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Building up relationships in asymmetric co-operation games between the cleaner wrasse *Labroides dimidiatus* and client reef fish

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Abstract It has been suggested that individuals may prevent partners from cheating by building up relationships slowly, giving very little in the beginning and raising the stakes in subsequent moves if partners reciprocate. I tested this idea with field experiments on the cleaner-fish *Labroides dimidiatus* and its "client" reef fish. Clients visit cleaners at their small territories, so-called cleaning stations, to have parasites removed. Cleaners were first observed and then caught and either put back on their original territory or moved to a new site. I noted a variety of cleaner and client behaviour to evaluate how, if at all, relationships are built up. Cleaners and resident clients indeed build up relationships, but with heavy initial investment. There was no evidence that cleaners build up relationships with client species that have access to several cleaners. Finally, it appeared that cleaners constantly invest in relationships with predatory clients, possibly to reduce the risk that predators try to catch them. I propose that asymmetries between partners with respect to either payoff values or strategic options are the major reason why the results do not fit the so-called raising-the-stakes strategy.

Keywords *Labroides dimidiatus* · Cooperation · Mutualism · Prisoner's dilemma · Asymmetric game

Introduction

The iterated prisoner's dilemma game (Axelrod and Hamilton 1981) has long been used as a paradigm for the evolution of co-operation between unrelated individuals (Dugatkin 1997). Though each of two partners playing a prisoner's dilemma game gains more by defecting than by co-operating in each round, irrespectively of what the partner does, repeated interactions may allow each to overcome the temptation to cheat, since any cheating would be reciprocated during future interactions. Recently, Roberts and Sherratt (1998) altered the assumption of the original model that payoff-values are constant and allowed individuals to vary investment in their partners. They found that a strategy called "raising the stakes" was evolutionarily stable. The strategy specifies that an individual may initially invest a small unit in its partner and increase the size of the unit subsequently if each donation is matched by a larger reciprocal donation from the partner. Otherwise, no further investment will be made. The strategy thus avoids any large exploitation by a non-cooperative partner and enables co-operative partners to build up stable relationships with strong mutual benefits.

Though the logic of Roberts and Sherratt's model (1998) is clearly appealing, a major challenge is to come up with empirical data to test the model. Grooming data on baboons failed to fit the model (Barrett et al. 2000), but the approach was rather indirect, since interactions between individuals were not observed from scratch. Documenting the history of interactions from the very first one to an established relationship (or its failure) would be the ideal way to test the model. Some data on the behaviour of schoolchildren do not fit the model (see Keller and Reeve 1998). Instead, it appeared that children were willing to invest a lot in the beginning to build up relationships and generally exchanged less when the relationship was established. In addition, if a friend did not give, children responded by an increase in their donations rather than stopping their own investment.

Here, I use Roberts and Sherratt's model (1998) as a guideline to develop questions about if and how cleaner wrasses, *Labroides dimidiatus*, build up relationships with other reef-fish species. *L. dimidiatus* removes parasites and other material from the surface, the gills and sometimes the mouth of so-called “client” reef fish which actively visit them at their small territories, so-called cleaning stations (recent reviews: Losey et al. 1999; Côté 2000). Cleaner-fish are ideal subjects for catching and translocation in order to study how relationships with clients are built up. Nevertheless, it is important to acknowledge that the cleaner-fish mutualism is not suitable for explicit testing of the original model. This is because Roberts and Sherratt (1998) assumed that both partners have the same set of strategies available, i. e. both partners can invest anything between nothing and the maximal amount. The cleaner-fish mutualism, however, is defined by marked asymmetries between cleaners and clients in their strategic options. Consider first the interaction between a cleaner and a predatory client. Cleaners can cheat by feeding on healthy mucus and scales rather than parasites and dead or infected material (Randall 1958; Gorlick 1980; Bshary and Grutter 2002). Even so, the negative effects of cheating on the predator are small compared to the reverse effect of a cheating predator on a cleaner, since the latter would loose its life. There is therefore a strong payoff asymmetry in this game. A different game occurs between cleaners and non-predatory clients. Here, only the cleaner has the option to cheat, while the client simply lacks that option as long as it tries to maximise its own payoff (clients could be spiteful). There is therefore a strong asymmetry in the strategy available to the partners. In conclusion, my experiment tests if and how individuals have to build up relationships to reap the maximal benefits of co-operation in rather asymmetric games.

