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Geographic Variation in the Behaviour of the Cleaner Fish *Labroides dimidiatus* (Labridae)

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Abstract

Geographical variation in the outcome of interspecific interactions has a range of proximate ecological causes. For instance, cleaning interactions between coral reef fishes can result in benefits for both the cleaner and its clients. However, because both parties can cheat and because the rewards of cheating may depend on the local abundance of ectoparasites on clients, the interaction might range from exploitative to mutualistic. In a comparative analysis of behavioural measures of the association between the cleaner fish *Labroides dimidiatus* and all its client species, we compared cleaning interactions between two sites on the Great Barrier Reef that differ with respect to mean ectoparasite abundance. At Heron Island, where client fish consistently harbour fewer ectoparasites, client species that tended to pose for cleaners were more likely to receive feeding bites by cleaners than client species that did not pose for cleaners. This was not the case at Lizard Island, where ectoparasites are significantly more abundant. Client fish generally spent more time posing for cleaners at Lizard Island than their conspecifics at Heron Island. However, fish at Heron Island were inspected longer on average by cleaners than conspecifics at Lizard Island, and they incurred more bites and swipes at their sides per unit time from cleaners. These and other differences between the two sites suggest that the local availability of ectoparasites as a food source for cleaners may determine whether clients will seek cleaning, and whether cleaners will feed on parasites or attempt to feed on client mucus. The results suggest that cleaning symbiosis is a mosaic of different outcomes driven by geographical differences in the benefits for both participants.

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Introduction

Mutualisms are interactions between species in which both participants experience a net benefit (Cushman & Beattie 1991). It has largely been assumed that such interactions have single outcomes. Recent research has demonstrated, however, that geographical variation in behaviour does occur (Foster & Endler 1999). Proximate ecological conditions can affect the costs or benefits of mutualism, and a 'cooperative' interaction may have a range of outcomes, from beneficial to antagonistic, across its geographical range (Bronstein 1994).

Cleaning behaviour, in which a cleaner organism removes ectoparasites from clients, is an example of mutualism widespread on coral reefs (Losey 1987; Poulin & Grutter 1996). Most studies on the ecological significance of cleaning have concentrated on its benefits (Limbaugh 1961; Youngbluth 1968; Losey 1972; Gorlick et al. 1987; Grutter 1996a, 1997a, 1999) with only the latter study demonstrating that cleaners control parasite abundance on fish and that clients therefore benefit from cleaning. There are, however, costs involved in cleaning, which may affect the client's net fitness (Poulin & Vickery 1995; Poulin & Grutter 1996). The likelihood of cheating in cooperative interactions is high and both cleaners and clients can cheat. Cleaners feed on client mucus, scales or skin (Youngbluth 1968; Gorlick 1980; Grutter 1997b; Sazima et al. 1998), which may be costly to the client. Clients may also 'cheat' by eating cleaners (Lobel 1976). Using a game theory model, Poulin & Vickery (1995) demonstrated that honesty, rather than cheating, is the best strategy for clients under most circumstances. Similarly, honesty is the best strategy for cleaners only if feeding on ectoparasites is more profitable than feeding on client tissues. There is little empirical information on the strategies used by cleaners and clients and how these might covary with ectoparasite availability. Geographical variation in the abundance of ectoparasites might indicate that this usually mutualistic association deteriorates where the low availability of parasites makes cheating an attractive option for cleaners.

One way to approach geographical comparisons would be to examine the relationships between the different behaviours involved in cleaning; this would yield insight into the potential causes of specific behaviours, as well as determine how the responses of the two participants to one another vary with local ectoparasite abundance. Clients often solicit the attention of the cleaner by posing, one of the most characteristic features of cleaning interactions involving tail- or headstands, flaring of the gills, or erection of fins (Potts 1973a; Losey 1979). Not all client fish pose, and Kuwamura (1976) suggested that fish that are preferred by cleaners do not have to pose in order to be cleaned. Recently, Côté et al. (1998) proposed a model that suggests that posing may be related to parasite load. For external parasites, fish size is a good indicator of parasite load (Poulin & Rohde 1997; Grutter & Poulin 1998a). Cleaner fish therefore should seek out larger fish and larger fish should pose less. Before or after a client poses, the cleaner engages in inspection behaviour, swimming close to the client, facing it and touching it with its fins or mouth (Potts 1973b). While inspecting clients, cleaners may feed by taking small bites from the body, fins, and gills of the client. Some cleaners also take swipes at the sides of clients, scraping their open mouth along the skin of clients. The most likely function of swipes is the ingestion of client mucus, which is common in the gut of cleaners from areas with low ectoparasite abundance on clients (Gorlick 1980; Grutter 1997b). Swiping has been associated with mucus removal based on field observations of juvenile damselfish (Robertson 1973) and experimental evidence in juvenile cichlids (Ward & Barlow 1967). In captivity, the cleaner wrasse *Labroides dimidiatus* swipes the sides of unparasitized and lightly anaesthetized fish or mucus-coated plastic plates, even when alternative food sources are available (Bshary & Grutter, in preparation). Cleaners can remove significant amounts of mucus from a fish, especially since client fish often make numerous visits to cleaning stations every day (Grutter 1996b). The benefits of mucus for fish are well known and include protection from parasites and other pathogens, and reduction of friction during swimming (Ebran et al. 1999 and references therein); thus swiping may be a form of cheating by cleaners with costs for clients. Occasionally, clients appear to respond negatively to cleaners. They twitch while being cleaned, flee from an inspecting or approaching cleaner, or behave aggressively towards a cleaner and end the interaction by chasing it (Potts 1973a; Kuwamura 1976; Losey 1979). More information is needed on antagonistic interactions in cleaning to understand how it is maintained as a mutualism.

