

Does Competition for Clients Increase Service Quality in Cleaning Gobies?

Marta C. Soares[†], Redouan Bshary[†], Sónia C. Cardoso[‡] & Isabelle M. Côté[§]

[†] Institut de Zoologie, Eco-Ethologie, Université de Neuchâtel, Neuchâtel, Switzerland

[‡] School of Biological Sciences, University of East Anglia, Norwich, UK

[§] Department of Biological Sciences, Simon Fraser University, Burnaby, BC, Canada

Correspondence and present address

Marta C. Soares, Unidade de Investigação em Eco-Etologia, Instituto Superior de Psicologia Aplicada, Rua Jardim do Tabaco 34, 1149-041 Lisboa, Portugal and Department of Zoology, University of Neuchâtel, Emile-Argand 11, 2009 Neuchâtel, Switzerland.
E-mail: MSoares@ispa.pt (M. C. Soares)

Received: September 17, 2007

Initial acceptance: October 8, 2007

Final acceptance: February 22, 2008

(K. Reinhold)

doi: 10.1111/j.1439-0310.2008.01510.x

Abstract

In a biological market, members of one trading class try to outbid each other to gain access to the most valuable partners. Competition within class can thus force individuals to trade goods or services more cheaply, ultimately resulting in conflict (e.g. cheating) over the value of commodities. Cleaning symbioses among fish appear to be good examples of biological markets. However, the existence and effect of outbidding competition among either types of traders (cleaners or clients) have never been tested. We examined whether increasing competition among cleaning gobies (*Elacatinus* spp.) for access to clients results in outbidding in the form of provision of a better cleaning service. On reefs where fish clients visited cleaning stations less frequently, and thus competition among cleaners was higher, cleaning gobies ingested fewer scales relative to the number of ingested parasites, i.e. they cleaned more honestly. This shift in cleaner behaviour towards greater honesty is consistent with a greater market value of access to clients in the face of competition among cleaners. However, this pattern could have also arisen as a result of differences in ectoparasite availability across reefs and therefore in value of the commodity offered by clients. Experimental manipulations will be required to determine whether cleaning service quality by cleaning gobies was enhanced solely because of competitive outbidding.

Introduction

The idea of biological markets is emerging as a key paradigm to understand cooperation among unrelated individuals. In biological markets, two classes of traders exchange commodities to their mutual benefit. Such markets exhibit three defining characteristics: (1) competition within trader classes by contest or outbidding, (2) preference for partners offering the highest value, and (3) conflicts over the exchange value of commodities (see Noë & Hammerstein 1994; Noë 2001, 2006). The latter two characteristics have been demonstrated empirically in a variety of natural systems. For example, the mutual-

istic relationship between ants and lycaenid butterflies is based on an exchange of protection for nutrients (reviewed by Pierce et al. 2002). However, while ants would benefit from receiving higher quantities of secretions, these are costly for the butterflies to produce (Pierce et al. 2002); hence the number of droplets secreted by the butterflies and the levels of protection given by ants are both governed by the laws of supply and demand (Noë 2001).

In a biological market scenario, competition for access to the most valuable partners rarely takes an agonistic form. Instead, members of a given class will attempt to outbid each other for the most attractive

partner (Noë & Hammerstein 1994). There is ample evidence of supply and demand and outbidding competition as driving forces in mating markets (see review by Grossbard-Shechtman 1993) but both have been less often demonstrated in other contexts. One of the clearest, non-mating examples of outbidding competition is again an ant-lycaenid mutualism, specifically between the larvae of *Polyommatus icarus* and *Lasius* ants, in which the amount of nectar produced by each larva depends on the total number of attending ants (Axén et al. 1996). When fewer ants are present, the butterfly larvae compete with each other to attract ants by increasing the amount of nectar produced (see Noë 2001).

Hence, changes in the supply and demand ratio (i.e. competition levels) of a commodity can shift the direction of any exchange rate (Bshary & Noë 2003; Noë 2006) by altering its value and thus its trading costs (Noë 2001). For instance, increasing competition within one trader class may force individuals in that class to exchange their services for a lower exchange rate (Noë et al. 1991; Noë & Hammerstein 1994; Noë 2001, 2006), which will eventually produce a decrease in their individual fitness (Pfenning et al. 2007). These shifts in the extent of accessibility or value of any commodity, which are produced by dynamic supply and demand, can give rise to several forms of conflict between trader classes, particularly in the propensity of certain trading partners to cheat. Cheating will occur between trading partners when one partner (predictably the one which offers the service or commodity in highest demand) deceives the other by providing a dishonest or incomplete service (Dugatkin 1997, 2002; Noë 2001, 2006; Bshary & Noë 2003; Sachs et al. 2004).

