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Strategic adjustment of service quality to client identity in the cleaner shrimp, *Periclimenes longicarpus*

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Cleaning mutualism, in which cleaning organisms remove ectoparasites from cooperating 'clients', is widespread among marine animals. Until now, research has focused on fishes as cleaners, whereas cleaner shrimps have received little attention. The aim of this study was to investigate the cleaning behaviour of the cleaner shrimp, *Periclimenes longicarpus*, and to compare the results directly to data on the sympatric and well-studied cleaner wrasse, *Labroides dimidiatus*. We first compared the time spent cleaning and client diversity as indicators of the potential importance of the cleaner shrimp to client health and found strong similarities between shrimp and wrasse. We further looked at three correlates of service quality: duration of interactions, tactile stimulation of clients, and jolt rates as correlates of mucus feeding (=cheating). We specifically predicted that shrimps would cheat clients less frequently than the wrasses because they should be more vulnerable to aggressive responses by clients. Although the results partly support our hypothesis, they also suggest that both species strategically adjust cheating rates according to risk, as predatory clients jolted less frequently than nonpredatory clients. In conclusion, the results suggest that the shrimps play an important role in client health but that nonpredatory clients have to control the shrimps' behaviour to receive a good service.

Keywords:

cooperation, *Labroides dimidiatus*, mutualism, niche overlap, partner control, *Periclimenes longicarpus*

Understanding the evolution and maintenance of behaviours that increase the fitness of a recipient has been a key issue in behavioural ecology from the very beginning (Hamilton 1964; Trivers 1971; Axelrod & Hamilton 1981). Numerous frameworks and models have been developed, which try to conceptualize and categorize the strategies of cooperation (reviewed in Sachs et al. 2004; Lehmann & Keller 2006; Nowak 2006; Bshary & Bergmüller 2008). Kin selection has provided the conceptual framework for understanding helping between relatives (Hamilton 1964). However, the stability of interspecific cooperation, known as mutualism (West et al. 2007), is more difficult to explain because the benefits of helping are often conditional on investments by others, driving the evolution of control mechanisms that reduce the fitness of cheaters.

Marine cleaning mutualism, which involves more than 130 described cleaner species of fishes and crustaceans (Côté 2000) that remove ectoparasites from 'client' reef fishes, has been a model system for studying the stability of mutualism (reviews: Losey et al.

1999; Côté 2000; Bshary & Côté 2008). In the intensively studied cleaner wrasse, *Labroides dimidiatus*, the cleaners occupy small territories (termed 'cleaning stations'), where clients visit. There is an important conflict of interest because the cleaner fish prefers to eat client mucus over ectoparasites, which is considered cheating (Grutter 1997; Grutter & Bshary 2003). To keep the interaction mutualistic, clients apply various partner control mechanisms, depending on their strategic options. Resident clients (with access to only one cleaning station) punish cleaners for cheating by aggressively chasing them (Bshary & Grutter 2002a, 2005), whereas visiting client species (with access to several cleaning stations) use their choice options and flee in response to cheating by cleaners, visiting another station for the next interaction (Bshary & Schäffer 2002; Bshary & Grutter 2005). Only predatory clients do not seem to need to control the cleaners' behaviour as cleaners hardly ever cheat them (Bshary 2001). Apparently, the clients' control mechanisms result in a net gain from cleaning interactions as the wrasses remove large numbers of ectoparasites (Grutter 1996, 1999) and the presence of cleaner wrasse causes an increase in local reef fish diversity (Bshary 2003; Grutter et al. 2003).

Recent research on the Caribbean cleaning gobies, *Elacatinus* sp., suggests that the complexity of interactions found in the cleaner wrasse system may be not typical for marine cleaning mutualism in general. The two systems have in common that cleaners have small

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territories (cleaning stations), that they depend strongly on interactions with clients for their diet (Côté 2000), and that clients regularly jolt in response to cleaner fish mouth contact. Those jolts are a correlate of cheating by cleaners rather than an indicator of parasite removal because in both systems parasite-free clients jolt more frequently than parasitized clients (Bshary & Grutter 2002b; Soares et al. 2008a). Despite these similarities, the course of interactions is very different, as clients of gobies show neither punishment nor partner switching in response to jolts (Soares et al. 2008c). In addition, predatory clients jolt about as frequently as non-predatory clients in the goby system (Soares et al. 2007), whereas cleaner wrasses hardly ever cause predatory clients to jolt (Bshary 2001). Finally, cleaning gobies lack a behaviour called 'tactile stimulation' (and 'tactile dancing' in Grutter 2004; called 'host stabilization' by Potts 1973), which involves the cleaner riding on the client's back and stroking it with pelvic and pectoral fins. Tactile stimulation may serve many functions, but most important for the comparison between cleaners are observations that cleaner wrasses use this behaviour to reconcile with clients after a cheat and to manipulate client decisions to start/prolong an interaction (Bshary & Würth 2001). Overall, the apparent lack of strategic behaviour in both cleaning gobies and their clients suggests that conflicts are less important in the system than in the cleaner wrasse mutualism, although the reasons for this difference are currently unknown.

