

The cleaning goby mutualism: a system without punishment, partner switching or tactile stimulation

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Keywords

cleaning goby mutualism; *Elacatinus* spp.; cheating; partner choice; partner switching; punishment; tactile stimulation.

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Editor: Jean-Nicolas Volff

Received 2 March 2008; revised 17 June 2008; accepted 23 June 2008

doi:10.1111/j.1469-7998.2008.00489.x

Abstract

In the cleanerfish–client mutualism involving the Indo-Pacific cleaner wrasse *Labroides dimidiatus* and its reef fish clients, mechanisms such as ‘tactile stimulation’, partner switching and punishment are used by clients to control cheating by cleaners. We sought to establish whether these behaviours are general features of cleaning mutualisms by examining their presence in interactions between Caribbean cleaning gobies (*Elacatinus* spp.) and their clients. The cleaning goby–client mutualism bears several similarities to the cleaner wrasse system: clients visit cleaners frequently to have their ectoparasites removed while cleaners depend heavily on these visits for food, and cheating by cleaning gobies is also prevalent. However, our data revealed striking differences between the two cleanerfish systems: clients did not seem to attempt to control cheating by cleaning gobies and cleaning gobies did not perform tactile stimulation on their clients. We suggest three hypotheses that might explain these major differences between both systems, based on differences in mutual dependence between cleaners and clients or cognitive ability of cleaners, differences in costs of being cheated and differences in foraging preferences by cleaners. Interactions between *L. dimidiatus* and its clients should probably not be seen as the ‘standard’ marine fish cleaning mutualism.

Introduction

Cooperative interactions can be viewed as a trade whenever two or more individuals exchange goods and services in order to achieve net benefits (Noë, 2001). However, reduced investment, increased exploitation and manipulation of the partner are favoured as each participant should try to maximize personal net benefits by minimizing potential risks and/or costs. These behaviours may undermine cooperation, unless they can be controlled. Cheating has always played a dominant role in theoretical models for the evolution of cooperation between unrelated individuals (Trivers, 1971; Axelrod & Hamilton, 1981) and it affects the evolutionary dynamics of interspecific mutualistic interactions (Bronstein, 2001a).

Interacting organisms can prevent cheating by choosing their trade partners carefully (Noë, van Schaik & van Hooff, 1991; Ferrière *et al.*, 2002; Bshary & Grutter, 2002a; Bshary & Noë, 2003; Noë, 2006) or by punishing cheating partners (Clutton-Brock & Parker, 1995). Partner choice is considered to be a strong selective force to prevent cheating in biological markets, in which players are predicted to prefer partners offering the highest value, while the exchange value

of commodities has to be bargained according to the market law of supply and demand (Noë, 2001).

One of the best examples of the power of both partner choice and punishment for controlling cheating is the cleaner fish–client mutualism involving the bluestreak cleaner wrasse *Labroides dimidiatus* and its reef fish clients (see Bshary, 2001; Bshary & Grutter, 2002a,b, 2005; Bshary & Noë, 2003). These cleaners are visited by fish clients at their small territories (referred to as cleaning stations) to have their ectoparasites and dead or infected tissue removed (reviewed by Côté, 2000). From a client’s perspective, a good cleaning service includes not only getting an immediate inspection but also an honest service, that is a cleaner that searches for ectoparasites and refrains from eating healthy tissue (Bshary & Noë, 2003). However, it has been shown that *L. dimidiatus* prefers mucus over ectoparasites, at least on some client species (Grutter & Bshary, 2003, 2004). Mucus protects fish against sunburn and infections (Ebran *et al.*, 1999) and its high protein content (Arnal, Côté & Morand, 2001) suggests that it might be expensive to produce. Therefore, a cleaner that eats mucus and scales inflicts costs on the client and is deemed to be cheating. Client species with access to several cleaning stations appear

to control cleaner cheating through partner choice. Individual parrotfish *Hipposcarus harid*, for example, change cleaning partners after cleaners have ignored or cheated on them (Bshary & Schäffer, 2002). In contrast, clients without a choice of cleaners use punishment to control cleaner cheating: they terminate cheating interactions with an immediate aggressive chase, which results in the punished cleaners being more honest in subsequent interactions with the punishing clients (Bshary & Grutter, 2002a).