Cleaning symbioses among fish have been considered to be a good example of biological markets (Bshary 2001; Bshary & Noë 2003). In cleaning symbioses, two main protagonists exchange services: the cleaner fish and their clients. Cleaners offer to remove parasites (and thus obtain an easy meal) and clients provide the parasites on their body and benefit from their removal. There is evidence of preference for high-value traders: Caribbean cleaning gobies (*Elacatinus* spp.), for example, are known to inspect preferentially clients species with more ectoparasites (Soares et al. 2007) and client fish prefer Indo-Pacific cleaner wrasses (*Labroides dimidiatus*) that provide a better cleaning service (Bshary & Schäffer 2002). There is also evidence for trade conflicts: cleaners will readily remove not only their clients' ectoparasites but also their scales and mucus (Arnal & Côté 2000; Bshary & Grutter 2002;

Whiteman & Côté 2002a,b; Grutter & Bshary 2003, 2004; Cheney & Côté 2005). The relative proportions of honest vs. dishonest cleaning (i.e. cheating) provided by cleaners could form the basis of market competition among cleaners, but the presence and effect of competition among traders have not yet been examined in any cleaning market.

In this study, we investigated whether competition among cleaners for access to clients results in a better cleaning service quality for clients during cleaning interactions. We used the cleaning symbiosis involving Caribbean cleaning gobies (*Elacatinus* spp.) and their clients as a model system. These species are found on shallow-water coral reefs, and separate reefs hold separate populations of cleaning gobies and of most of their clients. Reefs differ in availability of coral habitat, which is necessary for the establishment of cleaning stations (Whiteman & Côté 2004), in population sizes of both cleaners and clients (M. C. Soares, pers. obs.), as well as in ectoparasite loads of clients (Cheney & Côté 2005). These differences should generate variation in the intensity of competition among cleaners to access food resources (i.e. clients). Decreased supply of a limiting food source (i.e. ectoparasites) should increase the value of that resource, thereby increasing competition among cleaners and thus the value of the commodity (i.e. honest cleaning) the cleaners are willing to offer in return. As such, we predicted that decreased client visit frequency should lead to increased keenness by cleaning gobies to interact with clients and higher rates of honest cleaning. We tested these predictions with field observations of interactions between cleaners and clients on eight Barbadian coral reefs.

Methods

Study sites and species

The study was carried out on eight fringing reefs on the west coast of Barbados, West Indies, between Mar. and Nov. 2005. To try to maximize differences in fish abundance and benthic characteristics among reefs, we selected four reefs (Sandy Lane, Vauxhall, Golden Palm, and North Bellairs reefs) inside the Barbados Marine Reserve, a marine protected area, and four reefs (Glitter Bay, Driftwood, Tropicana, and Long Shawl) out of the reserve. Our study reefs were distributed along a 4.8-km stretch of coastline, with distances between adjacent reefs varying from 100 to 900 m. The large expanses of sand between reefs precluded frequent inter-reef movement by the

vast majority of client fish. All study reefs exhibited a typical spur-and-groove formation at their seaward edge.

We focussed on the only two cleaning gobies species present on Barbadian fringing reefs: *Elacatinus evelynae* (sharknose goby) and *E. prochilos* (broad-stripe goby). These cleaning gobies are small (1.2–3.5 cm in total length), and both species show a prominent lateral stripe (yellow or white) extending from the snout to the tail. They can be found alone, in pairs or in groups on the surface of living coral (*Siderastrea* spp. and *Montastrea* spp.) or sponges. Sponge-dwelling cleaning gobies (mainly *E. prochilos*) feed primarily on non-client gleaned material (Arnal & Côté 2000; Whiteman & Côté 2002a,b). We therefore considered only cleaning gobies living on live coral.

Behavioural observations

On each study reef, 20–22 cleaning stations were selected haphazardly. Each cleaning station was observed once, for 30 min, between 10:00 AM and 17:00 PM, which coincides with the period of cleaning activity in these species (Johnson & Ruben 1988). Cleaning stations varied in depth 3–7 m, and were operated by one to two adult cleaning gobies. Observations began 2–5 min after the arrival of the diver, to allow the fish to acclimate to the observer, and were made from a distance of 2–3 m. A single cleaner fish was observed per cleaning station.

