Indo-Pacific parrotfish exert partner choice in interactions with cleanerfish but Caribbean parrotfish do not

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ARTICLE INFO

Cooperation theory puts a strong emphasis on partner control mechanisms that have evolved to stabilize cooperation against the temptation of cheating. The marine cleaning mutualism between the Indo-Pacific bluestreak cleaner wrasse, *Labroides dimidiatus*, and its reef fish 'clients' has been a model system to study partner control mechanisms and counterstrategies. These cleaners cooperate by eating ectoparasites; however, they can cheat by taking client mucus, which they prefer. Such a conflict may be the exception. For example, Caribbean cleaning gobies, *Elacatinus* spp., prefer to eat ectoparasites instead of mucus. While partner control mechanisms and counterstrategies seem to be absent in cleaning gobies, no study has directly compared cleaner wrasses and cleaning gobies by using the same methods. We examined systematic differences in cleaning interaction patterns and strategic behaviour exhibited by 12 closely related parrotfish species in the two systems. Parrotfish seeking cleaner wrasses visited them more often and spent more time with their cleaner than parrotfish seeking cleaning gobies. Moreover, the clients of cleaner wrasses returned more often to the same cleaner following a positive interaction, whereas the clients of cleaning gobies were less influenced by the outcome of previous interactions. We hypothesize that the higher frequency and repeated nature of interactions observed in the cleaner wrasse system, combined with the need to resolve conflicts, might have been prerequisites for the development of complex behavioural strategies.

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Cooperation theory places a strong emphasis on how cheating can undermine the stability of cooperation (Axelrod & Hamilton 1981). To maintain the continuing net benefit of cooperative partnerships, the risk of cheating can be reduced through the use of various strategies (Noë 2006), such as careful partner choice (Noë et al. 1991; Bshary & Grutter 2002a, b; Ferrière et al. 2002; Bshary & Noë 2003; Noë 2006) or trying to exclude cheaters by passive partner choice (sanctioning; Kiers et al. 2003), actively switching partners if a partner cheats (Bshary & Schäffer 2002; Ferrière et al. 2002; Bshary & Grutter 2005; Johnstone & Bshary 2008) and/or punishing cheaters (Clutton-Brock & Parker 1995).

In cleaning mutualisms, conflicts between Indo-Pacific bluestreak cleaner wrasse, *Labroides dimidiatus*, the classic model for cleaning interactions, and their clients over service quality are common. Cleaning interactions entail individual fish clients repeatedly visiting the territories (i.e. cleaning stations) held by

cleaners, to have their ectoparasites and dead or infected tissues removed (reviewed by Côté 2000). However, while cleaners search the body and gills of their clients (i.e. while they 'inspect'), they often feed instead on healthy tissue, scales and mucus, which constitutes cheating (Grutter & Bshary 2003, 2004). To enforce good cleaning service quality, clients use partner control mechanisms, while the specific nature of these mechanisms depends on a client's strategic options (Bshary & Bronstein 2011). For example, predators exert the 'threat of reciprocity' in which they could retaliate on cheating cleaners by eating them. On the other hand, nonpredatory clients punish cheaters by aggressive chasing unless they have access to several cleaning stations, in which case they simply switch cleaners (Bshary & Grutter 2002a, 2005). Furthermore, potential clients may observe the cleaner's services on other fish and thus avoid cheating cleaners (Pinto et al. 2011). Cleaner wrasses, in return, can manipulate client decisions by rubbing their pelvic and pectoral fins on their client's dorsal area (Bshary & Würth 2001; Grutter 2004). Such tactile stimulation has several effects: it makes clients that are initially unwilling to interact stop for inspection, it allows cleaners to prolong interactions with clients that are about to leave, it serves as preconflict management in

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interactions with predators and it allows cheating cleaners that have been punished to reconcile with their clients (Bshary & Würth 2001; Grutter 2004). Clients appear to accept tactile stimulation as payment since it lowers baseline and acute stress levels (e.g. cortisol levels; Soares et al. 2011), an effect that at least in humans is used as an indicator of improved health (Field 1996; Field et al. 2005).