Interactions between *L. dimidiatus* and its clients become even more complex due to the cleaners' ability to manipulate client decisions (Bshary & Würth, 2001; Grutter, 2004). These cleaners apply tactile stimulation, typically to the clients' dorsal area (with their pelvic and pectoral fins), to stop clients that are unwilling to interact, to prolong interactions with clients that are about to leave (including visitors fleeing in response to cleaner cheating), to reconcile with clients after receiving punishment and as pre-conflict management in interactions with predators (Bshary & Würth, 2001; Grutter, 2004). Tactile stimulation may thus allow cleaners to eat more mucus than the clients would accept otherwise.

We currently do not know whether punishment, partner switching and manipulation through tactile stimulation are general features of all cleaning mutualisms or whether the *L. dimidiatus* system is unique in these respects. It is therefore important to examine other cleaning mutualisms in similar detail. Here, we provide such comparative data in a detailed observational field study of the interactions between Caribbean cleaning gobies (*Elacatinus* spp.) and their clients. Cleaning gobies provide a good model for comparison with *L. dimidiatus* as their cleaning behaviour has evolved independently. In common with *L. dimidiatus*, they have cleaning stations where they wait for clients to visit, near-complete dependence on cleaning for their diet (Côté, 2000), and the ability to cheat as evidenced by the fish scales and mucus commonly found in their stomachs (Arnal & Côté, 2000; Whiteman & Côté, 2002a,b; Cheney & Côté, 2005; Soares *et al.*, 2008b). We asked the following four questions. First, do clients with broad choice options respond to cleaner cheating by swimming away while clients with narrow choice options respond with aggressive chasing? Second, are clients with broad choice options more likely to switch to another cleaning station following a negative (i.e. cheating) interaction than after an interaction without conflict? Third, do clients take longer to return to the same previous cleaner after being cheated than after receiving a good service? Finally, do cleaning gobies provide tactile stimulation to clients under similar circumstances as *L. dimidiatus* cleaners do?

Methods

Study sites and species

The study was conducted on four fringing reefs off the west coast of Barbados, West Indies, during February–August 2004 and March–November 2005. The reefs – North Bellairs,

South Bellairs, Glitter Bay and Tropicana reefs – ranged in area from 30 000 to 60 000 m², and the maximum depth was 8–9 m. All four reefs were very similar, having relatively low coral cover (~10%), high algal cover (~40%) and a typical spur-and-groove development at their seaward edge.

We studied the two species of cleaning gobies present on Barbadian reefs: the sharknose goby *Elacatinus evelynae* and broadstripe goby *Elacatinus prochilos*. Both are ubiquitous on shallow-water Caribbean reefs, associating particularly with the massive coral species *Siderastrea* spp. and *Montastrea* spp. They are small, ranging in total length from 1.2 to 3.5 cm.

We focussed on 12 different species of reef fish clients, which included seven species of parrotfish (*Scarus vetula*, *Scarus taeniopterus*, *Scarus iserti*, *Sparisoma aurofrenatum*, *Sparisoma rubripinne*, *Sparisoma chrysopterum*, *Sparisoma viride*), three damselfish (*Microspathodon chrysurus*, *Stegastes diencaeus* and *Chromis multilineata*), one goatfish *Mulloidichthys martinicus* and one surgeonfish *Acanthurus bahianus*. These species are among the most frequent customers to cleaning goby stations (see Arnal & Côté, 1998; Côté, Arnal & Reynolds, 1998; Arnal *et al.*, 2000, 2001; Whiteman & Côté, 2002a,b; Soares, Cardoso & Côté, 2007; Soares *et al.*, 2008b); however, they differ markedly in home range sizes and hence in the possibility of visiting more than one cleaning station.

