

Client preferences by Caribbean cleaning gobies: food, safety or something else?

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Abstract Predation risk is amongst the most pervasive selective pressures influencing behaviour and animals have been repeatedly shown to trade-off foraging success for safety. We examined the nature of this trade-off in cleaning symbioses amongst Caribbean coral reef fishes. We predicted that cleaning gobies (*Elacatinus evelynae* and *Elacatinus prochilos*) should prefer fish clients that pose a low risk of predation (e.g. herbivores) over clients that may have more ectoparasites but pose a higher risk (e.g. piscivores). Our field observations revealed that cleaners did clean preferentially client species with more parasites but predatory and non-predatory clients had similar ectoparasite loads. Despite the lack of a foraging advantage for inspecting predators, cleaners did not avoid risky clients. On the contrary, a larger proportion of visiting predators than non-predators was inspected, gobies initiated more interactions with predatory clients, and predators were attended to immediately upon arrival at cleaning stations. This preferential treatment of dangerous clients may allow the rapid identification of cleaners as non-prey item or may be due to the effect of predators on the rest of the cleaners' clientele, which avoided cleaning stations whilst predators were present. Dealing with potentially risky clients may allow gobies to regain access to their main food source: non-predatory clients.

Keywords Cleaning symbiosis · *Elacatinus* spp · Ectoparasites · Food–safety trade-off · Foraging preferences · Predation risk

Introduction

Predation is one of the most pervasive selection pressures faced by prey individuals over the course of their lives (Lima and Dill 1990; Kats and Dill 1998; Werner and Peacor 2003). There is much evidence that animals have the ability to weight the risk of predation against various benefits (such as foraging) when deciding which behavioural option to pursue (Lima and Bednekoff 1999). If predation risk varies between patches or prey types, then an animal is expected to opt for safer habitats or prey, particularly when patches have identical value (Dill and Fraser 1984; Lima and Dill 1990). When risk of predation covaries with patch or prey quality, food intake is effectively traded off for increased safety. The ensuing decisions can result, for example, in altered distributions, foraging times or migration times (see Lima and Dill 1990; Bateson 2002).

Cleanerfish potentially experience foraging–predation trade-offs daily. Some cleaners rely virtually entirely on the ectoparasites they glean from the body of the many fish clients they service every day (Côté 2000). Such cleanerfish prefer clients that are more parasitised, cleaning them more frequently and for longer than fish with fewer parasites (Gorlick 1984; Grutter 1995; Arnal and Morand 2001). However, different client species pose different risks to cleaners, ranging from no risk of predation in the case of herbivorous clients to a potentially high risk in the case of piscivorous clients. Whilst it has been suggested that cleanerfish may be immune to predation by clients (Feder

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1966), behavioural evidence indicates that cleaners are sensitive to predation risk (see Côté 2000 for review). Despite the fact that cleaners do service large piscivorous fishes and some even enter and clean the buccal cavity of these potential predators (Feder 1966), cleaners generally tend to clean ‘safer’ areas such as the tail and fins and avoid areas such as the head and the mouth (Potts 1973a; Sazima et al. 1998; Francini-Filho et al. 2000). It is unlikely that the distribution of ectoparasites on clients explains this cleaning pattern since ectoparasites are usually most abundant on the gills, head and flanks of fishes (Potts 1973b; Rohde 1980). Cleaners are also more likely to provide tactile stimulation to hungry predatory clients than to satiated ones, which has been interpreted as a pre-conflict management strategy that enables cleanerfish to avoid conflict with potentially dangerous clients (Grutter 2004).

In addition to posing a risk to cleanerfish, piscivorous clients can threaten the majority of a cleaner’s clientele. Potts (1973a) found that the number of clients available to be cleaned decreased when predators appeared. Some clients also abruptly interrupt cleaning interaction upon the arrival of piscivores (Hobson 1965). The responses of non-predatory clients to the risk of predation at cleaning stations may therefore exacerbate any food–safety trade-off costs for cleanerfish.

In this paper, we investigated the preferences of Caribbean cleaning gobies (*Elacatinus* spp.) for specific client species and asked whether these preferences are influenced by client ectoparasite load and/or the potential risk the clients pose to cleaners. We tested three specific predictions. First, client ectoparasite load should influence a cleaner’s choice of clients, which should be reflected in clients with more ectoparasites being more likely to be attended and given a more rapid cleaning service than less infested clients. Second, predation risk should influence a cleaner’s choice of client, with cleaners preferring safe clients. Finally, if ectoparasite loads and risk of predation covary, cleaners should trade-off risk of predation for a lower foraging rate. We also examined the effect of the presence of predatory clients on cleaning goby clientele to document indirect foraging costs of risk of predation.