During each observation period, we recorded on plastic slates the species and total length (estimated visually to the nearest cm) of each visiting client, the time each client waited before being attended by the cleaner, inspection duration, and the outcome of each cleaning interaction (i.e. whether the client was inspected or not). We also noted which party initiated each interaction: whether the client posed before receiving an inspection (client-initiated) or the cleaner began the inspection prior to client posing behaviour (cleaner-initiated).

Cleaning goby diet analysis

We collected a minimum of 20 adult cleaning gobies from each reef ($n = 165$ in total, including 77 *E. evelynae* and 88 *E. prochilos*). A mixture of clove oil (a natural anesthetic), ethanol and water was sprayed over each individual cleaning goby to induce a temporary reduction in activity. Gobies were then easily caught with hand nets and placed individually in sealed plastic bags filled with an overdose of clove

oil, which caused rapid death. While still underwater, fish were placed in 10-ml bottles filled with 75% alcohol to stop the digestive process. In the laboratory 30–60 min later, fish were transferred to new bottles, again filled with 75% alcohol but without saltwater dilution, for longer-term preservation.

The entire gut (stomach and intestine) was dissected under a binocular microscope. We counted the number of items in each food category (i.e. crustacean parasites, monogeneans, scales and non-parasitic crustaceans). Ectoparasites were identified to family, focussing on the following families of parasitic copepods: Bomolochidae, Caligidae, Ergasilidae, Hatschekiidae, Kroyeriidae, Pandaridae, and *Argulus* spp; and one family of parasitic isopods: Gnathiidae.

Statistical analysis

We first compared the species composition of cleaning goby clienteles among reefs. To do so, we performed an analysis of similarity (ANOSIM) using the software PRIMER (Plymouth Routines in Multivariate Ecological Research version 5.2.4; PRIMER-E Ltd, Plymouth Marine Laboratory, Plymouth, UK) on the number of visits by each client species recorded in each 30-min observation. Each cleaning station was considered a sample, and Bray–Curtis similarity coefficients between pairs of samples were computed (Clarke & Warwick 1994). Cleaning stations from the same reef were then grouped by creating a ‘reef’ factor. ANOSIM generates an R statistic, which varies between 0 (as much similarity within as between reefs) and 1 (all cleaning stations within reefs are more similar to each other than any cleaning stations across reefs) and which was tested for difference from zero with a permutation test ($N_{\max} = 999$ permutations). The overall ANOSIM was followed by pairwise comparisons of reef clienteles. The clients species that contributed most to differences in clientele between reefs were then identified using the similarity percentage analysis (SIMPER) routine in PRIMER.

The number of clients visiting each station per min observation was averaged across cleaning stations within each reef to generate a reef-specific index of extent of competition among cleaning gobies for access to clients. Reefs with higher client visit rates were deemed to have less intense competition among cleaners whereas cleaners on reefs with lower client visit rates were considered to be under more intense competition for access to clients. We measured keenness to interact with clients as the proportion of cleaning interactions initiated by

cleaning gobies. The proportions were obtained for each goby, and averaged across gobies within each reef.

We used four indicators of cleaning service quality. The first was a direct measure of the extent of honest cleaning by cleaners on each reef. This was quantified by averaging the ratios of number of ectoparasites to number of scales observed in the entire gut contents of individual cleaning gobies within each reef. We also measured three behavioural correlates of cleaning service quality: (1) client waiting time at cleaning stations, (2) the proportion of clients of each species that was inspected, and (3) client inspection duration (seconds). All measures were obtained over 30 min at each focal cleaning station and then averaged across cleaning stations within each reef. Cleaning service quality is considered to be higher when the extent of honest cleaning is high, waiting time for access to cleaners is low, a high proportion of clients are inspected and inspection duration is long.

The relationship between intensity of competition among cleaners for clients (independent variable) and keenness to interact was examined using a non-linear regression analysis (curve estimation). All the remaining relationships between competition and indices of cleaning service quality were examined using linear regression analyses. Our data met all assumptions underlying parametric testing.

Results

Overall, 38 different fish species were seen visiting cleaning stations across the eight study reefs (Table 1). Client species diversity per reef ranged from 14 to 25 species (mean \pm SE: 19.1 ± 1.4 species). Overall, there was significant variation in species composition of clients among reefs (ANOSIM, $R = 0.07$, $p = 0.001$), with 17 of 28 pairwise comparisons between reefs being significant ($R > 0.06$, $p < 0.04$ for all significant differences). Variation in the abundance of one client species, the brown chromis *Chromis multilineata*, accounted for the highest proportion (34–56%) of the differences in clientele between reefs in all pairwise comparisons. Only two other client species, the yellow goatfish *Mulloidichthys martinicus* and the princess parrotfish *Scarus taeniopterus*, contributed appreciably (i.e. $>10\%$) to differences among some pairs of reefs.