Behavioural observations

Data on client behaviour were collected between 10:00 and 17:00 h through focal-follow observations of an average of 28 individual clients (9–44 individuals; Table 1) per species. Focal clients were selected haphazardly by roving scuba divers and observations began immediately upon sighting. Each individual was observed for a maximum of 60 min, with a scuba diver following the focal fish from a minimum distance of 3–5 m. Casual observations made by snorkellers at the surface suggested that fish behaviour did not appear to be altered by the presence of a nearby diver: focal fish showed no evasive action or increased swimming speed, thus continuing to feed and visit cleaning stations.

During focal follows, we noted all visits to cleaning stations by focal fish and any interactions with cleaning gobies. Specifically, we recorded (1) the duration of inspection by the cleaning goby; (2) all client jolts and client behaviour after jolting (e.g. interruption of the cleaning interaction with aggressive chasing or prompt departure); (3) any instances of tactile stimulation and client behaviour before, during and after such events and (4) the time elapsed between visits to cleaners, as well as cleaner identity (i.e. same or different cleaner in subsequent cleaning interactions). Jolts appear to be painful reactions to cleanerfish bites and have been shown to be the result of dishonest cleaning (Bshary & Grutter, 2002b; Soares *et al.*, 2008a). Each client interaction with cleaning gobies was classified as either 'negative' when the interaction ended with a client jolting or when the client left without being attended to by

Table 1 Summary of focal-follow observations of clients of cleaning gobies, including client choice options (BC, broad choice options; NC, narrow choice options), number of individuals observed, total observation time (min), number of individuals that visited cleaning goby stations, total number of cleaning interactions and number of returns to a previous cleaning station

Family	Species	Common name	Choice options	No. of followed individuals	Time spent following (min)	No. of individuals that visited stations	No. of cleaning interactions	No. of returns to previous station
Acanthuridae	<i>Acanthurus bahianus</i> (Castelnau, 1855)	Ocean surgeon	BC	24	693	4	7	0
Mullidae	<i>Mulloidichthys martinicus</i> (Cuvier, 1829)	Yellow goatfish	BC	12	518	5	13	0
Pomacentridae	<i>Chromis multilineata</i> (Guichenot, 1853)	Brown chromis	NC	9	499	10	27	12
	<i>Microspathodon chrysurus</i> (Cuvier, 1830)	Yellowtail damselfish	NC	35	1214	22	78	55
	<i>Stegastes diencaeus</i> (Jordan & Rutter, 1897)	Longfin damselfish	NC	9	600	6	30	23
Scaridae	<i>Scarus iserti</i> (Bloch, 1789)	Striped parrotfish	BC	39	1225	19	43	11
	<i>Scarus taeniopterus</i> (Desmarest, 1831)	Princess parrotfish	BC	44	1299	29	76	25
	<i>Scarus vetula</i> (Bloch & Schneider, 1801)	Queen parrotfish	BC	32	1019	22	73	23
	<i>Sparisoma aurofrenatum</i> (Valenciennes, 1840)	Redband parrotfish	BC	41	1282	25	58	22
	<i>Sparisoma chrysopterus</i> (Bloch & Schneider, 1801)	Redtail parrotfish	BC	23	607	9	26	15
	<i>Sparisoma rubripinne</i> (Valenciennes, 1840)	Yellowtail parrotfish	BC	32	898	17	57	20
	<i>Sparisoma viride</i> (Bonnaterre, 1788)	Stoplight parrotfish	BC	30	801	21	51	24

the cleaning goby, or 'positive' when clients were attended by cleaning gobies and the interaction did not end with a client jolt. We defined tactile stimulation as cleaners swimming and hovering above the client while touching it using pectoral and pelvic fins (Potts, 1973; Bshary, 2001; Bshary & Würth, 2001). Because clients were not tagged during the study, it is possible that individuals were observed more than once. However, the relatively high density of these species on each reef made this unlikely. Nevertheless, fish from different parts of the reefs were selected during the focal follows to reduce the possibility of repeat observations.