I distinguished between three different client categories: (1) predators; (2) non-predatory resident clients with small territories or home ranges that cover one cleaning station only; and (3) non-predatory clients with larger home ranges that allow them to access several cleaning stations. The distinction between the last two client categories seemed reasonable, since individuals of these two categories differ in the way they respond to cheating by a cleaner (Bshary and Grutter 2002). Client species with access to several cleaning stations react by swimming off and visiting another station (Bshary and Schäffer 2002), while resident clients without a choice chase the cleaner (Bshary and Grutter 2002). The latter behaviour fulfils the criteria for punishment (Clutton-Brock and Parker 1995) in that clients suffer a momentary (energetic) cost from chasing which will benefit them only during their next interaction with the cleaner, which may be minutes later. Punishment theory relies on the ability to recognise partners (individually or through site fidelity), while the partner-switching of clients with choices could keep cheating by cleaners to acceptable levels in principle without any partner recognition. It is thus conceivable that cleaners may build up relationships with resident clients but not with clients with access to several cleaning stations.

I first observed individual *L. dimidiatus* at their cleaning stations. Then I caught them the next day and either released them at their original cleaning station or released them at a new site where no cleaner had been present during at least the previous 3 weeks. The cleaners were observed immediately after the release, 2 h later and 26 h later. I looked at the following aspects of interaction: (1) duration; (2) frequency of clients performing jolts in response to cleaner-fish mouth contact; (3) frequency of interactions that consisted purely of the cleaner providing tactile stimulation to its client (host stabilisation; see Potts 1973). Jolt frequency is a good correlate of cheating by cleaners (Bshary and Grutter 2002). Tactile stimulation was defined as the cleaner touching the client’s dorsal area with its pelvic and pectoral fins, while the relative spatial positions of both remain constant and the cleaner’s mouth points away from the client. This behaviour is thus incompatible with foraging (Potts 1973; Bshary and Würth 2001) and therefore a good indicator of investment by the cleaner-fish in the client. I also noted how often clients chased cleaners, without cleaners trying to interact with them, and how often clients responded to an approach by a cleaner by evasive behaviour that prevented an interaction. If cleaners and clients build up relationships according to the raising-the-stakes strategy, I predicted that cleaners increase the tactile stimulation and reduce the amount of cheating over repeated interactions. In turn, clients should become more and more tolerant towards cheating by cleaners, and the duration of interactions should increase. If both sides have to invest initially to establish a relationship, I predicted that cleaners initially provide more tactile stimulation and refrain from cheating. Clients could be more tolerant towards cheating initially, but, alternatively, they could make clear from the beginning that they would not tolerate any cheating by the cleaner. They could do that by chasing the cleaner without explicit reason and by showing evasive action when approached. If relationships are not to be established in the cleaning mutualism, then interactions should be “average” right from the beginning.

Methods

Study site and study animals

The study was conducted at Mersa Bareika, Ras Mohammed National Park, Egypt. The area consists mainly of isolated small coral heads (patch reefs) which are isolated from each other by sandy areas. Depth at the bottom of the patch reefs varied between 2 and 6 m. Each cleaner used in the experiment was a resident on one of these patch reefs and without a partner. Cleaners were either subadults or small adults, up to 6 cm in standard length. Data were collected in May–June 1999 and October–November 1999.

Experimental set-up

Each cleaner was first observed for 60 min at its cleaning station. The next day, but 2 h earlier, the cleaner-fish was caught with a barrier net. It was placed in a plexiglas tube and I either dived to another patch reef and released the cleaner there, or I dived in a circle and released the cleaner back at its original patch reef. Transferred cleaners were released at patch reefs that, to the best of my knowledge, were without a cleaner for at least the previous

3 weeks, and I tried to match fish species composition of the previous and the new patch reef as far as possible. I alternated between translocating a cleaner and releasing a cleaner at its original patch reef. Ideally, cleaners were observed immediately after their release, for 15 min, 2 h after they had been caught, for 60 min, and, in October–November 1999, again 26 h after they had been caught, for another 60 min. This schedule was not always possible, since transferred cleaners tended to disappear overnight. In three cases, the cleaners had apparently moved to adjacent patch reefs; these fish were not observed further. Note that, with the adopted observation schedule, cleaners were observed on three consecutive days at the same time of day. Time of day varied between cleaners. Cleaners were caught between 0700 hours and 1400 hours, so the main observation sessions started between 0900 hours and 1600 hours. During all observation sessions, cleaning interactions with clients were noted in the following way: (1) species identity according to Randall (1983); (2) duration; (3) number of client jolts; (4) tactile stimulation, or not, during the entire interaction. In addition, it was noted if a client chased a cleaner without being inspected and if a client reacted to a cleaner approach with evasive action, either aggression or flight.