Here, we present the first field study on the cleaner shrimp *Periclimenes longicarpus* with the goal of collecting data that are directly comparable to the behavioural data on cleaner fishes. The study should give us a broader view of potential variation in the course of interactions between cleaners and clients. Until recently, cleaner shrimps have received little research attention, although 40 species have been recorded as cleaners (Jonasson 1987; Spotte 1998; Côté 2000). From what is known, however, it seems clear that cleaner shrimps deserve more attention. For example, it has been shown that cleaner shrimps (including a member of the genus *Periclimenes*) eat ectoparasites and thereby significantly reduce ectoparasite loads (Jonasson 1986; Becker & Grutter 2004, 2005; Becker et al. 2005; Östlund-Nilsson et al. 2005). Therefore, the question arises as to how strategic cleaner shrimps behave in interactions with clients and how clients behave towards the shrimps in comparison to how they behave towards cleaner fishes. *Periclimenes longicarpus* seemed to be a good candidate species for such a comparison because preliminary observations at our study site at the Red Sea confirmed that they occupy small cleaning stations, like the cleaner wrasse, and suggested that the two species have relatively similar numbers of interactions with diverse client species.

For a thorough appreciation of the behaviour of the cleaner shrimp, we collected equivalent data on the cleaner wrasse for direct comparisons. Although the cleaner wrasse has been studied in detail at our study site (Bshary 2001, 2003), only parallel sampling can exclude the possibility that any differences between the wrasse and the shrimp are due to variation in key ecological parameters between years. Our first point of interest was to compare the shrimps and the wrasses with respect to the percentage of time spent cleaning and the composition of client species. These data should give us some further indications about the importance of cleaner shrimps for reef fish health. Our second aim was to compare the nature of interactions with clients in the two cleaner species. We were particularly interested in three parameters that have been used to compare the behaviour of cleaner wrasse with the cleaning gobies: duration of interactions, client jolt rate and the occurrence of tactile stimulation. In addition, we noted client behaviours after jolts. We expected the shrimp system to be more similar to that of cleaning gobies than to that of the wrasse, i.e. we expected the shrimp system to be a by-product mutualism (Brown 1983) in which the shrimps would prefer

ectoparasites over mucus. In such a case we predicted a lack of strategic behaviour in the shrimps and consequently an absence of client aggression in interactions with shrimps. This expectation was based on two arguments. First, cleaner shrimps lack a vertebrate brain and we therefore doubted that they possess the cognitive skills to distinguish predatory and nonpredatory clients and adjust service quality accordingly. Second, the shrimps should also be particularly vulnerable to aggressive responses by nonpredatory clients because of their fragile bodies and hence would avoid the risk of being punished entirely.

METHODS

Study Site and Cleaning Organisms

This study was conducted at Mersa Bareika, Ras Mohamed National Park, South Sinai, Egypt. Data were collected between September and mid-November 2007. The two study species co-occur in the area and can be found in the same habitat at the same depths, within a few metres' distance of each other, with the cleaner fish even visiting the shrimps' cleaning stations occasionally.

The cleaner wrasse is an obligate cleaner fish ranging from Japan to South Africa, including Polynesia, the Red Sea and the Arabian Gulf (Lieske & Myers 2004). It is one of the main cleaning organisms of the underwater fauna, interacting with more than 2000 clients per day (Grutter 1996). The cleaner shrimp is an obligate cleaner found in the Red Sea and around the Arabian Peninsula. It is often associated with corals and anemones including *Xenia*, *Pleurogyra*, *Entacmaea quadricolor* and *Heteractis crista*, and it usually lives in groups (Debelius 2001; Lieske & Myers 2004). Our study groups of cleaner shrimps ranged from 2 to 50 shrimps (median = 7).