These control mechanisms do not exist in all cleaning mutualisms. A comparison between various cleaner wrasse species in the Red Sea suggests that cleaning evolved as a by-product mutualism (Brown 1983), in which cleaners initially grazed and ingested small benthic invertebrates and later picked these food items from fish, while more complex behavioural interactions and signalling might have evolved only in more specialized species (Barbu et al. 2011). For example, in Caribbean cleaning gobies, *Elacatinus* spp., the level of conflict between cleaners and clients appears to be lower than in the cleaner wrasse system (Soares et al. 2008c, 2010). Indeed, Soares et al. (2008c) found no evidence for punishment, partner switching and manipulation through tactile stimulation. The absence of control strategies and counterstrategies may be explained by the foraging preferences of cleaning gobies: in contrast to cleaner wrasses, cleaning gobies prefer ectoparasites over mucus (Soares et al. 2010). Nevertheless, gobies still eat some mucus from their clients, which is confirmed by clients' jolting behaviour. Jolts are whole-body shudders that occur in response to cleanerfish mouth contact, and their frequency appears to be a good correlate of cheating by cleaners, since they are largely absent when the client is parasitized and frequent when the client is parasite-free (Bshary & Grutter 2002b; Soares et al. 2008b). Moreover, in both systems client jolt frequency is reduced when cleaners inspect in pairs rather than on their own (Bshary et al. 2008; Soares et al. 2009). Thus, there are both similarities and dissimilarities between the cleaner species with respect to cheating behaviour.

In this study, we carried out a first direct comparison between Indo-Pacific cleaner wrasses and Caribbean cleaning gobies. To exclude potential effects of differences in client composition, we focused on the family Scaridae (parrotfish). Parrotfish are ideal for a comparison because members of this family are found in both oceans. Moreover, representatives of some genera (e.g. the genus *Scarus*) are present in both regions; thus *Scarus* species exposed to cleaners in different oceans are more closely related to each other than they are to other sympatric parrotfish species. Using identical methods, we quantified the degree to which parrotfish clients depend on cleaning, the use of tactile stimulation, the extent of cheating and the use of partner switching to control cheating in each system. The notion that client species with access to several cleaner wrasses exert partner choice is based on observations of a single parrotfish species, namely *Hipposcarus harid* (Bshary & Schäffer 2002). Thus, our study allowed us to compare the two cleaning mutualisms and also to evaluate how general partner switching is as a strategy against cheating by cleanerfish.

METHODS

Study Sites and Species

Our study focused on Caribbean cleaning gobies and Indo-Pacific bluestreak cleaner wrasses. In the Caribbean, observations were conducted on four fringing reefs off the west coast of Barbados, West Indies, between March and November 2005. All reefs showed a typical spur-and-groove development at their seaward edge, and all were degraded, with relatively low live coral cover and high algal cover. In the Red Sea, behavioural observations were carried out in Mersa Bareika (Egypt), a protected bay with many reef patches within Ras Mohammed National Park. Three sets

of observations were obtained: between May and July in 1998 and 1999 and between August and October in 2009. Approval for the study was obtained from the Portuguese National Authority for Animal Health (oficio circular no. 9–0420/000/000, 20 January 2011) and the Egyptian Environmental Affairs Agency.

At both locations, we focused on the commonest species of parrotfish on the study reefs. In Barbados the species included members of the genera *Scarus* and *Sparisoma*: *Scarus vetula*, *Scarus taeniopterus*, *Scarus iserti*, *Sparisoma aurofrenatum*, *Sparisoma rubripinne*, *Sparisoma chrysopterum* and *Sparisoma viride*, while in Egypt the species also included the genus *Scarus* but also representatives of the genera *Chlorurus* and *Hipposcarus*: *Chlorurus sordidus*, *H. harid*, *Scarus gibbus*, *Scarus niger* and *Scarus ferrugineus*. In total, our focal species belong to two clades: one comprising the genus *Sparisoma* and the other comprising all other genera. All these species exhibit sex change, switching from a relatively drab-coloured initial phase characteristic of females (and primary males in some species) to a brilliantly coloured, usually larger male terminal phase (Deloach 1999).