As a control, I also transferred 12 other wrasses of the species *Pseudocheilinus hexalineatus, Thalassoma klunzingeri* and *T. lunare*. The last two species are facultative cleaners that often clean as juveniles. The fish were observed for the first 15 min following transfer, and the focus of attention was on whether or not other fish responded to their presence with either unprovoked aggression or unprovoked flight.

Data analysis

For each cleaner, observation session and client category, I calculated the mean duration of interactions, client jolt frequency and percent of cleaning interactions that consisted of tactile stimulation only. In addition, I calculated the frequency of interactions that consisted purely of clients chasing the cleaner and the frequency of interactions in which inspection did not take place because the client evaded an approaching cleaner.

Statistics

Data were analysed with the statistical programme SPSS-X. All tests were non-parametric and two-tailed.

Results

The data could be analysed in two different ways. One could ask whether, for each cleaner, treatment had a significant effect on behaviour, or compare cleaners that have been transferred with cleaners that have been released at their original patch reef. I concentrate on the latter analysis. Prior to manipulation, cleaners that were to be translocated did not differ significantly from cleaners that were to be returned to their original patch reef, with respect to any but one of the measured parameters for any client category (Mann–Whitney U tests: all NS; see Figs. 1, 2, 3, 4 and 5). The only exception was that cleaners that were to be moved were avoided more often when they approached a resident client than were cleaners that were to be caught and returned to their reef (Mann–Whitney U tests: m=12, n=10, U=27, P=0.03; Fig. 2c).

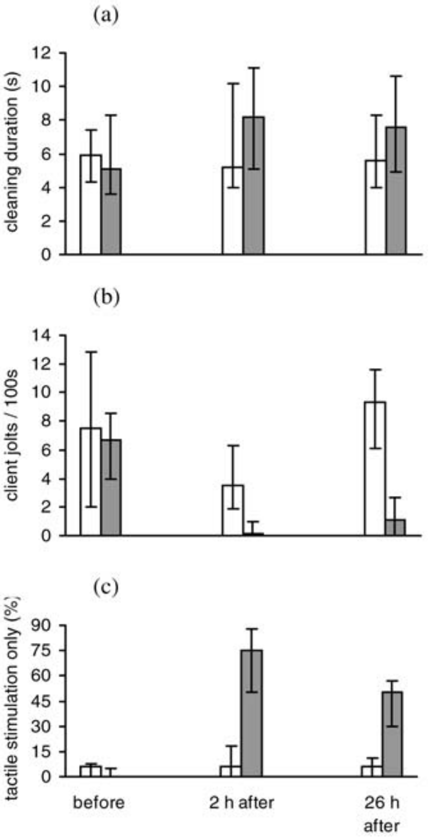

Fig. 1a–c Interactions between cleaners and non-predatory resident species. Cleaning duration (**a**), client jolt rate (**b**) and interactions that consisted of tactile stimulation only (**c**)—before, 2 h after and 26 h after the manipulation. *Open columns* Cleaners caught and put back; *shaded columns* cleaners caught and moved to another patch reef; *vertical capped lines* median and interquartiles of values for individual cleaners

Interactions between cleaners and non-predatory residents

Manipulations had no significant effect on cleaning duration (Mann–Whitney U tests: after 2 h, m=12, n=10, U=47, P=0.41; after 26 h, m=7, n=6, U=17, P=0.62; Fig. 1a). However, residents that interacted with translocated cleaners jolted less frequently (Mann–Whitney U tests: after 2 h, m=12, n=10, U=28.5, P=0.036; after 26 h, m=7, n=6, U=5, P=0.022; Fig. 1a) and received more tactile stimulation (Mann–Whitney U tests: after 2 h, m=12, n=10, U=6, P<0.001; after 26 h, m=7, n=6, U=0, P<0.001; Fig. 1a). In addition, translocated cleaners ignored residents less frequently after 2 h and tended to do so still after 26 h (Mann–Whitney U tests: after 2 h, m=12, n=10, U=10, P<0.001; after 26 h, m=7, n=6, U=10.5, P=0.09; Fig. 2a). Resident clients, on the other hand, chased translocated cleaners spontaneously, which never happened to cleaners that were returned to their original reef (Mann–Whitney U tests: after 2 h, m=12, n=10, U=0, P<0.001; after 26 h, m=7, n=6, U=5, P=0.03; Fig. 2b). They also avoided translocated cleaners more often (Mann–Whitney U tests: after 2 h, m=12,