Cleaning Behaviour Observations

Fourteen cleaning stations of cleaner wrasse were chosen for convenient accessibility, at depths of between 1 and 12 m, as well as 14 stations of cleaner shrimp, at depths of between 1 and 17 m, with the mean depth being not significantly different (Mann-Whitney *U* test: $W = 56.5$, $N = 14$, $M = 14$, $P > 0.05$). All observations were done by scuba diving. The data were collected while sitting on sandy patches at a distance of ~1.5 m in front of the station, always by the same observer. Observations were done early in the morning and late in the afternoon, which correspond to the times the cleaner shrimps appeared to be the most active (determined by preliminary studies). Each station was observed four times for 30 min. Immediately after each interaction between a cleaner and a client, the following data were written on a Plexiglas plate: client species, as determined according to Lieske & Myers (2004); client total length, estimated with the help of a reference gradation on the Plexiglas plate; duration of the interaction in seconds, measured with a stopwatch; number of client jolts; the client's reaction to the jolts (no further reaction, fleeing or aggressive chasing of the cleaner); and the maximum number of shrimps cleaning the client at the same time.

Data Analysis

An overlap index (Pianka 1973) was calculated to establish the niche overlap of the two cleaners. Niche overlap increases as Pianka's index increases and the overlap is usually considered biologically significant if the value exceeds 0.60 (Zaret & Rand 1971).

To analyze the interaction data, the client species were used as independent units instead of the cleaning stations, because each of the latter had a unique set of clients. Individual clients were not recognized and may appear several times at the same cleaning

station as well as at different stations in the case of visitor species. The values obtained for one client species for each cleaning station were summed and divided by the number of stations in which the client species had been observed. This resulted in one mean value per client species. The following variables were calculated: the mean length of client, the mean duration of cleaning interactions, the total duration of cleaning interactions, the client jolt rate as the number of jolts divided by total interaction time, the percentage of jolts followed by a reaction from the client (either flight or aggression), and for these reactive jolts, the percentage of 'a fleeing reaction' and of 'an aggressive chase'.

We ran separate analyses for nonpredatory visitor clients, non-predatory resident clients, and predatory clients. Species were classified according to Bshary (2001) for the cleaner wrasse. For the cleaner shrimp we used information about the client species' diet described in Lieske & Myers (2004) to determine predatory clients. Twelve species (representing 7.5% of total observations) that could not readily be classified according to our categories predatory/nonpredatory and resident/visitor were excluded from the analyses.

For any comparison between the two cleaner species with respect to our indicators of service quality (cleaning duration, jolt rates and tactile stimulation) and client responses to jolts (frequency of response and percentage aggressive response), we used only client species that had interacted with both cleaner species for a matched pair comparison. To compare client jolt rates, only client species with a minimum of 10 s interaction time were considered to reduce the variance in the data (which would favour the null hypothesis of no difference between the cleaner species). In addition, we were interested in consistent variation in cleaner behaviour as an indication of whether the cleaners distinguished between predatory clients, nonpredatory resident clients and nonpredatory visiting clients. For these analyses we ran separate analyses per cleaner species in which each client species provided an independent data point that was attributed to one of the three client categories.

Statistics

Data were analysed with the statistical program R. All tests were nonparametric and two tailed.

RESULTS

Niche Description

Interactions of cleaner shrimp groups lasted on average 1.4 times longer than interactions of cleaner fish, yielding a significant difference (Wilcoxon signed rank test: $V = 130$, $N = 35$ shared client species, $P < 0.01$). However, the cleaner fish had on average 1.8 times more cleaning interactions than the cleaner shrimp groups (Mann-Whitney U test: $W = 165.5$, $N = 14$ cleaner wrasses, $M = 14$ cleaner shrimp stations, $P < 0.01$). When the frequency of cleaning interactions was taken into account, the total time of testing was similar for the two cleaner species (Mann-Whitney U test: $W = 104$, $N = 14$ cleaner wrasses, $M = 14$ cleaner shrimp stations, $P = 0.60$).

There was a significant niche overlap between the cleaner fish and the cleaner shrimp (Pianka's niche overlap index = 0.61). A total of 35 client species visited both cleaners. For the comparisons relating to service quality, we focus on these shared client species.