In the only geographical comparison of cleaning, Losey (1974) suggested that variation in parasite load may, in part, explain the differences in cleaning he found between Hawaiian and Caribbean cleaner fish. This comparison, however, involved different cleaner fish species. The low numbers of parasites on fish in Hawaii (Losey 1972) may explain why the Hawaiian cleaner fish *Labroides phthirophagus* eats so few parasites (Youngbluth 1968) and much host mucus, suggesting it parasitizes client fish (Gorlick 1980). Intraspecific comparisons between populations are needed to assess the role of parasite abundance or other factors in creating spatial variation in cleaning interactions. This is a promising avenue, as many fish species display sets of behavioural traits that vary across populations (e.g. Bakker 1986; Endler 1995; Houde 1997; Magurran 1999).

On the Great Barrier Reef, *Labroides dimidiatus*, the most ubiquitous cleaner fish in the Indo-Pacific (Randall 1958), cleans hundreds of different fish species (Kuwamura 1976; Grutter & Poulin 1998b), providing a large number of replicates of behavioural interactions with cleaners. It feeds selectively on large numbers of ectoparasitic gnathiid isopods and on low numbers of parasitic copepods (Grutter 1997b). At Lizard Island, *L. dimidiatus* feeds primarily on ectoparasitic gnathiid isopods. In contrast, at Heron Island, 1000 km south of Lizard Island, it eats fewer gnathiids and more (although in small amounts) mucus and nonparasitic copepods (Grutter 1997b). These dietary differences are supported by differences in the abundance of gnathiids between locations, with clients from Heron Island consistently having fewer gnathiids than clients from Lizard Island in pairwise comparisons within the most common fish species (Grutter & Poulin 1998a). The *L. dimidiatus*–client fish system is thus an ideal model for examining geographical variation in cleaning.

We approached this question in two ways. First, we performed separate comparative analyses across client species for each of the two locations. Assuming that low ectoparasite abundance can promote cheating in cleaners (see Poulin & Vickery 1995), we expected that client and cleaner behaviours should relate differently at each location. More specifically, we expected that, across client species, as the tendency to pose or the duration of inspection increased, the likelihood of antagonistic behaviours (swiping by cleaner; twitching, fleeing or chasing of the cleaner by clients) would increase at Heron Island but not at Lizard Island. Secondly, in pairwise comparisons within client species but between locations, we expected that the tendency of clients to pose should be lower at Heron Island where their mucus is more at risk than at Lizard Island, but that the duration of inspections by cleaners should be longer at Heron as they spend more time searching for the rarer parasites than they would at Lizard Island. Also, we expected that the likelihood of antagonistic behaviours should be greater at Heron than at Lizard Island.

Methods

Focal animal sampling was used to observe the behaviour of adult *Labroides dimidiatus*. One cleaner at a time was observed by a snorkeller or scuba diver for 40 min; this observation period was selected as Grutter & Poulin (1998b) showed that the number of new species interacting with a cleaner after 30 min was low. A total of 46.67 h of observations were made with 35 observations at each location. Observations were spread randomly throughout the day (i.e. among 2-h periods from 06:00 to 18:00 h) and taken from different sites around Heron Island (23°27′S, 151°55′E) and nearby Wistari Reef between 1 Apr. and 12 May 1998, and the inner reefs of Lizard Island (14°40′S, 145°26′E) between 6 and 15 Mar. 1999. A different cleaner was chosen haphazardly for consecutive observation periods at the same site. The areas covered each contained several hundred cleaners, and any individual cleaner is unlikely to have been used more than once as the focal animal. Each cleaning interaction was recorded separately and each client species was identified. The variables measured are defined in Table 1. The complete data set is available from the authors upon request.