Materials and methods

Study site and species

The study was carried out in Barbados, West Indies, between February and August 2004. All observations were made on the North and South Bellairs fringing reefs in the Barbados Marine Reserve, a 2.2-km stretch of coast containing fringing reefs, on the west coast of the island. These reefs are largely degraded, with relatively low coral cover.

Two species of cleaning goby are present on Barbadian fringing reefs: *Elacatinus evelynae* (sharknose goby) and *Elacatinus prochilos* (broadstripe goby). Both species are small (1.2–3.5 cm total length) with a prominent lateral stripe (white in *E. prochilos*, yellow in *E. evelynae*) running from snout to the base of the tail. Both species are common across the Bellairs reefs and inhabit the surface of living coral, usually *Siderastrea* spp. and *Montastrea* spp., but *E. prochilos* is also abundant on sponges. Only gobies on coral were considered in this study because sponge-dwelling *E. prochilos* feed predominantly on non-client-gleaned material (Arnal and Côté 2000) and spend less time inspecting clients than both species living on coral (Whiteman and Côté 2002).

Behavioural observations

Observations were made whilst diving or snorkelling between 10:00 and 17:00 hours, encompassing the hours during which *E. evelynae* and *E. prochilos* are active (Johnson and Ruben 1988; Arnal and Côté 1998). Cleaning stations were selected haphazardly across the reefs and varied in depth between 1.8 and 6.4 m. Each cleaning station was observed for 30 min on up to four occasions. None of the cleaning stations was observed more than once per week. Observations were made from a distance of 2–3 m and began after a 2- to 5-min delay to allow the fish to become accustomed to the presence of the observer.

During each observation period, we recorded on plastic slates the species and total length of each client (estimated visually to the nearest centimeter) visiting the cleaning station, the time it spent waiting before being attended by cleaning gobies or swimming away without being cleaned and whether it adopted the species-specific immobile pose, which signals the need to be cleaned (Côté et al. 1998), before or after the onset of cleaning by the cleaning goby. Clients posing before the onset of cleaning goby inspection were deemed to have initiated the cleaning interaction, whilst interactions starting without prior client posing were deemed to have been initiated by cleaning gobies. In the latter case, cleaning gobies usually hopped onto fish swimming near cleaning stations; these fish often did not slow down even upon the onset of cleaning goby inspection. Such cleaning interactions ended with the cleaner having to swim some distance back to the cleaning station. We also recorded the duration (in s) of inspection of each client’s body by the cleaning goby, instances of client switching (i.e. when a cleaner abandoned inspection of a current client immediately upon arrival of a new client) and the number of jolts by clients. Jolts are apparently painful reactions to a cleanerfish bite and have previously been shown to be dishonest bites by cleaners (Bshary and Grutter 2002).

The position and depth of each cleaning station were recorded on maps of the two reefs, together with information on the species, number, length and gender of cleaning gobies. A total of 52 h of observation of 59 cleaning stations (23 on South Bellairs and 36 on North Bellairs) were made, during which 46 different client species were seen visiting.

Ectoparasite load assessment

Ectoparasite loads were assessed on 114 individuals of 26 client species (Table 1). The client species were chosen in part to represent wide variation in visiting frequency to cleaning stations and in part because of their abundance on the reefs. All specimens were collected between 10:00 and 13:00 hours, between March and August 2004.

The ectoparasite extraction method followed Sikkel et al. (2004). Individual fish were herded into a barrier net placed close to the locations of behavioural observations. The fish were caught with a hand net and quickly placed individually into hermetically sealed plastic bags filled with seawater. These were then taken to the laboratory and placed into individual containers with a variable amount of

seawater and two to three drops of clove oil, a natural anaesthetic. Fish were identified (species and development stage), measured to the nearest millimeter (total length) and then transferred for 10 min to a freshwater bath, during which time we brushed gently their entire body surface. Finally, fish were placed in seawater-filled recovery containers and released at their capture relocation. All fluids were filtered using a plankton net (100- μ m mesh size) and ectoparasites were preserved in 70% alcohol. These samples were later examined under a binocular microscope. Ectoparasites were counted and identified to family, focussing on the families Bomolochidae, Caligidae, Gnathiidae and Hatschekiidae.