Jolt Frequencies

There was no significant difference in the jolt frequencies of clients when interacting with cleaner wrasse and with cleaner

shrimp (Wilcoxon signed rank test: $V = 194$, $N = 32$ shared client species, $P = 0.43$). However, we found a positive correlation between the jolt frequencies and the maximum number of shrimps cleaning the client at the same time (Spearman's rank correlation: $r_s = 0.30$, $P < 0.01$). If one corrects the jolt frequencies of clients for the number of inspecting cleaners, the clients of the cleaner shrimp jolted less frequently than the clients of the cleaner wrasse (Wilcoxon signed rank test: $V = 329$, $N = 32$ shared client species, $P < 0.05$; Fig. 1).

For both cleaner species, we found that predatory clients jolted less frequently than nonpredatory clients (Mann-Whitney U tests, for cleaner wrasse: $W = 91$, $N = 28$ nonpredatory client species, $M = 4$ predatory client species, $P < 0.05$; for cleaner shrimp: $W = 220.5$, $N = 16$ nonpredatory client species, $M = 19$ predatory client species, $P < 0.05$; Fig. 2). In contrast, there were no significant differences in the jolt rates of nonpredatory resident clients and nonpredatory visiting clients for either cleaner species (Mann-Whitney U tests, for cleaner wrasse: $W = 50$, $N = 12$ resident client species, $M = 9$ visitor client species, $P = 0.81$; for cleaner shrimp: $W = 17$, $N = 5$ resident client species, $M = 6$ visitor client species, $P = 0.78$; Fig. 2).

The Nonpredatory Clients' Responses to Jolts

The clients responded (with either a flight or an aggressive chase) more frequently to jolts caused by the wrasse (mean 45% of observations) than to jolts caused by the shrimp (mean 11% of observations) (Wilcoxon signed rank test: $V = 65$, $N = 14$ shared client species that were observed to jolt in interactions with both cleaner species, $P < 0.01$). If a client reacted, resident species showed a tendency to respond more aggressively to the cleaner wrasse (mean 25% of responses) than to the cleaner shrimp (mean 6% of responses) (Wilcoxon signed rank test: $V = 19$, $N = 6$ resident client species that responded, $P = 0.09$).

Tactile Stimulation

We did not observe any behaviour of the shrimps that would classify as tactile stimulation. As all cleaner wrasses were observed

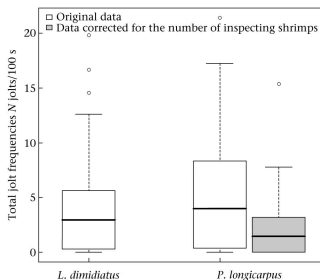


Figure 1. Box plot comparing the jolt frequencies per 100 s of 32 client species during interactions with the cleaner fish, *L. dimidiatus*, and with the cleaner shrimp, *P. longicarpus*. The jolt frequencies, in grey, are corrected for the number of inspecting cleaner shrimps.

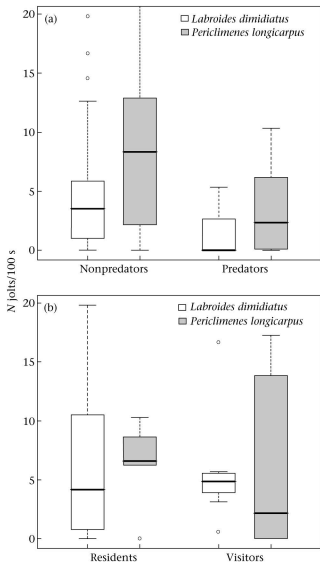


Figure 2. (a) Box plots comparing jolt frequencies per 100 s of interaction between predatory and nonpredatory clients for the cleaner fish, *L. dimidiatus*, and the cleaner shrimp, *P. longicarpus*. (b) Box plots comparing jolt frequencies per 100 s of interaction between nonpredatory resident and visitor clients for the cleaner fish ($N = 21$) and the cleaner shrimp ($N = 11$).

to provide clients with tactile stimulation, the difference was highly significant (Wilcoxon signed rank test: $V = 253$, $N = 32$ shared client species, $P < 0.001$).

DISCUSSION

In this study, we provide the first detailed observations on cleaner shrimp–client interactions in the field aiming at advancing our understanding of both their ecological importance for reef fish health and the game structure of their interactions. Overall, our results suggest that the cleaner shrimp–client relationships are quite similar to cleaner wrasse–client relationships with respect to both questions.

