- Heyes, C. M. 1998 Theory of mind in non human primates. *Behav. Brain Sci.* **21**, 101.
- Johnstone, R. A. 2001 Eavesdropping and animal conflict. *Proc. Natl Am. Soc.* **98**, 9177–9180.
- Johnstone, R. A. & Grafen, A. 1993 Dishonesty and the handicap principle. *Anim. Behav.* **46**, 759–764.
- Krebs, J. R. & Davies, N. B. 1993 *An introduction to behavioural ecology*, 3rd edn. Oxford: Blackwell Scientific.
- Leimar, O. & Hammerstein, P. 2001 Evolution of cooperation through indirect reciprocity. *Proc. R. Soc. Lond. B* **268**, 745–753. (DOI 10.1098/rspb.2000.1573.)
- Losey, G. C., Grutter, A. S., Rosenquist, G., Mahon, J. L. & Zamzow, J. P. 1999 Cleaning symbiosis: a review. In *Behaviour and conservation of littoral fish* (ed. V. C. Almada, R. F. Oliveira & E. J. Gonclaves), pp. 379–395. Lisbon: Instituto Superior de Psicologia Aplicada.
- McGregor, P. K. 1993 Signalling in territorial systems: a context for individual identification, ranging and eavesdropping. *Phil. Trans. R. Soc. Lond. B* **340**, 237–244.
- Naguib, M. & Todt, D. 1997 Effects of dyadic vocal interactions on other conspecific receivers in nightingales. *Anim. Behav.* **54**, 1535–1543.
- Nowak, M. A. & Sigmund, K. 1998 Evolution of indirect reciprocity by image scoring. *Nature* **393**, 573–577.
- Oliveira, R. F., McGregor, P. K. & Latruffe, C. 1998a Know thine enemy: fighting fish gather information from observing conspecific interactions. *Proc. R. Soc. Lond. B* **265**, 1045–1049. (DOI 10.1098/rspb.1998.0397.)
- Oliveira, R. F., McGregor, P. K., Burford, F. R. L., Custodio, M. R. & Latruffe, C. 1998b Functions of mudballing behaviour in the European fiddler crab, *Uca tangeri*. *Anim. Behav.* **55**, 1299–1309.
- Potts, G. W. 1973 The ethology of *Labroides dimidiatus* Cuv. and Val. Labridae, Pisces on Aldabra. *Anim. Behav.* **21**, 250–291.
- Premack, D. & Woodruff, G. 1978 Does the chimpanzee have a theory of mind? *Behav. Brain Sci.* **4**, 515–526.
- Randall, J. E. 1958 A review of the labrid fish genus *Labroides*, with descriptions of two new species and notes on ecology. *Pacific Sci.* **12**, 327–347.
- Randall, J. E. 1983 *Red Sea reef fishes*. London: Immel.
- Roberts, G. 1998 Competitive altruism: from reciprocity to the handicap principle. *Proc. R. Soc. Lond. B* **265**, 427–431. (DOI 10.1098/rspb.1998.0312.)
- Robertson, D. R. 1972 Social control of sex reversal in a coral-reef fish. *Science* **177**, 1007–1009.
- Sherratt, T. N. & Roberts, G. 2001 The importance of phenotypic defectors in stabilizing reciprocal altruism. *Behav. Ecol.* **12**, 313–317.
- Sikkel, P. C., Fuller, C. A. & Hunte, N. 2000 Habitat/sex differences in a time at cleaning stations and ectoparasite loads in a Caribbean reef fish. *Mar. Ecol. Prog. Ser.* **193**, 191–199.
- Szamado, S. 2000 Cheating as a mixed strategy in a simple model of aggressive communication. *Anim. Behav.* **59**, 221–230.
- Trivers, R. L. 1971 The evolution of reciprocal altruism. *Q. Rev. Biol.* **46**, 35–57.
- Wedekind, C. & Milinski, M. 2000 Cooperation through image scoring in humans. *Science* **288**, 850–852.
- Whiten, A. & Byrne, R. W. (eds) 1998 *Machiavellian intelligence*, vol. 2. Cambridge University Press.
- Zahavi, A. 1995 Altruism as a handicap—the limitations of kin selection and reciprocity. *J. Avian Biol.* **26**, 1–3.

As this paper exceeds the maximum length normally permitted, the author has agreed to contribute to production costs.