Ethical note

In our assessment of client ectoparasite loads, we tried to minimise stress and other negative effects on individuals. We used large plastic bags to allow us to place the captive fish in a large volume of water. We also collected few fish (average of five individuals) per sampling dive to minimise the time between capture and release as much as possible.

Table 1 Mean body size (\pm SE), mean ectoparasite numbers (\pm 1 SE), and frequency of visits to cleaning stations over 52 h of observations of Barbadian coral reef fish species (*indicates predatory species)

Family	Species	No. individuals collected	Total length (cm)	Ectoparasite load	No. visits to cleaning stations
Acanthuridae	<i>Acanthurus bahianus</i> (Castelnaud 1855)	6	13.88 \pm 2.40	4.67 \pm 2.37	19
	<i>Acanthurus coeruleus</i> (Bloch & Schneider 1801)	7	13.18 \pm 2.05	2.57 \pm 1.02	20
Aulostomidae	<i>Aulostomus maculatus</i> Valenciennes 1837*	5	46.54 \pm 1.67	11.20 \pm 5.60	11
Chaetodontidae	<i>Chaetodon striatus</i> Linnaeus 1758	4	10.32 \pm 1.01	1.75 \pm 1.44	7
Haemulidae	<i>Haemulon chrysargyreum</i> (Gunther 1859)	7	17.15 \pm 1.02	0.57 \pm 0.20	18
	<i>Haemulon flavolineatum</i> (Desmarest 1823)	7	13.51 \pm 0.78	0.43 \pm 0.29	60
Holocentridae	(<i>Myripristis jacobus</i> Cuvier 1829)*	2	19.00 \pm 0.90	0	3
Kyphosidae	<i>Kyphosus sectatrix</i> (Linnaeus 1758)	6	27.83 \pm 1.21	9.50 \pm 2.65	21
Labridae	<i>Bodianus rufus</i> (Linnaeus 1758)*	2	24.55 \pm 9.45	136.50 \pm 130.50	12
Lutjanidae	<i>Lutjanus mahogoni</i> (Cuvier, 1828) *	7	15.25 \pm 1.98	1.28 \pm 0.52	4
Monacanthidae	<i>Cantherhines pullus</i> (Ranzani 1842)*	1	18.70 \pm 0	2.00 \pm 0	1
Mullidae	<i>Mulloidichthys martinicus</i> (Cuvier 1829)	6	18.1 \pm 2.55	2.00 \pm 0.25	13
Pomacentridae	<i>Chromis multilineata</i> (Guichenot 1853)	6	8.61 \pm 0.34	0.16 \pm 0.16	235
	<i>Microspathodon chrysurus</i> (Cuvier 1830)	5	15.78 \pm 0.69	20.00 \pm 10.73	57
	<i>Stegastes adustus</i> (Troschel 1865)	5	7.62 \pm 0.36	0.40 \pm 0.24	3
	<i>Stegastes diencaeus</i> (Jordan & Rutter 1897)	5	10.44 \pm 0.21	1.40 \pm 0.67	72
	<i>Stegastes partitus</i> (Poey 1868)	4	6.87 \pm 0.29	0.50 \pm 0.50	4
Scaridae	<i>Stegastes planifrons</i> (Cuvier, 1830)	2	7.80 \pm 1.10	0.50 \pm 0.50	2
	<i>Sparisoma aurofrenatum</i> (Valenciennes, 1840)	5	20.42 \pm 1.66	9.60 \pm 2.29	25
	<i>Sparisoma chrysopterum</i> (Bloch & Schneider, 1801)	1	13.40 \pm 0	0	9
	<i>Sparisoma viride</i> (Bonnaterre, 1788)	5	11.84 \pm 1.89	1.40 \pm 0.67	24
	<i>Sparisoma rubripinne</i> (Valenciennes, 1840)	2	30.45 \pm 2.05	108.00 \pm 21.00	16
	<i>Scarus iserti</i> (Bloch, 1793)	6	18.35 \pm 1.61	3.83 \pm 2.16	45
Serranidae	<i>Scarus taeniopterus</i> Desmarest, 1831	5	22.20 \pm 0.51	7.00 \pm 0.89	127
	<i>Scarus vetula</i> Bloch & Schneider, 1801	2	20.50 \pm 7.55	2.50 \pm 2.50	97
	<i>Rypticus saponaceus</i> (Bloch & Schneider, 1801) *	1	27.00 \pm 0	4.00 \pm 0	5

We elected to use the freshwater bath method of parasite extraction because it usually entails a lower rate of mortality than alternative methods (e.g. dilute formalin solution). Unfortunately, in our case, mortality was high (73 fish died), the cause of which we eventually identified as high levels of chlorine in the tap water. When we replaced tap with bottled water, no further mortality occurred. The time elapsed between capture and release of the surviving fish was 120–240 min.