The home range of each client was mapped during the focal follows by recording the position of the focal fish, relative to obvious underwater landmarks, on maps of the study reefs at the end of each observation period. This was possible because each diver was very familiar with each of the study reefs, having carried out numerous roving surveys before the study. The longest axis of each range was used as a proxy for home range size. To verify the robustness of our home range length estimates, we plotted home range length in relation to time observed for each species. A positive association between the two variables without evidence of an asymptote would suggest that the duration of observation was insufficient to characterize the home range length.

For two species (*C. multilineata* and *A. bahianus*), it was not possible to examine this association because the observation time was constant across all individuals. For all other client species, there was either no association between the home range length and observation time, or the association was curvilinear with a clear asymptote, suggesting that the estimates of the home range length were adequate.

Statistical analysis

Clients were categorized as having more or fewer choice options on the basis of territory or home range length. In general, smaller territories or home ranges were less likely to encompass more than one cleaning station than larger territories/home ranges. The bimodal distribution of home range sizes of our study species allowed us to identify unambiguously nine of the 12 focal species as having large home ranges (mean \pm SE = 14.11 \pm 2.32 m) and broader choice options, and the remaining three species (all damselfish) as having small home ranges (mean \pm SE = 3.47 \pm 0.39 m) and narrower choice options. For a matter of accuracy and to make sure that both divers collecting jolt-related data were at the exact same level, the first 2 months of observations (during 2004) were not considered for all analyses in which cheating (i.e. jolts) was involved.

To answer our first question, that is whether the strategy used by clients to punish cheating cleaners depends on choice options, we calculated for each client species the proportions of jolting individuals that reacted by either chasing the cleaning goby or by immediately terminating the cleaning interaction and leaving the cleaning station. We then compared these responses to cleanerfish cheating between species with narrow and broad choice options using independent-samples *t*-tests.

We examined whether the nature of an interaction (i.e. negative or positive) with a cleaner influenced the likelihood of clients returning to this cleaning station on a consecutive visit (Question 2). For these analyses, we used only individual clients that had visited cleaners at least twice. For those that had visited cleaning gobies more than twice, only the first pair of visits was considered. The analyses were carried out at two levels using 2×2 contingency tables: first, overall by considering all individuals of all species observed for clients with broad choice and, separately, narrow choice options, and second, within each species, to examine whether all species followed a pattern similar to the overall pattern.

To test our third question, we considered all clients that had repeatedly visited a cleaner. We calculated the times elapsed between all consecutive visits to a given cleaner and compared these between visits that had ended positively and negatively. This was examined again at two levels using independent-samples *t*-tests: first, overall, using species averages (obtained from individual averages) separately for clients with broad and narrow choice options, and second, within species, using values from individual clients.

Results

More than half of our focal individuals visited cleaning gobies during their observation period (56.7%; $n = 187$ of a total of 330 fish; Table 1). Similar proportions of clients with broad or narrow choice options visited cleaning stations (with broad choice options: mean \pm SE = $54.5 \pm 16.9\%$ of individuals; with narrow choice options: mean \pm SE = $66.5 \pm 10.0\%$; independent-samples *t*-test: $t_{10} = -1.15$, $P = 0.28$).

Client reactions to cheating cleaning gobies

Overall, clients jolted in 41% of observed cleaning interactions. Clients with broad choice options jolted in 43.3% ($\pm 13.0\%$) of interactions compared with 33.8% ($\pm 14.5\%$) for clients with narrow choice options ($t_{10} = 1.06$, $P = 0.31$). Client jolt rate did not differ between both categories of clients (with broad choice options: mean \pm SE = 8.9 ± 6.7 jolts 100 s^{-1} of inspection; with narrow choice options: mean \pm SE = 8.0 ± 6.8 jolts 100 s^{-1} of inspection; $t_{10} = 0.20$, $P = 0.84$).