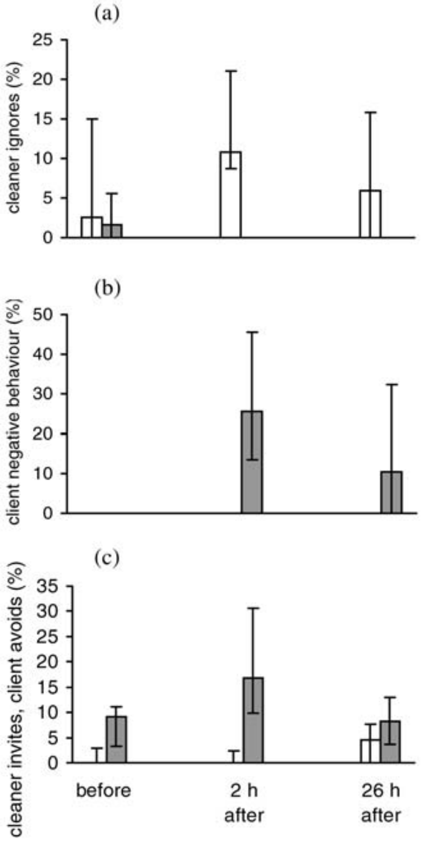

Fig. 2a–c Interactions between cleaners and non-predatory resident species. Frequencies of cleaners ignoring inviting clients (**a**), client spontaneous negative behaviour (aggression or fleeing) (**b**) and client avoiding cleaners that invite an interaction (**c**)—before, 2 h after and 26 h after the manipulation. *Open columns* cleaners caught and put back; *shaded columns* cleaners caught and moved to another patch reef; *vertical capped lines* median and interquartiles of values for individual cleaners

n=10, U=0, P<0.001; after 26 h, m=7, n=6, U=3.5, P=0.008; Fig. 2c). Since this result was obtained prior to manipulation, I also tested whether there were any significant changes in a matched-pair design. Cleaners were avoided significantly more often after translocation (Wilcoxon test: n=10, T=0, P=0.002), whereas catching and release at their original patch reef had no effect on avoidance frequencies.

Resident clients did not chase or avoid the 12 individuals of other wrasse species that were transferred to a new patch reef during the first 15 min following release. The only exception was an olive dottyback, *Pseudochromis olivaceus*, which attacked a six-stripe wrasse that entered its coral. Also the 12 cleaners that were put back on their original cleaning station were not chased or avoided by residents. In contrast, translocated cleaners experienced such behaviour frequently, between 5 and 34 times (median 10, n=10). Most often, the residents chased the new cleaners without any apparent reason (median 7, range 3–34), and sometimes they fled from the cleaner.

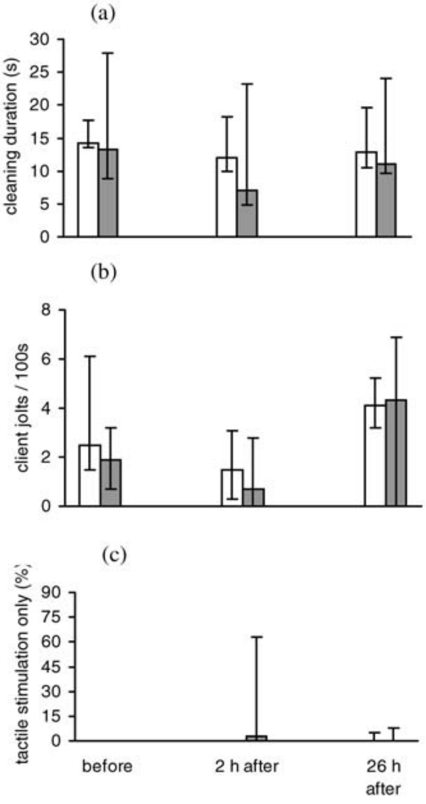

Fig. 3a–c Interactions between cleaners and non-predatory client species with access to several cleaning stations. Cleaning duration (**a**), client jolt rate (**b**) and interactions that consisted of tactile stimulation only (**c**)—before, 2 h after and 26 h after the manipulation. *Open columns* Cleaners caught and put back; *shaded columns* cleaners caught and moved to another patch reef; *vertical capped lines* median and interquartiles of values for individual cleaners