Statistical analysis

We investigated differences between the North and South Bellairs reef by comparing the length, ectoparasite loads and behaviour of fish occurring on both reefs in a series of paired tests. There were no differences between the reefs in most of the variables considered. Data were therefore combined in subsequent analyses.

Cleaning goby preference for specific client species can be measured by the likelihood of being cleaned or by the quality of the cleaning service provided. Each of these measures in turn has several behavioural correlates. Hence, we measured the species-specific likelihood of being cleaned as: (1) the proportion of clients of each species which was inspected, (2) the proportion of cleaning interactions initiated by gobies and (3) client waiting time at cleaning stations. Whilst the first two measures are expected to correlate positively with the likelihood of being cleaned, the third should correlate negatively.

Measures of species-specific cleaning service quality included (1) mean duration of inspection by cleaning gobies, (2) the number of cleaning gobies switching from a current client to a newly arrived client of the focal species and (3) the number of jolts per minute of inspection. The first two measures are expected to correlate positively with cleaning service quality, whilst the third should correlate negatively. Proportions and mean values of each variable were obtained for each species at each station and then averaged across all cleaning stations. Each of the measures of cleaning goby preference was then related to ectoparasite load and compared between clients posing no risk or some risk of predation to cleaners.

Of the 46 species observed at cleaning stations, we considered only frequent visitors (i.e. more than five visits), reducing the sample to 25 client species. Ectoparasite load was obtained for each of the captured species ($n=26$) by averaging the number of ectoparasites across all individuals collected. We removed from this set those species for which only one individual was sampled, as well as species that were never observed at cleaning stations, thus reducing the sample to 18 species. Total ectoparasite load was sig-

nificantly and positively correlated with client length (Spearman's rank correlation: $r_s=0.75$, $n=18$, $p<0.0001$). For this reason, we examined relationships between measures of preference and total ectoparasite load, as well as total ectoparasite load per unit length of client. Because the results were very similar, we report only those obtained with uncorrected ectoparasite loads.

Each client species observed at cleaning stations was categorised as either harmless to cleaning gobies or potentially predatory based on published information on the diet of Caribbean reef fish (Randall 1967).

Non-parametric tests were only used when the assumptions for parametric testing were not met. All tests are two-tailed.

Results

Do cleaning gobies prefer highly parasitised clients?

Cleaning gobies were more likely to attend to more parasitised clients according to two of the three measures of likelihood of being cleaned. The proportion of clients of each species which was inspected increased with client ectoparasite load (Spearman's rank correlation, $r_s=0.59$, $n=18$, $p=0.009$). The proportion of cleaning events initiated by gobies was not correlated to client ectoparasite load ($r_s=-0.11$, $n=18$, $p=0.66$). Waiting time at cleaning stations decreased with increasing client ectoparasite load ($r_s=-0.68$, $n=18$, $p=0.002$). Clients with the most ectoparasites did not wait at all before being inspected.

Cleaning gobies did not provide a more rapid cleaning service to more parasitised clients. Cleaning gobies did not spend more time inspecting more parasitised clients ($r_s=-0.02$, $n=18$, $p=0.95$). Client switching by cleaners was not correlated with the ectoparasite load of newly arrived clients ($r_s=-0.14$, $n=18$, $p=0.58$). Jolt rate was also not significantly correlated with client ectoparasite load ($r_s=-0.33$, $n=18$, $p=0.18$).

Do cleaners prefer clients that pose a low risk of predation?