Behavioural Observations

Data on parrotfish behaviour were collected throughout the day (0600–1700 hours) through focal follow observations of an average of 30 individuals per species at each location. Focal clients were selected haphazardly by snorkellers or roving scuba divers and observations began immediately upon sighting. Each individual was observed for a maximum of 90 min, with a snorkeller diver or a scuba diver following the focal parrotfish from a minimum distance of 3–5 m. During focal follows, we noted all visits to cleaning stations by focal fish and any interactions with cleaners. Specifically, we recorded (1) the duration of inspection by the cleaner, (2) all client jolts and parrotfish behaviour after jolting (e.g. interruption of the cleaning interaction with prompt departure) and (3) any instances of tactile stimulation by cleaners and parrotfish behaviour before, during and after such events. Each client interaction with cleaners was classified as either 'negative' when the interaction ended with a client swimming away after a jolt, or 'positive' when clients were attended by cleaners and the interaction did not end with a client jolt. We defined tactile stimulation as occurring when cleaners hovered above the client while touching it using pectoral and pelvic fins (Potts 1973; Bshary & Würth 2001). Because clients were not tagged during the study, it is possible that individuals were observed more than once. However, we selected parrotfish from different parts of the reefs during the focal follows to reduce the possibility of repeated observations.

Statistical Analysis

To measure the degree to which parrotfish clients depend on cleaning, the use of tactile stimulation and the extent of cheating, we calculated mean values for each parrotfish species for (1) the frequency of parrotfish visits to cleaning stations (number of visits per 10 min observation), (2) the mean duration of inspection by cleaners (mean length of inspection bouts for each parrotfish, and then an overall mean per species), (3) the proportion of interactions in which the cleaners used tactile stimulation on clients (calculated for each individual, and then averaged within species), and (4) the frequency of jolts (number of jolts per 100 s of inspection). We first investigated the influence of time of day (morning versus afternoon observations), using just the data collected in 2009, on inspection duration, client jolt rates and the proportion of tactile stimulation provided and found no differences (independent-samples t tests: inspection duration: $t_{304} = -1.53$, $P = 0.12$; frequency of jolts: $t_{304} = -0.65$, $P = 0.52$; proportion of interactions with tactile

stimulation: $t_{304} = -1.65$, $P = 0.10$). Similarly, we tested for influence of client size on these three behavioural variables and found no significant relationships (Pearson correlations: inspection duration: $r_{306} = -0.02$, $P = 0.71$; frequency of jolts: $r_{306} = 0.007$, $P = 0.91$; proportion of interactions with tactile stimulation: $r_{306} = 0.008$, $P = 0.89$). Time of day and client size were therefore not considered further.

We then compared the species-specific means (seven species in Caribbean versus five species in Red Sea) between cleanerfish systems with independent-samples t tests. In the case of the proportion of interactions with tactile stimulation, we used a t test with unequal variances. To examine the effect of service quality on client return probabilities, we selected only observations in which the focal parrotfish experienced both a positive interaction (i.e. it left the cleaner without jolting) and a negative interaction (i.e. it left immediately after jolting). We calculated for each species the proportion of parrotfish returns after positive events (number of returns after positive events divided by the sum of all interactions with positive outcome) and the proportion of parrotfish returns after negative events (number of returns after negative events divided by the sum of all interactions with negative outcome). We then used paired t tests to compare species' return probabilities for each cleanerfish system.

RESULTS

Overall, parrotfish seeking cleaner wrasses visited cleaning stations more often (independent-samples t test: $t_{10} = 5.88$, $P < 0.001$; Fig. 1a) and spent significantly more time being inspected ($t_{10} = 2.53$, $P = 0.03$; Fig. 1b) than parrotfish seeking cleaning gobies. In addition, a larger proportion of parrotfish interactions with cleaner wrasses entailed tactile stimulation, while tactile stimulation was never provided by Caribbean cleaning gobies (t test for unequal variances: $t_{10} = 3.8$, $P = 0.02$; Fig. 1c). In contrast, jolt rates did not differ significantly between clients of cleaner wrasses and cleaning gobies (mean $\pm$ SEM: cleaner wrasses: 14.49 ± 6.44 jolts per 100 s inspection; cleaning gobies: 20.27 ± 4.55 jolts per 100 s inspection; $t_{10} = -0.76$, $P = 0.47$).