Interactions between cleaners and non-predatory clients with choices

There were no significant differences between the two cleaner-fish groups with respect to cleaning duration, client jolt rate and interactions consisting of tactile stimulation only after the manipulations (Mann–Whitney U tests: all NS; Fig. 3). Cleaners never ignored a client with choices (unless they had to choose between several that were present simultaneously), and these clients never showed any spontaneous aggression towards cleaners. Therefore, these data are not shown graphically. Nevertheless, clients with choices were more likely to flee from a translocated approaching cleaner than from a cleaner that was put back on its patch reef 2 h after the manipulation (Mann–Whitney U test: m=11, n=8, U=16.5, P=0.025; Fig. 4).

Interactions between cleaners and predatory clients

There were no significant differences between the two cleaner-fish groups with respect to cleaning duration or

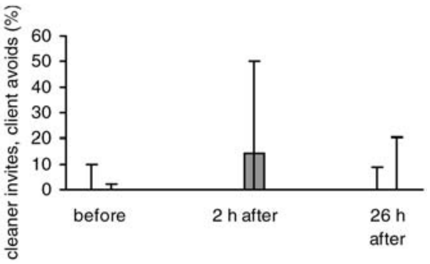

Fig. 4 Interactions between cleaners and non-predatory client species with access to several cleaning stations. Frequencies of clients avoiding cleaners that invite an interaction—before, 2 h after and 26 h after the manipulation. *Open columns* Cleaners caught and put back; *shaded columns* cleaners caught and moved to another patch reef; *vertical capped lines* median and interquartiles of values for individual cleaners

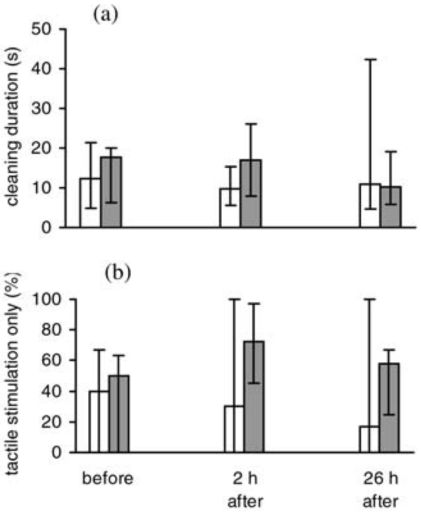

Fig. 5a, b Interactions between cleaners and predatory client species. Cleaning duration (**a**) and interactions that consisted of tactile stimulation only (**b**)—before, 2 h after and 26 h after the manipulation. *Open columns* Cleaners caught and put back; *shaded columns* cleaners caught and moved to another patch reef; *vertical capped lines* median and interquartiles of values for individual cleaners

interactions consisting of tactile stimulation only after the manipulations (Mann–Whitney U tests: all NS; Fig. 5). Client jolts were too infrequent for any statistical analysis. A predatory client was ignored once during all observations (n=149). Predators did not show any spontaneous aggressive behaviour towards cleaners. A specific behaviour of a few groupers was to remain motionless and open their mouth in a very exaggerated way initially after a cleaner had been translocated, at distances of about 1 m from the cleaners. Five individuals of *Cephalopholis hemistiktos* did so 2–5 times, and one individual *C. miniata* did so twice. Such extreme opening of the mouth is often observed when groupers have their mouth inspected by cleaner-fish or cleaner shrimps (personal observation). Predatory clients did not flee from approaching cleaners. In contrast, cleaners fled from predators on seven occasions during observations, once before the experimental manipulation and six times after being translocated. Thus, they were more likely to flee from a resident predator after translocation than otherwise (binomial test: n=7, probability of event = (observation time after translocation)/(total observation time) =0.33, observed events =6, P=0.013).

Cleaners interacted with resident predators more frequently 2 h after translocation than before (Wilcoxon test: n=9, T=6, P=0.04).