For the interspecific comparative analysis, we used only client species for which at least five observations had been made. To remove potential phylogenetic influences, we used the method of phylogenetically independent contrasts (Felsenstein 1985) which consists in deriving independent contrasts between sister taxa in a phylogeny of client fish species. The computations were made on log-transformed data following the procedures outlined in Garland et al. (1992), using the CAIC program, version 2.0 (Purvis & Rambaut 1994). To derive contrasts we used the proposed fish phylogeny and taxonomy of Nelson (1994). No corrections for true branch lengths could be made, but the method is robust

Table 1: Description of cleaner and client behaviours recorded during field observations

Behaviour	Description
Inspection time	The total time that a cleaner spent inspecting a client visually within 5 cm of it.
Pose	The presence or absence of posing, defined as remaining motionless with spreading out of the fins, opening of the mouth or the gill operculae, or orienting of the head up or down.
Bite	The number of bites per cleaner fish inspection was counted. A bite was recorded as contact of the cleaner's mouth to part of the client's surface, usually in a feeding context.
Swipe	The number of swiping bites was recorded separately from normal bites and differed in that the cleaner would swipe its mouth along the surface of its client. The distance swiped varied but was greater than that of a normal 'pecking' bite. These bites appeared visually more aggressive than a normal bite.
Twitch	The number of twitches was counted for every cleaning bout. A twitch was an obvious jolt of the client's body, usually in response to some stimuli provided by the cleaner.
Flee	The presence or absence of fleeing by the client. Fleeing was considered avoidance behaviour and involved the client swimming away from the cleaner.
Chase	The presence or absence of chasing, i.e. rapid pursuit, of the cleaner by the client.

and the lack of correction should not inflate Type I error rates (Purvis et al. 1994). Relationships among contrasts were assessed with correlations and regressions forced through the origin (see Garland et al. 1992 for justification). When significant outliers were identified, following the method of Pearson & Hartley (1954), analyses were repeated after their exclusion. When contrasts in one behavioural trait correlated significantly with contrasts in client body size, we regressed the contrasts in that trait on contrasts in body size and used the residuals as measures of the trait corrected for body size. The measure of client body size used was the maximum length of the species provided in Randall et al. (1997), and the parasite (gnathiid isopod) data were from Grutter & Poulin (1998a).

To test for differences between locations in the presence or absence of a behaviour in a species, the proportion of client species that posed, received bites from cleaners, were swiped by cleaners, twitched, chased cleaners, and fled from cleaners was compared; all species were included and Yate's corrected chi-square tests were used (Zar 1999). To examine whether the mean intensity of these behaviours per species differed between locations, only the 58 species that were found at both locations and had at least five observations each were used. We used paired *t*-tests when the assumption of equal variances was met using Levene's test; when the variances were not equal Wilcoxon's rank sums test was used.

To determine whether the total amount of time that *L. dimidiatus* spent cleaning and whether the total number of fish per observation periods differed between locations, the sum of all inspections and the frequency per observation period were calculated. As the variances between locations were not homogeneous (Levene's test) (they were more variable at Heron Island), Wilcoxon's rank sums tests were used. To estimate the total time cleaners spent cleaning per day and the total number of fish they cleaned per day, the mean duration and mean frequency per observation period were multiplied by the number of hours that cleaners were active (estimated at 12 h following Grutter 1996b).

Results

Cleaning Behaviour at Heron Island

Labroides dimidiatus cleaned 124 species at Heron Island. The 81 client species for which we had at least five observations generated a total of 38 sets of phylogenetically independent contrasts on which the following results are based. Client body size was not correlated with average inspection time ($r = 0.278$, ns) and the tendency to pose ($r = –0.272$, ns) but it was correlated with the tendency to chase cleaners ($r = 0.369$, $p < 0.01$). However, after removing single outlier points in all three analyses, client body size was no longer correlated with the tendency of clients to chase cleaners ($r = 0.042$, ns) and it was still not correlated with the tendency of clients to pose ($r = –0.096$, ns); whereas there was now a positive relationship between client body size and average inspection time (Fig. 1a). Thus only the latter variable was corrected for client body size in subsequent analyses.

The client's tendency to pose and the mean inspection time by cleaners were strongly correlated across client species (Fig. 1b). Longer inspection times were also associated, although not quite significantly, with fewer swipes per unit time ($r = –0.312$, $0.1 > p > 0.05$), but were not related to the client's tendency to either chase cleaners ($r = –0.062$, ns) or flee from them ($r = 0.020$, ns).