Cleaning gobies never preferred harmless clients, according to all measures of likelihood of being cleaned. The proportion of visiting clients that was cleaned was higher for predators than for harmless clients (Mann–Whitney test: $U=10.0$, $n_1=20$, $n_2=5$, $p=0.005$; Fig. 1a). Cleaning gobies also initiated interactions more often with predatory clients (independent samples t test: $t_{23}=-4.8$, $p<0.0001$; Fig. 1b). Moreover, predatory clients waited for a significantly shorter time than harmless clients to be attended by cleaning gobies ($U=10.0$, $n_1=20$, $n_2=5$, $p=0.005$; Fig. 1c). In fact, predatory clients were usually attended

immediately upon arrival at a cleaning station. This appeared to be due to the fact that when predators arrived at cleaning stations, there were usually no other clients being cleaned (median [interquartile range] number of clients present upon arrival of predatory client: 0 [0–0]; upon arrival of harmless client: 1 [0–1]; $U=22.5$, $n_1=20$,

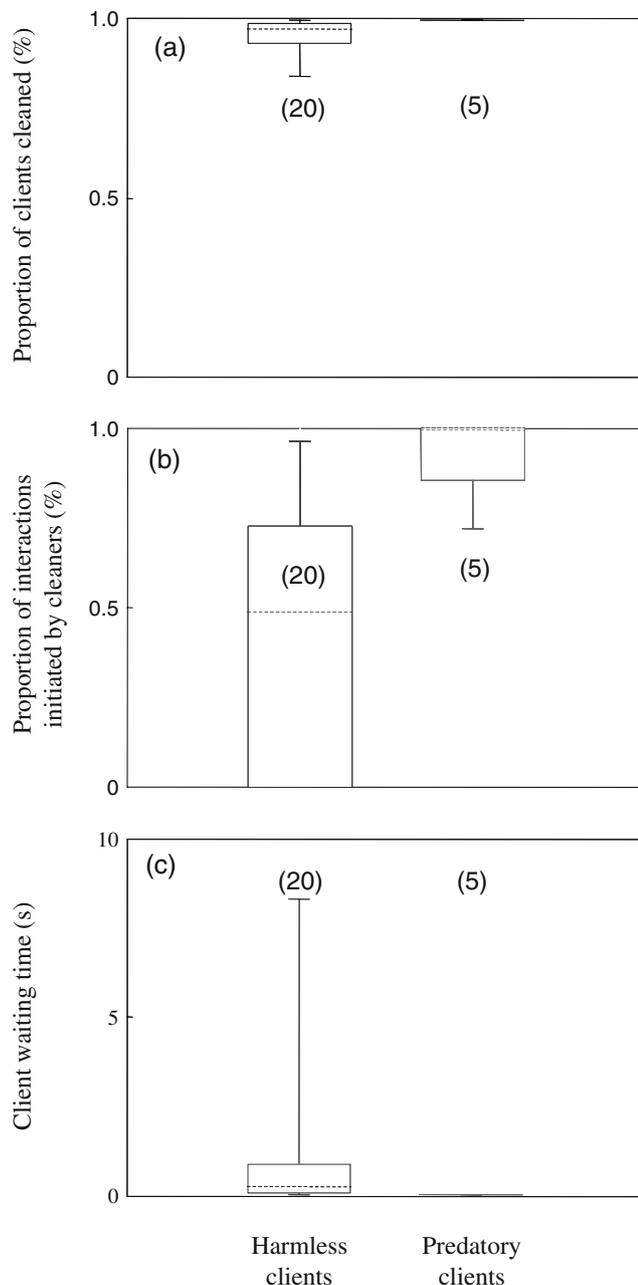


Fig. 1 (a) Proportion of visiting clients that were cleaned (number of clients cleaned/total number of visits), (b) proportion of cleaner-initiated cleaning events (number of cleaning events initiated by gobies/total number of cleaning events), and (c) client waiting time (in seconds) at cleaning stations, for harmless and predatory clients of Caribbean cleaning gobies. Medians (*dashed lines*) and interquartile ranges are shown. Sample sizes are given in parentheses

$n_2=5$, $p=0.04$). However, a comparison of predators with non-predatory clients that were alone at cleaning stations revealed that harmless clients still waited longer to be inspected than predatory clients (median [interquartile range] harmless clients: 0.2 s [0–0.34 s]; predatory clients: 0 [0 s–0 s]; $U=22.5$, $n_1=20$, $n_2=5$, $p=0.04$). The rate of client visits to cleaning stations was significantly lower whilst predatory clients were being cleaned than when they were absent ($U=21.5$, $n_1=20$, $n_2=5$, $p=0.05$; Fig. 2).