Discussion

I looked at three different potentially co-operative games, i. e. the game between cleaners and predatory clients, the game between cleaners and non-predatory clients with a choice of several cleaners, and the game between cleaners and non-predatory resident clients with a choice of one cleaner only. I asked whether potentially co-operative partners have to build up a relationship first in order to receive the highest payoffs obtainable from co-operation. If that was the case, I asked whether investment in the partner and the relationship was initially low, as predicted by Roberts and Sherratt (1998), or whether initial investment was high, as previously observed in school children (see Keller and Reeve 1998).

Interactions between cleaners and non-predatory residents

The data clearly show that initial interactions between cleaners and non-predatory residents differ markedly from interactions the cleaners had at their established cleaning stations. Cleaners put in quite an effort initially as they provided plenty of tactile stimulation, which is incompatible with foraging and therefore a purely altruistic act from their perspective (Potts 1973; Bshary and Würth 2001). In addition, they hardly ever took bites that made clients jolt, indicating that they refrained from cheating (Bshary and Grutter 2002). Thus cleaners start with an initial heavy investment in their relationships with non-predatory residents. It will be interesting to look at other forms of co-operation or mutualism in which one partner may profit from cheating while the other one does not, to see whether initial heavy investment by the potential cheater is a general phenomenon in such systems.

Also, the residents invested initially in the relationship. However, they did not invest to benefit the cleaners but inflicted costs on them through unprovoked chases and avoidance of approaching cleaners. It thus seemed that residents started to punish cleaners even before the latter had any opportunity to cheat them. Since residents did not chase other wrasses that were transferred, it appears unlikely that the aggression towards cleaners was due to a general aggression towards unfamiliar individuals. Instead, resident clients, as potential victims of cleaner-fish cheating, might have to show right from the beginning that they will not tolerate any exploitation to increase the co-operative level of the potential cheater.

Interactions between cleaners and non-predatory clients with choices

Clients with access to several cleaners evaded approaching cleaners more often if the cleaners had been moved to a new patch reef. This could be interpreted as an initial doubt about the cleaners' willingness to co-operate, which cleaners should have to overcome by providing a good service. However, cleaners did not offer any special service to clients with choices after translocation. A previous study revealed that clients that arrive at a cleaning station reproduce the behaviour of the previous client if they could observe the cleaner's last interaction (Bshary 2002). It is therefore most likely that, in the present study, clients with choices sometimes saw resident clients evading or chasing the new cleaner and therefore avoided an interaction when approached by the cleaner. Clients with choices appear to control the behaviour of cleaners simply by switching partners if the service was bad (Bshary and Schäffer 2002). A cleaner that cheats thus risks that one of his food patches will be at least temporarily unavailable. The results presented here suggest that this partner-control strategy makes the establishment of a personal relationship unnecessary. The results directly contrast existing models that predict that mobility of partners hinders the evolution of co-operation (Dugatkin and Wilson 1991; Enquist and Leimar 1993). In the present example, stability arises because the potential cheater is stationary while the potential victim is the rover and can exert choice. This is more similar to a model proposed by Ferriere and Michaud (1995), in which co-operators move to find co-operators.

Interactions between cleaners and predatory residents

Similar to interactions between cleaners and clients with choices, the data do not suggest that cleaners and predatory residents have to establish a relationship to reap the benefits of co-operation. As in previous studies (Bshary 2001; Bshary and Würth 2001), predators hardly ever jolted during interactions and received plenty of tactile stimulation. I suggest that cleaners might simply provide a service quality that is above the predator's threshold at which it switches from co-operation to trying to eat the cleaner. As long as predators constantly re-evaluate the cleaners' value as either cleaner or food source, the cleaners will never alter their service quality, so their investment in the relationship with predators will remain constant. An important open question is whether a predator's decision-making depends on the integration of expected future benefits of repeated parasite removal, as suggested by Trivers (1971), or whether the predator has no temptation to cheat as long as a cleaner co-operates, even during one interaction. Trivers (1971) suggested that only the repeated removal of parasites eventually outweighs the high but only once achievable payoff for eating the cleaner. However, given that a cleaner-fish would certainly try to escape any predation attempt and terminate the interaction if successful, a predator's payoff for cheating might as well be below its payoff for co-operation within each interaction as long as the cleaner co-operates.