Parrotfish visiting cleaner wrasses were more likely to return to the same cleaner for a second inspection when the previous interaction had been positive (paired t test: $t_4 = 3.50$, $P = 0.02$; Fig. 2a) than parrotfish visiting cleaning gobies ($t_6 = 0.002$, $P = 0.99$; Fig. 2b).

DISCUSSION

Fish clients interacting with Red Sea cleaner wrasses behaved differently from those interacting with Caribbean cleaning gobies,
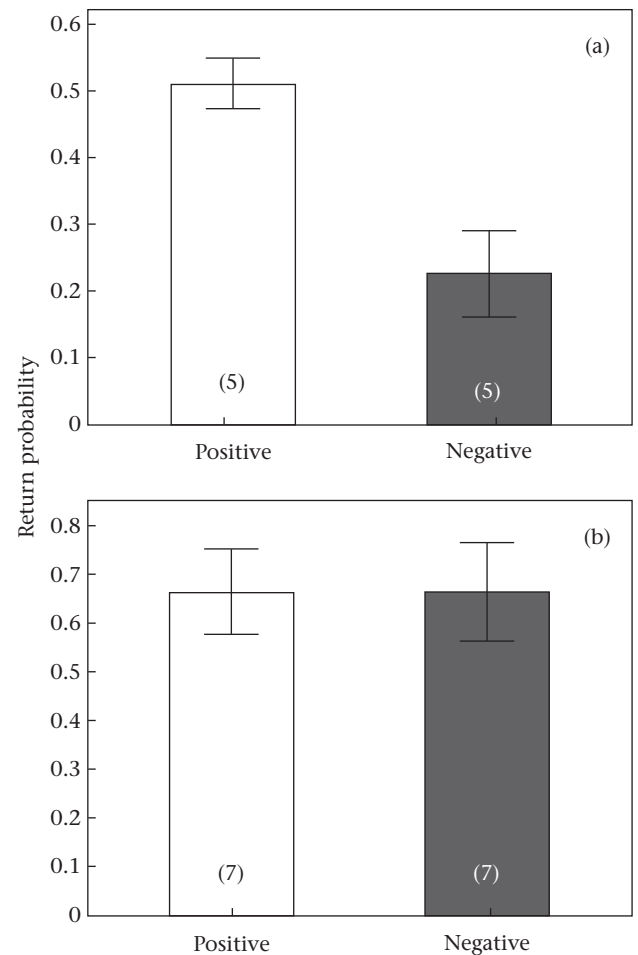

Figure 2. The probability of returning to the same cleaner after a positive event and after a negative event (on a consecutive visit) for parrotfish species interacting with: (a) cleaner wrasses, *Labroides dimidiatus*, in the Red Sea and (b) cleaning gobies (*Elacatinus* spp.) in the Caribbean (see the Methods for more detailed explanation). Sample sizes are given in parentheses. Means are shown ± 1 SEM.