The extent of competition among cleaners for access to clients varied widely on the study reefs, ranging from 12.7 clients per cleaner per 30 min on North Bellairs reef to 26.7 clients per cleaner per

30 min on Driftwood reef (Fig. 1). Overall, 97.6% of cleaning gobies examined ($n = 165$) had ingested ectoparasites; 74.5% of individuals had also ingested fish scales. The number of ectoparasites ingested by cleaning gobies varied from (mean \pm SE) 7.35 ± 1.41 on Long Shawl reef to 25.55 ± 10.18 on Vauxhall reef, while the number of client-gleaned scales ranged from (mean \pm SE) 4.76 ± 1.57 on North Bellairs reef to 51.14 ± 15.05 on Driftwood reef.

Overall, cleaners initiated 26% of all cleaning interactions (SE = 4%, range = 13–44%). The keenness of cleaning gobies to interact with clients, as measured by the proportion of cleaning interactions initiated by cleaning gobies, was not related to the intensity of competition for access to clients ($r^2 = 0.08$, $F_{1,6} = 0.55$, $p = 0.49$, slope = -0.007 , SE = 0.01).

The extent of honest cleaning, as measured by the ratio of numbers of parasites to scales ingested by cleaning gobies, decreased with decreasing intensity of competition (i.e. with increasing client visit rate) ($r^2 = 0.84$, $F_{1,6} = 14.66$, $p = 0.009$, slope = -2.60 , SE = 0.68; Fig. 2). However, none of the other indices of cleaning service quality namely client waiting time before inspection, likelihood of being inspected and inspection duration, was significantly related to competition intensity (waiting time: $r^2 = 0.32$, $F_{1,6} = 0.20$, $p = 0.67$, slope = 0.01, SE = 0.03; likelihood of being inspected: $r^2 = 0.39$, $F_{1,6} = 3.88$, $p = 0.10$, slope = -0.01 , SE = 0.005; inspection duration: $r^2 = 0.01$, $F_{1,6} = 0.07$, $p = 0.81$, slope = 0.09, SE = 0.34).

Discussion

Our results suggest that intense competition among cleaners for access to clients can promote cleaning goby honesty. On reefs where fish clients visited cleaning stations less frequently, and hence competition among cleaners was highest, cleaning gobies ingested a higher proportion of parasites relative to scales. Although our main result is consistent with the expectation based on the market value of the service provided by cleaning gobies, it is also consistent with an alternative explanation based on the offer (i.e. the parasite loads) made by the clients.

Clients outnumber cleaners on reefs. Competition among clients for access to cleaners might therefore be expected, but not the reverse. However, not all clients are equal. Some are more preferred (e.g. clients with more parasites; Soares et al. 2007), generating the potential for competition among cleaners

Table 1: Percentage of total visits to cleaning stations performed by various species of coral reef fish on each of eight Barbadian reefs