There were, however, no differences in any of the three measures of cleaning service quality. Inspection duration did not differ between harmless and predatory clients ($U=26.0$, $n_1=20$, $n_2=5$, $p=0.10$). There was no difference in the rate of switching from a current client to a newly arrived harmless or predatory client ($U=35.0$, $n_1=20$, $n_2=5$, $p=0.17$). Although harmless clients jolted more than twice as often as predatory clients during inspections, this difference was not significant (mean \pm SE for harmless clients, 1.37 \pm 0.33 jolts min^{-1} ; predatory clients, 0.55 \pm 0.28 jolts min^{-1} ; $t_{23}=1.2$, $p=0.24$).

Covariation between ectoparasite load and risk of predation

We could not detect a difference in ectoparasite load between harmless and predatory clients (median [interquartile range] harmless clients, 2.25 ectoparasites [0.52–8.95]; predatory clients, 1.28 ectoparasites [0–11.20]; $U=23.0$, $n_1=20$, $n_2=3$, $p=0.57$). Moreover, although predators were larger than harmless clients, this difference was not significant (mean \pm 1 SE for harmless clients, 16.14 \pm 1.51 cm; predatory clients 26.99 \pm 9.82 cm; $t_{21}=2.09$, $p=0.38$). Therefore, there appears to be no covariation between client ectoparasite load and risk of predation posed to cleaning gobies and their clients.

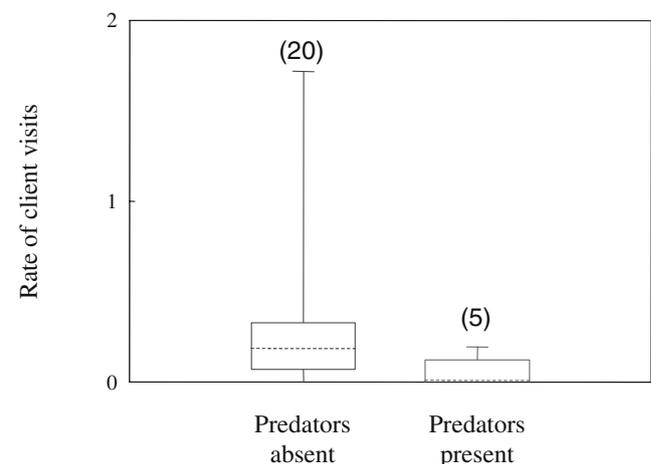


Fig. 2 Number of clients visiting cleaning stations per minute in the presence or absence of predatory clients. Medians (*dashed lines*) and interquartile ranges are shown. Sample sizes are given in parentheses

Discussion

Our results suggest that cleaning gobies do not experience a conventional trade-off between foraging intake and predation risk. Cleaning gobies did inspect preferentially client species with more parasites over those with fewer parasites. However, ectoparasite load did not covary with predation risk. Even in the absence of higher foraging benefits from cleaning predators, cleaners did not avoid risky clients. On the contrary, they provided a more rapid cleaning service to predatory clients: a larger proportion of these was inspected immediately upon arrival at a cleaning station and gobies initiated more interactions with predatory clients than with harmless clients. The immediate service given by cleaners to predators may be a tactic to be identified readily as cleanerfish rather than prey and/or to reduce the negative impact of the predators' presence on the rest of the clientele.

Ectoparasite load is an important determinant of cleaning goby preference for specific client species. Our findings that having more parasites increases a client's attractiveness to cleaners and reduces client waiting time are consistent with experimental (Gorlick 1984) and observational evidence (Grutter 1995; Arnal and Morand 2001) for a key role of ectoparasites in client choice by cleaners. Gorlick (1984), in particular, showed that cleaners associated preferentially with parasitised over experimentally deparasitised clients and that cleaner preference for client species could be reversed with a reversal in ectoparasite levels. Arnal et al. (2001) failed to find a relationship between client ectoparasite load and the likelihood of being inspected by the same cleaning goby species as those we studied. However, their study included only eight client species and, thus, had low statistical power. Interestingly, whilst client ectoparasite load increased the likelihood of a client being cleaned, it did not increase the quality of the cleaning service as we measured it. Clients with more ectoparasites were not inspected for longer, preferentially switched to when cleaners were already engaged in cleaning, or cleaned more honestly. Although cleaning inspection time has been observed to be related to ectoparasite load (e.g. Grutter 1995; Arnal and Morand 2001), a negative relationship could reasonably be expected between these two parameters if high ectoparasite loads of clients lead to more rapid satiation of cleaners. Alternatively, no relationship may exist if cleaners search for ectoparasites and other items, which is the case for cleaning gobies (Arnal and Côté 2000; Whiteman and Côté 2002; Cheney and Côté 2005; M.C. Soares, unpublished data). The lack of effect of client ectoparasites on client jolting rate, an index of dishonest cleaning, is puzzling because cleaner wrasses have been found to cheat more on individual

clients with fewer parasites (Bshary and Grutter 2002). Our result may be caused by the coarseness of the species-level analysis carried out. Alternatively, jolts by clients of cleaning gobies may not indicate cheating as they do in interactions with cleaner wrasses.