Transferred cleaners were more likely to flee from predators without being attacked, a behaviour that usually occurred extremely rarely, and thus indicates that cleaners are weary of potentially-cheating predators or of predators making mistakes. These observations and the increase in interaction frequency between transferred cleaners and resident predators (there are hardly any data on interactions between cleaners and visiting predators) suggest that some trust has to be built up. The latter result has to be treated with caution, however, since it was not predicted and the explanation is therefore post hoc. Even so, the observation that some groupers widely opened their mouth initially indicates that cleaners and resident predators build up relationships. Groupers engulf their prey by a sucking action with a rapid opening of their mouth, so the exaggerated opening of the mouth might make any attempt at predation very unlikely to be successful. The behaviour might thus function as a signal to the cleaner that the client wants to co-operate.

In conclusion, it appears that, depending on the nature of asymmetry (payoffs or strategic options) and the corresponding control mechanisms that clients use to control cleaner-fish behaviour, relationships have to be established or not. No data set supports the idea that relationships are built up by increasing investment in the partner (Roberts and Sherratt 1998). On the contrary, cleaners and non-predatory residents invest initially, the cleaner in the client and the client in the control mechanism of punishment. This means that a roving strategy is very costly for a cleaner, since the resident clients will harass it initially wherever it goes. There is thus a strong pressure on cleaners to show site fidelity. From the clients' perspective, however, the option to switch between partners appears to be a very reliable partner-control option that is based on very simple rules and does not warrant any relationship with the cleaners. In this context, it is interesting to note that some other cleaner-fish species are less territorial than *L. dimidiatus* and cover much larger areas (see Henriques and Almada 1997). In these species, roving strategies might therefore be found. In interactions with predators, cleaners are initially wary of cheating, but also seem to try to establish a relationship quickly. This might be important for cleaners to avoid any attack while inspecting other clients. Overall, the data clearly emphasise our need for further empirical studies and new models on the evolution of co-operation between unrelated individuals.

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References

Axelrod R, Hamilton WD (1981) The evolution of cooperation. Science 211:1390–1396

Barrett L, Henzi SP, Weingrill T, Lycett JE, Hill RA (2000) Female baboons do not raise the stakes but they give as good as they get. Anim Behav 59:763–770

Bshary R (2001) The cleaner-fish market. In: Noë R, Hooff JARAM van, Hammerstein P (eds) Economics in nature. Cambridge University Press, Cambridge, pp 146–172

Bshary R (2002) Biting cleaner-fish use altruism to deceive image scoring reef fish. Proc R Soc Lond B (in press)

Bshary R, Grutter AS (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

Clutton-Brock TH, Parker GA (1995) Punishment in animal societies. Trends Ecol Evol 373:209–215

Côté IM (2000) Evolution and ecology of cleaning symbioses in the sea. Oceanogr Mar Biol Annu Rev 38:311–355

Dugatkin LA (1997) Co-operation among animals. Oxford University Press, New York

Dugatkin LA, Wilson DS (1991) Rover: a strategy for exploiting cooperators in a patchy environment. Am Nat 138:687–701

Enquist M, Leimar O (1993) The evolution of cooperation in mobile organisms. Anim Behav 45:747–757

Ferriere R, Michod RE (1995) Invading wave of cooperation in a spatially iterated prisoner's dilemma. Proc R Soc Lond B 259:77–83

Gorlick DL (1980) Ingestion of host fish surface mucus by the Hawaiian cleaning wrasse, *Labroides phthirophagus* (Labridae), and its effect on host species preference. Copeia 1980:758–762

Henriques M, Almada VC (1997) Relative importance of cleaning behaviour in *Centrolabrus exoletus* and other wrasses at Arrábida, Portugal. J Mar Biol Assoc UK 77:891–898

Keller L, Reeve HK (1998) Familiarity breeds cooperation. Nature 394:121–122

Losey GC, Grutter AS, Rosenquist G, Mahon JL, Zamzow JP (1999) Cleaning symbiosis: a review. In: Almada VC, Oliveira RF, Goncalves EJ (eds) Behaviour and conservation of littoral fishes. Instituto Superior de Psichologia Aplicada, Lisbon, pp 379–395

Potts GW (1973) The ethology of *Labroides dimidiatus* (Cuv. and Val.) (Labridae, Pisces) on Aldabra. Anim Behav 21:250–291

Randall JE (1958) A review of the labrid fish genus *Labroides*, with descriptions of two new species and notes on ecology. Pac Sci 12:327–347

Randall JE (1983) Red Sea reef fishes. Immel, London

Roberts G, Sherratt TN (1998) Development of cooperative relationships through increasing investment. Nature 394: 175–179

Trivers RL (1971) The evolution of reciprocal altruism. Q Rev Biol 46:35–57