Jolting clients never chased the attending cleaning gobies, but the majority terminated interactions immediately. The overall probability of a client leaving immediately after a jolt was 93% ($n = 120$ out of 129 interactions where client jolting occurred), and this probability did not significantly

differ between clients with and without choice options (*t*-test: $t_{10} = -0.79$, $P = 0.45$). The duration of interactions between cleaner and client was similar for clients that did and did not jolt (mean duration with jolt \pm SE = 10.36 ± 4.34 ; mean duration without jolt \pm SE = 7.53 ± 1.04 ; paired *t*-test: $t_{42} = 0.48$, $P = 0.63$).

Likelihood of revisiting a cleaner in relation to nature of previous interaction

In the overall analysis, when all individuals were combined regardless of species identity, clients were not more likely to return to the same cleaner for a second inspection if the previous one had ended without conflict. This result held for clients with broad choice options (Pearson's χ^2 -test, $\chi^2_1 = 1.90$, $P = 0.17$) as well as clients with narrow choice options ($\chi^2_1 = 1.19$, $P = 0.28$). Almost one-third (30.8%, $n = 16$) of the clients with broad choice options returned to their previous cleaners after an interaction ended in conflict while 39.1% ($n = 36$) returned to the same station after the previous interaction had ended without apparent conflict. Among individuals with narrow choice options, 33.3% ($n = 7$) returned after a cheating event whereas 50.0% revisited following a positive interaction ($n = 14$). Regardless of the outcome of the previous interaction, more than half of the clients with narrow choice options (55.3%, $n = 21$) returned to their previous cleaners, while only 34.9% ($n = 52$) did so among clients with broad choice options ($\chi^2_1 = 5.28$, $P = 0.02$).

There were sufficient data for within-species analysis for 10 of the client species: *Sc. vetula* ($n = 22$ repeat visits), *Sc. taeniopterus* ($n = 29$), *Sc. iserti* ($n = 19$), *Sp. aurofrenatum* ($n = 25$), *Sp. rubripinne* ($n = 17$), *Sp. chrysopterum* ($n = 9$), *Sp. viride* ($n = 19$), *M. chrysurus* ($n = 23$), *St. dienciaeus* ($n = 6$) and *C. multilineata* ($n = 10$). An association between the likelihood of returning to a cleaning station and the outcome of a previous interaction was never observed within species ($\chi^2_1 < 2.76$, $P > 0.10$ in all cases).

Time elapsed between consecutive visits to cleaners

Overall, for both clients with broad and narrow choice options, there was no significant difference in the intervals of time between consecutive visits following a positive and a negative interaction (with broad choice options: $t_{12} = -0.52$, $P = 0.61$; with narrow choice options: $t_4 = 0.80$, $P = 0.47$). There were also no significant differences in return times to the same cleaning stations between prior positive and negative interactions in the 10 individual species for which sufficient data were available [*Sc. vetula* (positive interactions: $n = 20$; negative interactions: $n = 3$), *Sc. taeniopterus* ($n = 10, 13$), *Sc. iserti* ($n = 6, 8$), *Sp. aurofrenatum* ($n = 6, 2$), *Sp. rubripinne* ($n = 16, 4$), *Sp. chrysopterum* ($n = 13, 2$), *Sp. viride* ($n = 17, 7$), *M. chrysurus* ($n = 39, 18$), *St. dienciaeus* ($n = 13, 10$) and *C. multilineata* ($n = 9, 3$); $P > 0.08$ in all cases].

Tactile stimulation

Cleaning gobies were never observed performing any form of tactile stimulation to their clients.