and these differences did not arise solely from differences in client identity. Focusing solely on parrotfish species, several of which are closely related across ocean basins, we found that clients of cleaner wrasses visited cleaning stations more often, spent more time with them and were more likely to switch partners in response to a poor service than the clients of cleaning gobies. Thus, while parrotfish
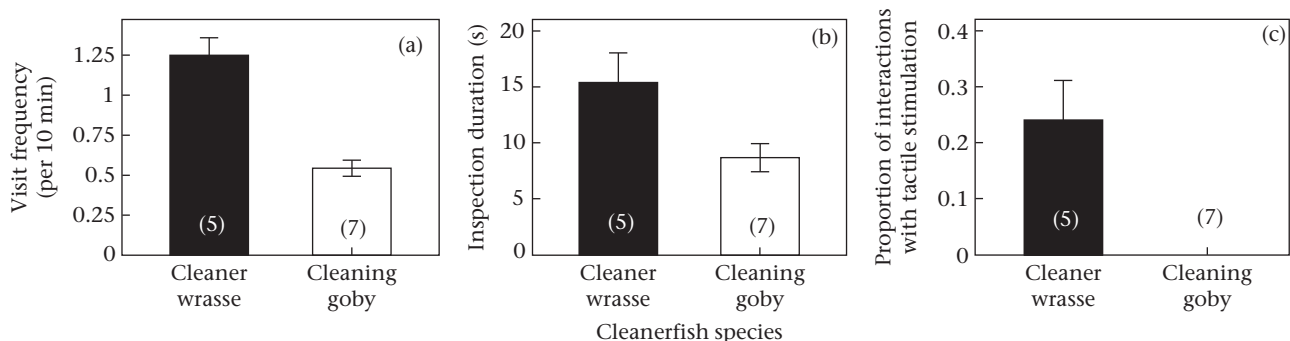

Figure 1. Behavioural responses of parrotfish species interacting with cleaner wrasses, *Labroides dimidiatus*, in the Red Sea (black bars) and cleaning gobies (*Elacatinus* spp.) in the Caribbean (white bars), in terms of: (a) client visit frequency to cleaning stations (per 10 min of observation), (b) inspection duration (s) and (c) proportion of interactions in which tactile stimulation was applied to clients (number of cleaning events in which cleaner performed tactile stimulation/total number of cleaning events). Sample sizes (number of client species; each contributing species mean comprises observations of about 30 individuals) are given in parentheses. Means are shown ± 1 SEM.

visiting cleaner wrasses were more likely to return to the same cleaner if the interaction had ended without conflict (see also Bshary & Schäffer 2002), parrotfish visiting cleaning gobies did not seem to distinguish between interactions that ended with and without conflict. This appears to be consistent among other clients of cleaning gobies (Soares et al. 2008c). Thus, the parrotfish clients of cleaner wrasses seem to use partner switching as a control mechanism against cheating while parrotfish clients of cleaning gobies do not.

Are the differences observed between the two cleanerfish systems idiosyncratic site-specific differences rather than fundamental biological differences? We do not think so. The behavioural metrics we compared are widely used in studies of cleaning mutualisms, so some information about visit frequency and/or inspection duration is available to examine within-system geographical variation. For the Caribbean damselfish, *Stegastes diencaeus*, interacting with *Elacatinus evelynae*, Cheney & Côté (2005) reported a range of inspection durations of 9–20 s per 30 min across six Caribbean islands spanning the region, with Barbados being in the middle of the group. If these data are representative of Caribbean parrotfish (for which there are only data from Barbados), then our estimates of parrotfish inspection durations, obtained at an 'average' location in the Caribbean, could vary by about 50% (up or down), depending on location. Observations of interactions between Indo-Pacific bullethead parrotfish, *C. sordidus*, and *L. dimidiatus* available from several sites spanning both oceans in their ranges (see Table 1) suggest some variation in visit frequencies and inspection durations. However, given the magnitude of the differences observed here (i.e. behavioural metrics were 2–2.5 times higher for Indo-Pacific parrotfish), it seems unlikely that parrotfish at many locations in the Caribbean visit cleaners more often and for longer than parrotfish at many locations in the Indo-Pacific. Also, it seems that data from different locations all fit into one picture (Red Sea: Bshary & Schäffer 2002; Australia: Pinto et al. 2011; Moorea: Adam 2010), suggesting that the results presented in this study are of general validity. Nevertheless, future studies should confirm the general applicability of our results by extending observations to other sites in the Indo-Pacific and Caribbean regions.