Family	Species	SL (209)	V (222)	GP (211)	NB (206)	GB (211)	D (294)	T (169)	LS (237)
Acanthuridae									
	<i>Acanthurus bahianus</i> Castelnau, 1855	4.8	0.9	0.9	0	3.3	4.1	1.8	1.3
	<i>Acanthurus coeruleus</i> Bloch & Schneider, 1801	0.5	1.8	2.4	0	2.4	2.4	4.1	0.8
Anguilliformes									
	<i>Gymnothorax ocellatus</i> Agassiz, 1831	0	0	0	0	0.5	0	0	0
	<i>Gymnothorax miliaris</i> (Kaup, 1856)	0	0	0	0	0	0	0.6	0
Aulostomidae									
	<i>Aulostomus maculatus</i> Valenciennes, 1837	0	0.5	1.4	0	1.4	0	0	5.5
Chaetodontidae									
	<i>Chaetodon striatus</i> Linnaeus, 1758	0	0.9	0.5	0	0	0	0	0
Diodontidae									
	<i>Diodon holocanthus</i> Linnaeus, 1758	0	0	0	0	1.0	1.0	0	0
Haemulidae									
	<i>Haemulon carbonarium</i> Poey, 1860	0	0	0	0.5	0	0	0	0
	<i>Haemulon chrysargyreum</i> Gunther, 1859	0	0.5	0	0.5	0	0.3	1.8	0
	<i>Haemulon flavolineatum</i> (Desmarest, 1823)	0	9.5	5.2	2.9	0.5	0.3	0.6	7.6
Holocentridae									
	<i>Holocentrus rufus</i> (Walbaum, 1792)	0	0	0.5	1.0	2.4	0	0.5	0
	<i>Myripristis jacobus</i> Cuvier, 1829	0.5	0.9	0.9	1.0	0.9	0.7	0	0.4
Labridae									
	<i>Bodianus rufus</i> (Linnaeus, 1758)	0	0.5	0	0.5	1.0	2.0	0	0
	<i>Halichoeres garnoti</i> (Valenciennes, 1839)	0	0	0.5	0	0	0.7	0	0
Lutjanidae									
	<i>Lutjanus mahogoni</i> (Cuvier, 1828)	0.5	0	0	0.9	0	0	0	0
Monacanthidae									
	<i>Cantherhines pullus</i> (Ranzani, 1842)	0	0.5	0	0	0	0.3	0	0
Mullidae									
	<i>Mulloidichthys martinicus</i> (Cuvier, 1829)	18.7	2.7	3.8	34.3	0	4.1	0	20.3
Ostraciidae									
	<i>Lactophrys triqueter</i> (Linnaeus, 1758)	0	0	0	0	0	0	0.6	0
Pomacentridae									
	<i>Chromis multilineata</i> (Guichenot, 1853)	53.1	31.5	51.2	28.2	45.5	54.1	35.5	47.7
	<i>Microspathodon chrysurus</i> (Cuvier, 1830)	7.7	3.6	3.3	1.9	4.3	4.8	8.9	5.9
	<i>Stegastes adustus</i> (Troschel, 1865)	0	0.5	0	0	0.5	0	0	0
	<i>Stegastes dienaecus</i> (Jordan & Rutter, 1897)	2.4	0.5	0.5	2.4	2.4	0	0	0.4
	<i>Stegastes partitus</i> (Poey, 1868)	3.3	0.9	1.4	0	1.9	0.3	4.1	0.8
	<i>Stegastes planifrons</i> (Cuvier, 1830)	0	0.5	0	0	0	0	0.6	0
Priacanthidae									
	<i>Heteropriacanthus cruentatus</i> (Lacepède, 1801)	0	0	1.4	0	0	0	0	0
Scaridae									
	<i>Sparisoma aurofrenatum</i> (Valenciennes, 1840)	2.4	4.1	3.8	1.5	1.9	3.1	1.8	0
	<i>Sparisoma chrysopterum</i> (Bloch & Schneider, 1801)	1.9	0	0	0.5	0.5	0	0	0
	<i>Sparisoma viride</i> (Bonnaterre, 1788)	1.4	8.1	1.9	1.9	2.8	4.4	0	1.3
	<i>Sparisoma rubripinne</i> (Valenciennes, 1840)	0	0	1.0	0	0.5	0	0.6	0
	<i>Scarus iserti</i> (Bloch, 1793)	0	6.3	6.6	2.4	3.3	3.7	7.7	4.2
	<i>Scarus taeniopterus</i> Desmarest, 1831	0.5	13.1	9.5	11.2	15.6	8.2	22.5	2.1
	<i>Scarus vetula</i> Bloch & Schneider, 1801	1.0	11.7	1.4	2.9	1.9	3.7	1.2	0
Serranidae									
	<i>Cephalopholis fulva</i> (Linnaeus, 1758)	0	0	0	0	3.3	0	0	0
	<i>Epinephelus adscensionis</i> (Osbeck, 1765)	0	0	0	0	0.5	0	0	0
	<i>Epinephelus cruentatus</i> (Lacepède, 1802)	1.4	0.5	0	1.5	1.4	1.7	1.2	1.7
	<i>Hypoplectrus nigricans</i> (Poey, 1852)	0	0.5	0	0	0	0	0	0
	<i>Rypticus saponaceus</i> (Bloch & Schneider, 1801)	0	0	1.0	0	0	0	5.9	0
Tetraodontidae									
	<i>Canthigaster rostrata</i> (Bloch, 1786)	0	0	0	0	0.5	0	0	0

Reef codes: SL, Sandy Lane; V, Vauxhall; GP, Golden Palm; NB, North Bellairs; GB, Glitter Bay; D, Driftwood; T, Tropicana; LS, Long Shawl. The total number of visits per reef is given in parentheses.