Discussion

The clients of cleaning gobies did not seem to use their choice options to promote honesty in cleaning gobies, which is in clear contrast to the *L. dimidiatus* system. The likelihood and time taken to return to a cleaner that had previously cheated were not clearly linked to the outcome of that previous interaction, either in species with access to several cleaning stations or in species with restricted choice options. In addition, clients rarely chased cleaners after a cheating event, as was expected particularly of species with restricted choice options or smaller home ranges (Bshary & Grutter, 2002a). Clients do chase cleaning gobies during cleaning interactions, but this is an extremely rare event ($n = 3$ clients in a total of 2919 clients visiting cleaning stations; M. C. Soares, pers. obs.), which was not witnessed during the present study. We thus did not find any evidence that clients attempted to control cheating by cleaning gobies through partner switching, delayed revisiting of cleaning stations after a negative interaction, or through aggressive chasing of gobies after a jolt, as is observed in *L. dimidiatus*. Instead, clients of cleaning gobies, regardless of their choice options, used a simple strategy to deal with cleaner cheating: they interrupted cleaning interactions by swimming away. This strategy is reminiscent of sanctions, that is curtailment of investment by one partner in the face of cheating by the other partner, which have been shown to be effective in maintaining the stability of interspecific mutualisms (e.g. West *et al.*, 2002a,b).

The differences noted between cleaning gobies and cleaner wrasses are unlikely to stem from methodological differences in the studies of the two systems. We followed a behavioural observation protocol that was similar to that of Bshary & Schäffer (2002), who detailed the strategies used by clients of cleaner wrasses to control cleaner cheating. Their study was carried out using snorkelling, whereas ours required diving because of the depth of the sites, although in both cases, there was no evidence that fish were disturbed by observers. Bshary & Schäffer (2002) followed individual clients for 90–120 min, whereas ours were followed for 60 min, but the same behavioural events were recorded. The largest difference between the studies is that while Bshary & Schäffer (2002) focused on a single species of client – the parrotfish *H. harid* – with large home ranges and choice options of cleaners (43 individuals, total observation time: 56 h), we observed 12 different client species that differed in home range sizes and choice options [330 individuals (including 241 parrotfish), total observation time: 177 h]. The inclusion of multiple client species in our study allowed us to investigate more thoroughly the generality of the previously reported patterns. However, this also created the potential issues of phylogenetic relatedness among species. The distinction between client species with and

without choice options unfortunately fell almost strictly along family lines, that is clients with options were mainly parrotfishes and clients without options were damselfishes, thus precluding phylogenetically controlled analyses. However, results of within-species analyses supported those of cross-species analyses, suggesting a lack of phylogenetic artefact.

A clear difference uncovered between *L. dimidiatus* and cleaning gobies is the fact that the latter do not seem to perform tactile stimulation on their clients. Yet, cleaning gobies commonly face situations similar to those experienced by *L. dimidiatus*, during which the latter are frequently observed to manipulate their clients. While we cannot give a conclusive explanation as to why the two cleaning systems are so different, we present three ‘non-mutually’ exclusive hypotheses that may account for the differences and which are amenable for future research. The hypotheses are based on (1) constraints, (2) low costs of being cheated and (3) cleaning goby foraging preferences.

(1) *The constraint hypothesis*: Two potential constraints may explain why the cleaning goby mutualism might not have yet evolved to the complexity observed in the *L. dimidiatus* system. (a) *Possible constraints due to lower dependency*: Cleaning gobies depend less on cleaning interactions for their diet than *L. dimidiatus*. In the latter species, individuals gain more than 99% of their diet from cleaning interactions while among cleaning gobies, ‘only’ 85% of their diet is gained through cleaning (Arnal & Côté, 2000; Côté, 2000; Whiteman & Côté, 2002b). Lower levels of dependency on cleaning may have exerted weaker selection for client manipulation through tactile stimulation. Clients of cleaning gobies may also depend less on cleaners. We found that some individual fish visited cleaning stations up to 16 times per hour. This translates, by rough extrapolation to a 12-h-long day, into nearly 200 daily visits by some individual clients to cleaning stations, which is similar to that observed for some clients of *L. dimidiatus* (144 times a day; Grutter, 1995). However, most clients of cleaning gobies should visit far less frequently than this as parasite loads of fish across the Caribbean (Sikkel, Fuller & Hunte, 2000; Cheney & Côté, 2001, 2005) are much lower than those found on fish clients in Australia and visits rates are usually linked to parasite loads (Grutter, 1995, 1996, 1999; Bansemmer, Grutter & Poulin, 2002). (b) *Possible cognitive constraints*: Punishment is not a simple control mechanism as it relies on highly developed cognitive abilities. The punished individual must be able to remember the interaction and the punisher’s identity so that it can adjust its behaviour during future interactions with the punisher. The punisher, on the other hand, must not fall in the psychological trap of disregarding future benefits, which would reduce the willingness to incur an immediate cost for the act of punishment (Clutton-Brock & Parker, 1995; Stevens & Stephens, 2002). It is not immediately obvious as to why Indo-Pacific fish possess all the prerequisites for punishment to be effectively imposed while Caribbean fish might lack the necessary cognitive basis. One possible explanation might be that lower parasite loads in the Caribbean lead to longer