Niche Description

Because the shrimp stations were just as active as the wrasse stations, our study supports the hypothesis that the cleaner shrimp is an important cleaner and that it plays an ecological role similar to

that of the cleaner wrasse. The same argument has been made in earlier studies that showed that cleaner shrimps, including a species of the genus *Periclimenes*, do indeed eat ectoparasites (Becker & Grutter 2004) and that clients with access to shrimp have a low cortisol response to confinement stress, comparable to that of clients with access to cleaner wrasse (Bshary et al. 2007). Removal and translocation experiments have revealed that cleaner wrasse is a key organism for local reef diversity (Bshary 2003), with a strong influence on the movement patterns, habitat choice and activity of a wide variety of fish species (Grutter et al. 2003). Such experiments should be conducted on the cleaner shrimp in a future study. Furthermore, stomach contents of the shrimps should be analysed to evaluate their diet rather than relying entirely on data collected on other shrimp species at a different site (Becker & Grutter 2004). As the composition of clients was quite similar between both species, the extent to which the two species compete because of niche overlap and the factors that promote coexistence currently remain unclear.

Strategic Behaviour of Cleaners

We had predicted that cleaner shrimp would show an overall higher service quality than cleaner wrasse for two reasons. First, shrimps have fragile bodies and consequently should be particularly vulnerable to a client's aggressive response to cheating (Poulin & Vickery 1995). Second, we assumed that cleaner shrimps lack the basic cognitive abilities necessary to cheat clients in a strategic way: a strategic adjustment of service quality relies on the capacity to distinguish between predatory and nonpredatory client species and specifically reduce service quality for the latter class of clients. Although we did find significant differences in client jolt rates between cleaner wrasse and cleaner shrimp, this result was evident only when we corrected for the number of simultaneously inspecting cleaners. The differences based on this analysis may be confounded by interference between individuals as the number of shrimps increases, leading to both less cleaning and fewer jolts. In any case, clients jolted regularly when interacting with shrimps. At this stage we cannot exclude the possibility that, contrary to the evidence collected for cleaner fish (Bshary & Grutter 2002a; Soares et al. 2008b), client jolts do not correlate with mucus feeding by shrimps. The observation that jolts caused by shrimps elicited fewer responses by clients than jolts caused by cleaner fish suggests that the correlation between jolts and cheating might be at least weaker for cleaner shrimps than for cleaner fish. This alternative explanation remains to be tested, especially because jolts caused by shrimps were regularly followed by client aggression, suggesting that a cleaner shrimp cheated.

A further indication of the cleaner shrimps' ability to cheat clients was the clear indication that cleaner shrimps strategically adjust service quality to the risk of predation by clients, contrary to our predictions. Such strategic adjustment is apparently absent in cleaning gobies (Soares et al. 2008c), a genus that is highly dependent on cleaning interactions for its diet and that is equipped with a vertebrate brain that should be better able to process the relevant information than a shrimp brain. If cleaner shrimp were indiscriminately cooperative and client jolts were a side effect of errors in parasite removal, no such differences in client jolt rates would be predicted. Thus, the different jolt rates of nonpredatory and predatory clients suggest that the shrimp are sometimes able to cheat and actively feed on mucus instead of ectoparasites, depending on the client's identity. Such strategic adjustment of behaviour shows a further level of complexity, as previously described for cleaner wrasse only (Bshary 2001), in addition to findings from laboratory experiments showing that shrimps adjust signalling levels to their hunger state to attract clients (Becker et al.

2005). We have no specific hypothesis as to how cleaner shrimps could potentially distinguish between predatory and nonpredatory clients. Whereas piscivorous clients typically share some features necessary for fast acceleration, fish species that include small crustaceans in their diet seem to be very diverse in form and size.

Evidence for tactile stimulation remains restricted to the genus *Labroides*. In this respect, the shrimps appear to be similar to the cleaning gobies (Soares et al. 2008c). However, we noted that shrimps are constantly in body contact with the client as they walk on its surface. The walking gives a soft tickling sensation on human hands (personal observations), which may qualify as tactile stimulation by default, rendering more specific stimulation behaviours unnecessary. Measures of client heart rates and/or frequency of operculum openings as a proxy (Brown et al. 2005) may help to address the issue further: if a shrimp's walking on a client has the same effects as pelvic fin touching by a cleaner wrasse, then one could conclude that cleaner shrimps provide default massages.

In conclusion, our results are in line with the hypothesis that cleaner shrimps are key organisms for local reef fish health. In addition, we found indications that cleaner shrimp behave strategically during inspections and adapt service quality to the identity of their clients. This result raises questions about the role of cheating and partner control in this mutualism as well as about potential cognitive processes underlying the flexible service quality given by shrimp.

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