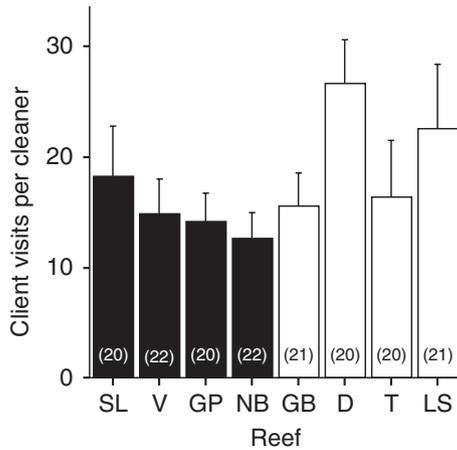


Fig. 1: Extent of competition among cleaners for access to fish clients, as measured by client visit rate to cleaning stations (per 30 min), on eight Barbadian reefs. Reef codes: SL, Sandy Lane; V, Vauxhall; GP, Golden Palm; NB, North Bellairs; GB, Golden Palm; D, Driftwood; T, Tropicana; LS, Long Shawl. Black bars represent reefs within a marine protected area. Means are shown ± 1 SE. Sample sizes (number of cleaning gobies observed) are given in parentheses.

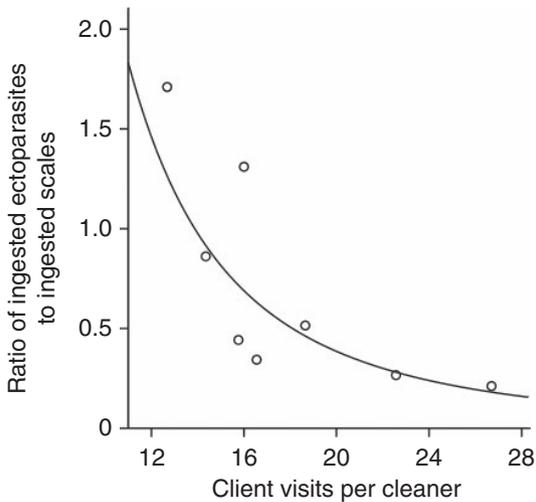


Fig. 2: The relationship between intensity of competition among cleaners for access to fish clients, as measured (inversely) by client visit rate to cleaning stations (visits per 30 min), and the extent of honest cleaning by cleaning gobies, represented by the ratio of number of ingested ectoparasites to ingested scales. The line represents the best fit to a power curve (ratio of parasites to scales = $954.5 \times \text{client visits}^{-2.6}$).

for access to the best clients. Overt aggression between cleaning gobies to attract such clients should generally be unlikely because of their dispersed distribution on the reef and of their limited swimming ability. This sets the stage for various forms of non-physical, outbidding competition.

In the cleaner wrasse *L. dimidiatus* and in cleaner shrimp *Urocaridella* spp., ‘tactile dances’ and ‘rocking dances’, respectively, serve to advertise cleaning services to potential clients (Youngbluth 1968; Grutter 2004; Becker et al. 2005) and their rate could be an expression of outbidding competition. Cleaning gobies do not dance. Instead of obvious advertising, cleaning gobies can outbid their competitors by attempting to initiate more cleaning interactions when clients are rarer. Cleaning gobies sometimes swim onto fish that are passing near cleaning stations and try to inspect them while in motion (M. C. Soares, pers. comm.). Some of these clients react negatively to the unrequested cleaning service and swim away rapidly, but others continue grazing or even stop and pose while cleaners continue to inspect them. It was therefore surprising that the proportion of interactions initiated by cleaning gobies did not vary with the intensity of competition for clients.

However, the ultimate form of outbidding by cleaner fish is to provide the most honest or best-quality service. For instance, clients have been shown to be sensitive to cheating by cleaner wrasses and to visit wrasses that appear to be honest (Bshary & Schäffer 2002). In contrast, there is no evidence that clients of cleaning gobies switch to another station for their next inspection if the current interaction ends with the cleaner cheating (M. C. Soares, unpubl. data). Dishonest cleaning by cleaning gobies is prevalent, as evidenced by the large number of fish scales usually found in dietary analyses of these species (Arnal & Côté 2000; Whiteman & Côté 2002a,b; Cheney & Côté 2005). We found that the extent of dishonest cleaning varied in relation to the intensity of competition for access to clients, as predicted from market theory (Noë 2001). That is, when the supply of clients was higher, competition among cleaning gobies was lower, the cleaning service exchange rate was also smaller and thus lower quality (i.e. less honest cleaning) was provided to clients. However, such a relationship – emerging from an unmanipulated system – could also arise as a simple result of reef differences in ectoparasite availability.

Ectoparasite availability to cleaning gobies depends on the number of clients visiting cleaning stations – which was captured by our index of competition among cleaning gobies – and ectoparasite load on these clients – which was not captured by our index because information on parasite intensities for our study reefs was not available. Because ectoparasite loads on individual clients influence the propensity for cleaners to clean dishonestly (Bansemmer et al.