Client species with a higher frequency of posing were more likely to receive bites ($r = 0.385$, $p < 0.01$) and received more bites per unit time (Fig. 1c). Client species with a greater tendency to pose were also more likely to twitch during an inspection event (Fig. 1d). Although not significant, the tendency to pose was negatively associated with the number of swipes per unit time across client species ($r = –0.272$, ns).

The likelihood that a fish species received bites correlated strongly with its tendency to twitch (Fig. 1e) and with the number of twitches shown per unit time (Fig. 1f). Similar results were obtained when the number of bites received per unit time was used in the analysis instead of the likelihood of getting bitten. Neither the likelihood that a fish species received swipes nor the number of swipes received

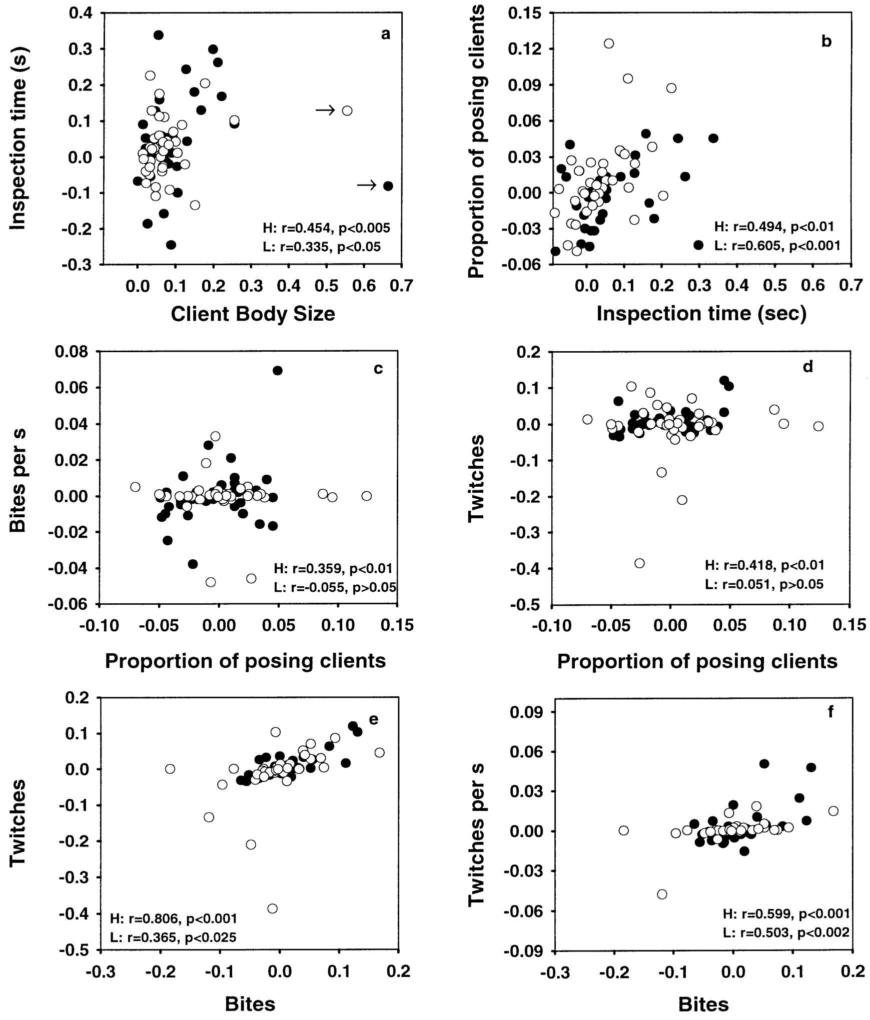

Fig. 1: Relationships among phylogenetic contrasts in behaviours observed between the cleaner fish *Labroides dimidiatus* and its client fish species at Heron Island (H, black symbols) and Lizard Island (L, open symbols). See Table 1 for definitions of behaviours. Arrows indicate outliers that were excluded from the analyses; correlation coefficients shown were computed after exclusion of the outliers

per unit time correlated with the tendency of the fish to show aversive responses such as chasing cleaners or fleeing from them (all $r \leq 0.180$, ns).

Parasite load data were only available for 18 of the 81 fish species used in the analysis, and the following results are therefore based on 14 sets of independent contrasts. After variables were corrected for fish body size, no correlations were found between parasite load and either average inspection time (Fig. 2a) or the client's tendency to pose for cleaners (Fig. 2b).