The pattern of partner switching in the two-cleanerfish systems is consistent with earlier studies of foraging preferences, which documented conflict between cleaners and clients in Indo-Pacific cleaner wrasses but not in the Caribbean cleaning gobies. The former prefer mucus over ectoparasites when given an unconstrained choice between the two whereas the reverse is true for cleaning gobies (Grutter & Bshary 2003; Soares et al. 2010). In addition, the partner control strategies used by clients of cleaner wrasses may partially explain why these cleaners have evolved tactile stimulation to manipulate client decisions. This counterstrategy to partner control is used as a means of reconciliation after

feeding on client mucus (Bshary & Würth 2001; Grutter 2004). Given the presence of reconciliation strategies in cleaner wrasses, we expected the jolt rates to be higher for the clients of cleaner wrasses than for those of cleaning gobies since wrasses can immediately atone for their misbehaviour. However, we did not find any difference. The lack of differences in client jolt frequencies may potentially be explained by geographical differences in ectoparasite levels. Ectoparasite loads are one of the main factors driving fish clients to seek cleaners in the wild and a good predictor of the time spent by clients at cleaning stations (Côté & Molloy 2003; Sikkel et al. 2004). In Barbados, our study site in the Caribbean, ectoparasite abundance is very low at a regional scale (Cheney & Côté 2005) and compared to the Red Sea study site (Soares et al. 2008a). It is possible that low parasite loads prompt cleaning gobies to cheat because of the difficulty in finding their preferred food items, while higher ectoparasite loads in the Red Sea make it advantageous for wrasses to forage against their preference (Johnstone & Bshary 2002; Bshary et al. 2008). These opposing forces could lead to similar client jolt rates despite the differences in food preferences between cleaner species.

Game-theoretic models assume that individuals act like rational or pseudorational players, i.e. having access to full information at no cost (Nowak 2012). However, optimal behaviour may change when explicit mechanisms and costs of information are included (or excluded) in the decision-making process (Fawcett et al. 2013). The differences between the cleaner wrasse and cleaning goby systems could arise if the clients of cleaning gobies are somehow constrained in showing more sophisticated control strategies. With respect to partner switching, Bshary & Schäffer (2002) found that the likelihood of long-nose parrotfish, *Hipposcarus longiceps*, revisiting a cleaner wrasse was no longer affected by the outcome of prior interactions if the time interval to the next inspection exceeded 5 min. Thus, the fact that Caribbean parrotfish visited cleaning gobies less frequently than their Red Sea counterparts (once per 20 min for Caribbean parrotfish versus once per 8 min, on average, for Red Sea parrotfish; see Fig. 1) raises the possibility that memory constraints led to a lack of partner switching in response to poor service quality in the clients of cleaning gobies. Prolonged intervals between consecutive interactions have also been proposed to alter the clients' strategic options in the mutualism involving the roving cleaner wrasse *Labroides bicolor*: roving might allow these interactions to function as one-off encounters since partners will not remember the outcome of their last interaction when they meet again (Dugatkin & Wilson 1991; Oates et al. 2010a, b). The higher frequency and repeated nature of the interactions between clients and cleaner wrasses and the need to resolve conflicts and adjust investments might have been prerequisites for the development of higher cognitive abilities not only in cleaner wrasse (Bshary 2011; Salwiczek & Bshary 2011; Salwiczek et al. 2012) but also in their clients.

Further research should focus on the direct cognitive consequences of interacting with different cleanerfish species that vary in their levels of cheating and manipulation skills to determine whether the emergence of sophisticated control decisions is linked to cleaning interactions. The ability to cooperate and deceive in the context of mutualistic and cooperative interactions might play an important role in the evolution of species' cognitive capacities.

Table 1
Frequency of visits and inspection duration by Indo-Pacific bullethead parrotfish, *Chlorurus sordidus*, to the cleaning stations of the Indo-Pacific cleaner wrasse, *Labroides dimidiatus*

Locations	Frequency of visits (visits per 30 min)	Inspection duration (s per 30 min)	Source
Lizard Island (Australia)	3.8	30.0	Grutter 1995
Wakatobi (Indonesia)	4.4	37.2	I. M. Coté, unpublished data
Hoga Island (Indonesia)	2.2	42.0	Soares et al. 2008c
Guam	7.2	51.9	Soares et al. 2008c
Egypt	2.3	32.7	Present study

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