2002; Cheney & Côté 2005), cleaning gobies visited frequently (i.e. apparent low competition) by clients harbouring few parasites might clean dishonestly more often than gobies visited infrequently (i.e. apparent high competition) by clients with more parasites. On Barbadian reefs, there is in fact a negative covariation between overall client density and individual ectoparasite load (Pearson's correlation, $r = -0.90$, $n = 5$ reefs, $p = 0.037$; data from Cheney & Côté 2003). In addition, the differences in client species composition observed among reefs also support the notion that ectoparasite loads were spatially variable. Brown chromis, which were the commonest visitors to cleaning stations (Table 1), were the most important contributors to clientele differences between reefs. This species also consistently exhibits among the lowest ectoparasite loads (Arnal et al. 2001; Soares et al. 2007). Reef differences in client ectoparasite load, caused wholly or partly by differences in client species composition, could therefore have led to an apparent negative relationship between the intensity of competition among gobies, as measured by client visit frequency, and extent of honest cleaning.

Interestingly, the other aspects of cleaning service quality considered were not significantly affected by the intensity of competition among cleaners. It was surprising to observe that even on reefs with more clients per cleaner, the proportion of clients inspected remained constant, which may indicate that some clients are never considered suitable regardless of overall client availability. Most aspects of cleaning service quality by cleaning gobies are perhaps more likely to be determined by client-specific features, such as risk of predation (see Soares et al. 2007), than by the number of clients visiting cleaning stations.

According to biological market theory, supply and demand largely determine the outcome of cooperative interactions (Noë & Hammerstein 1994; Noë 2001). Our data indicate that in the cleaning goby mutualism, changes in intensity of competition may determine the exchange rate of cleaning service and thus influence the dynamics of cooperative behaviour. At this stage, however, it is difficult to say whether it is the change in this ratio *per se* or differences in client parasite loads that influence service quality. In any case, cleaners are able to alter their cleaning strategies (for instance, to provide more honest cleaning) in accord to either the market value of the service they provide or in accord to the offer (the parasite loads) made by the clients. Only experimental manipulation of client visit frequencies

will allow us to elucidate the precise market mechanisms that cause shifts in the service quality of cleaning gobies.

Acknowledgements

We thank the staff of the Bellairs Research Institute for logistical support. We thank Stanton Thomas for support and friendship during the collection of fish samples. The data collection complied with the ethical laws of Barbados. 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.

Literature Cited

- Arnal, C. & Côté, I. M. 2000: Diet of the broadstripe cleaning gobies on a Barbadian reef. *J. Fish Biol.* **57**, 1075–1082.
- Arnal, C., Côté, I. M. & Morand, S. 2001: Why clean and be cleaned? The importance of client ectoparasites and mucus in a marine cleaning symbiosis. *Behav. Ecol. Sociobiol.* **51**, 1–7.
- Axén, A. H., Leimar, O. & Hoffmann, V. 1996: Signalling in a mutualistic interaction. *Anim. Behav.* **52**, 321–333.
- Bansemer, C., Grutter, A. S. & Poulin, R. 2002: Geographic variation in the behaviour of the cleaner fish *Labroides dimidiatus* (Labridae). *Ethology* **108**, 353–366.
- Becker, J. H. A., Curtis, L. M. & Grutter, A. S. 2005: Cleaner shrimp use a rocking dance to advertise cleaning service to clients. *Curr. Biol.* **15**, 760–764.
- Bshary, R. 2001: The cleaner fish market. In: *Economics in Nature* (Noë, R., van Hooff, J. A. R. A. M. & Hammerstein, P., eds). Cambridge Univ. Press, Cambridge, pp. 146–172.
- Bshary, R. & Grutter, A. S. 2002: Asymmetric cheating opportunities and partner control in a cleaner fish mutualism. *Anim. Behav.* **63**, 547–555.
- Bshary, R. & Noë, R. 2003: Biological markets. The ubiquitous influence of partner choice on the dynamics of cleaner fish – client reef fish interactions. In: *Genetic and Cultural Evolution of Cooperation* (Hammerstein, P., ed.). Dahlem Workshop Reports, MIT Press, Cambridge, UK, pp. 167–184.
- Bshary, R. & Schäffer, D. 2002: Choosy reef fish select cleaner fish that provide high-quality service. *Anim. Behav.* **63**, 557–564.
- Cheney, K. L. & Côté, I. M. 2003: Do ectoparasites determine cleaner fish abundance? Evidence on two spatial scales. *Mar. Ecol. Prog. Ser.* **263**, 189–196.