time intervals between consecutive visits to cleaning stations by individual clients, which exceed the memory limits of cleaners and/or result in too much discounting of the future by clients.

(2) *The low cost of being cheated hypothesis*: Bronstein (2001a,b) and Bronstein (2003) suggested that the costs of most kinds of cheating associated with mutualisms are low or perhaps even negligible. It is well known that cleaning gobies can cheat, as scales and mucus are often prevalent in goby stomach contents (Arnal & Côté, 2000; Whiteman & Côté, 2002a,b; Cheney & Côté, 2005; Soares *et al.*, 2008b, unpubl. data), but the actual cost to clients of losing these items to cleaners is currently unmeasured. The small size of cleaning gobies (up to 4 cm), compared with the wrasse *L. dimidiatus* (12 cm), may limit the impact of their cheating, at least in terms of the capacity to cause injuries. It is therefore possible that the persistence of cleaner cheating, alongside an apparent absence of client strategies to enforce cleaner honesty, may be due to the inability of cleaning gobies to inflict significant fitness costs on their partners.

(3) *The foraging preference hypothesis*: An important feature of the *L. dimidiatus* system is the preference by these wrasses for client mucus over ectoparasites (Grutter & Bshary, 2003, 2004). At the moment, the foraging preferences of cleaning gobies are unknown. Results of previous studies (Arnal *et al.*, 2001) suggest that cleaning gobies may prefer client ectoparasites over client mucus. Such a foraging preference would ensure that cleaning gobies begin all interactions cooperatively and only switch to mucus and scale eating at later stages when ectoparasites become rare (see Arnal *et al.*, 2001 for a similar argument). In this scenario, a jolt-inducing bite by the goby might inform the client that the goby is unable to find more parasites and that it is time to leave. Causing a client to jolt could also reflect the cleaning goby's selfish intention to make the client leave to create a vacancy for new clients. Both ideas would predict the observed similar duration of inspections with and without jolts. This hypothesis could also explain the absence of benefit to cleaning gobies in manipulating their clients' decisions, as clients that are unwilling to interact or ready to leave may have fewer parasites and are thus unattractive food sources.

In summary, the interactions between cleaning gobies and their clients are strikingly different from interactions between the cleaner wrasse *L. dimidiatus* and their clients. Currently, we can only offer hypotheses that may explain these differences. Future research on the constraint hypothesis should involve a comparison of visit frequencies coupled with memory tasks and temporal discounting tasks to shed light on potential cognitive constraints in cleaning gobies. It would also be interesting to conduct a large-scale comparison of cleaner fish species that vary with respect to their degree of dependency on cleaning interactions for their diet. In any case, the results from the present study indicate clearly that the *L. dimidiatus* cleaning mutualism should not be seen as the 'standard' marine fish cleaning mutualism. Instead, further comparisons of different cleaner fish mutualisms are necessary to be able to extract general principles underlying this mutualism complex.

Acknowledgements

We thank the staff of the Bellairs Research Institute for logistical support, and Kevin Foster and an anonymous reviewer for constructive criticism of the paper. M.C.S. was supported by Fundação para a Ciência e a Tecnologia studentship from the Portuguese Ministry of Science and Technology. R.B. is supported by the Swiss Science Foundation. I.M.C. is supported by the Natural Science and Engineering Research Council of Canada. The data collection complied with the laws of Barbados.

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