A foraging–predation trade-off depends on positive covariation between foraging benefits and risk of predation. In our cleanerfish system, this covariation was not detectable and harmless and predatory clients exhibited similar ectoparasite loads. In the absence of a foraging advantage to cleaning predatory species, one may have expected avoidance of such species and preference for harmless species by cleaning gobies. Our results suggest the opposite: harmless clients had a lower likelihood of being inspected and were not given a more rapid service than predatory clients. In fact, cleaning gobies ignored or interrupted cleaning interactions only with non-dangerous clients. Predators were generally inspected immediately upon arrival to the cleaning station, with most interactions being initiated by cleaners. This was not simply the result of lack of competition for cleaning service because non-predatory clients that were alone at cleaning stations were still made to wait by cleaners before inspection began. This surprising preference for predatory clients can be explained if (1) rapid attendance of piscivores reduces predation rate on cleaners, (2) piscivores do not actually present a high risk of predation and/or (3) the presence of predators causes other negative effects on cleaners, which are attenuated by providing immediate cleaning service.

Immediate attendance of predatory fish could reduce the likelihood of predation on cleaning gobies if this results in quicker identification of cleanerfish as non-prey items. Cleaners appear to be recognised at a distance by clients through a suite of signals, which include size and colour (Stummer et al. 2004; Arnal et al. 2006), but short-distance cues are provided by physical contact between cleaner and client (Potts 1973a; Bshary and Würth 2001). This benefit of rapid attendance would, however, depend on whether predators do really pose a risk to cleaners. It has long been thought that cleaners are immune to predation, at least when they are cleaning (Feder 1966; Hobson 1971). Although occurrences of predation on cleaners have been noted, as evidenced by gut content analyses, there have been no recorded attempts at predation by clients during cleaning events (Côté 2000; Francini-Filho et al. 2000). Colin (1975) also suggested that some cleaning gobies may be unpalatable. The fact that cleaning gobies inflicted jolt-causing bites at a similar rate on non-predatory and predatory clients suggests that the latter may pose a lower risk of predation to cleaners than their piscivorous diet would suggest. However, note that this conclusion may not apply to all cleanerfish. The predatory clients of the Indo-Pacific cleaner wrasse *Labroides dimidiatus* rarely jolt in

response to inspection (Bshary and Noë 2003), despite the fact that the overall rate of harmful bites delivered by cleaner wrasses (~3.75 jolts per 100 s, on average; Bshary 2001) is higher than that of cleaning gobies (1.37 jolts per 60 s, on average; this study). Piscivores may therefore pose a real risk to cleaner wrasses.

Predatory clients also appear to have indirect effects on cleaning gobies. We found that the presence of predators at cleaning stations reduced the rate of client visits to these stations. The grouper *Epinephelus cruentata* alone was responsible for a 58% decrease in visits to cleaning stations whilst it was being cleaned, with small-sized clients responding most strongly (M.C.S. unpublished data and personal observations). A similar predator-induced decline in client numbers was noted by Potts (1973a) at cleaning stations operated by the wrasse *L. dimidiatus* on Pacific reefs. This effect is also reminiscent of the sharp reduction in client visits to *L. dimidiatus* stations caused by the presence of nearby cleanerfish mimics, which attack passing fish to remove tissues and scales (Côté and Cheney 2004). Immediate handling by cleaners of predatory clients that wish to be inspected should reduce the opportunity cost of these visits.

In conclusion, the client preferences of cleaning gobies are usually governed by a conventional motive: they prefer clients that yield a higher foraging benefit because of their greater parasite load. However, these preferences are altered in an unusual manner by the indirect negative impacts that some rare clients (predators) have on visits by other more abundant clients (non-predatory species). Dealing efficiently with predatory clients may allow gobies a faster access to their main food source: harmless clients.

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