- Cheney, K. L. & Côté, I. M. 2005: Mutualism or parasitism? The variable outcome of cleaning symbioses. *Biol. Lett.* **2**, 162–165.
- Clarke, K. A. & Warwick, R. M. 1994: Similarity-based testing for community pattern: the 2-way layout with no replication. *Mar. Biol.* **118**, 167–176.
- Dugatkin, L. A. 1997: *Cooperation Among Animals: An Evolutionary Perspective*. Oxford Series in Ecology and Evolution. Oxford Univ. Press, Oxford.
- Dugatkin, L. A. 2002: Cooperation in animals: an evolutionary overview. *Biol. Philos.* **17**, 459–476.
- Grossbard-Shechtman, S. 1993: *On the Economics of Marriage. A Theory of Marriage, Labor and Divorce*. Westview Press, Boulder, CO.
- Grutter, A. S. 2004: Cleaner fish use tactile dancing behaviour as a preconflict management strategy. *Curr. Biol.* **14**, 1080–1083.
- Grutter, A. S. & Bshary, R. 2003: Cleaner wrasse prefer client mucus: support for partner control mechanisms in cleaning interactions. *Proc. R. Soc. Lond. B. Biol. Sci.* **270**(Suppl. 2), S242–S244.
- Grutter, A. S. & Bshary, R. 2004: Cleaner fish, *Labroides dimidiatus*, diet preferences for different types of mucus and parasitic gnathiid isopods. *Anim. Behav.* **68**, 583–588.
- Johnson, W. S. & Ruben, P. 1988: Cleaning behaviour of *Bodianus rufus*, *Thalassoma bifasciatum*, *Gobiosoma evelynae*, and *Periclimenes pedersoni* along a depth gradient at Salt River Submarine Canyon, St Croix. *Environ. Biol. Fish* **23**, 225–232.
- Noë, R. 2001: Biological markets: partner choice as a driving force behind the evolution of mutualism. In: *Economics in Nature* (Noë, R., van Hooff, J. A. R. A. M. & Hammerstein, P., eds). Cambridge Univ. Press, Cambridge, pp. 146–172.
- Noë, R. 2006: Digging for the roots of trading. In: *Cooperation in Primates and Humans: Mechanisms and Evolution* (Kappeler, P. M. & van Schaik, C. P., eds). Springer-Verlag, Berlin Heidelberg, pp. 233–261.
- Noë, R. & Hammerstein, P. 1994: Biological markets: supply and demand determine the effect of partner choice in cooperation, mutualism and mating. *Behav. Ecol. Sociobiol.* **35**, 1–11.
- Noë, R., Van Schaik, C. P. & Van Hooff, J. A. R. A. M. 1991: The market effect: an explanation for pay-off asymmetries among collaborating animals. *Ethology* **87**, 97–118.
- Pfenning, B., Poethke, H. J. & Hovestadt, T. 2007: Dealing with time constraints on development: the effect of food availability. *Ecol. Entomol.* **32**, 273–278.
- Pierce, N. E., Braby, M. F., Heath, A., Lohman, D. J., Mathew, J., Rand, D. B. & Travassos, M. A. 2002: The ecology and evolution of ant association in the Lycaenidae (Lepidoptera). *Ann. Rev. Entomol.* **47**, 733–771.
- Sachs, J. L., Mueller, U. G., Wilcox, T. P. & Bull, J. J. 2004: The evolution of cooperation. *Q. Rev. Biol.* **79**, 135–160.
- Soares, M. C., Cardoso, S. C. & Côté, I. M. 2007: Client preferences by Caribbean cleaning gobies: food, safety or something else? *Behav. Ecol. Sociobiol.* **61**, 1015–1022.
- Whiteman, E. A. & Côté, I. M. 2002a: Cleaning activity of two Caribbean cleaning gobies: intra- and interspecific comparisons. *J. Fish Biol.* **60**, 1443–1458.
- Whiteman, E. A. & Côté, I. M. 2002b: Sex differences in cleaning behaviour and diet of a Caribbean cleaning goby. *J. Mar. Biol. Assoc. UK.* **82**, 655–664.
- Whiteman, E. A. & Côté, I. M. 2004: Individual differences in microhabitat use in a Caribbean cleaning goby: a buffer effect in a marine species? *J. Anim. Ecol.* **73**, 831–840.
- Youngbluth, M. J. 1968: Aspects of the ecology and ethology of the cleaning fish, *Labroides phthirophagus* Randall. *Z. Tierpsychol.* **25**, 915–932.