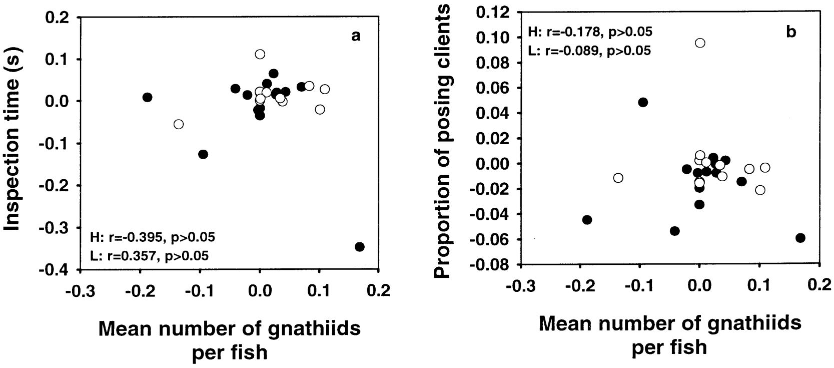

Fig. 2: Relationships among phylogenetic contrasts in parasite (gnathiid isopods) load and behaviours observed in cleaning interactions involving different species of client fish at Heron Island (H, black symbols) and Lizard Island (L, open symbols)

Cleaning Behaviour at Lizard Island

At Lizard Island, *L. dimidiatus* cleaned 111 species. The 83 client species for which we had at least five observations generated a total of 38 sets of phylogenetically independent contrasts on which the following results are based. Similar to Heron Island, client body size correlated positively with average inspection time ($r = 0.396$, $p < 0.025$); this relationship still remained after an outlier was removed (Fig. 1a). As for the Heron Island data, client body size did not correlate significantly with the tendency to pose ($r = 0.028$, ns) and with the tendency to chase cleaners ($r = 0.172$, ns). Thus, neither of these variables has been corrected for client body size in subsequent analyses.

As for the Heron Island data, the client's tendency to pose and the mean inspection time by cleaners were strongly correlated across client species (Fig. 1b). Again, longer inspection times were associated with fewer swipes per unit time, although not significantly ($r = -0.243$, ns), and had no apparent relationship with the client's tendency to either chase cleaners ($r = 0.005$, ns) or flee from them ($r = 0.062$, ns).

Unlike the patterns observed at Heron Island, client species with a greater tendency to pose were not more likely to receive bites ($r = -0.047$, ns) nor did they receive more bites per unit time (Fig. 1c). Client species with a greater tendency to pose were also no more likely to twitch during an inspection event (Fig. 1d) than species that posed less frequently, and the tendency to pose did not correlate with the number of swipes per unit time across client species ($r = -0.133$, ns).

Similar to Heron Island, the likelihood that a fish species received bites correlated positively with its tendency to twitch (Fig. 1e) and with the number of twitches shown per unit time (Fig. 1f). Similar results were obtained when the number of bites received per unit time was used in the analysis instead of the likelihood of getting bitten. Consistent with the Heron Island results, neither the likelihood that a fish species received swipes nor the number of swipes received per unit time correlated with the tendency of the fish to show aversive responses such as chasing cleaners or fleeing from them (all $r \leq 0.202$, ns).

Parasite load data were only available for 19 of the 84 fish species used in the analysis, and the following results are based on the 12 sets of independent contrasts that could be generated from these species. After variables were corrected for fish body size, no correlations were found between parasite load and either average inspection time, although there was a positive trend (as we predicted) (Fig. 2a), or the client's tendency to pose for cleaners (Fig. 2b).

Comparison of Behaviours Between Locations

The number of species that posed at Lizard Island (88%) was significantly higher than that at Heron Island (70%) (Yate's corrected $\chi^2 = 10.32$, df = 1, $p < 0.001$). In contrast, the percentage of client species (percentage of species at Lizard Island/Heron Island) that received bites from cleaners (70/60), were swiped by cleaners (35/32), twitched (62/48), chased cleaners (35/36), and fled from cleaners (59/62) did not differ between locations (all ns).

On average, client species at Heron Island were inspected 1.3 times longer than their conspecifics from Lizard Island ($t = -3.051$, df = 57, $p < 0.005$); however, a client species' tendency to pose did not vary between locations ($t = 0.0452$, df = 57, ns) (Fig. 3). Although the number of bites taken per species did not varysignificantly between locations ($t = 0.8301$, df = 57, ns) the number of bites taken per unit time did, with cleaners at Heron Island taking 3.5 times more bites per client species than those from Lizard Island ($z = 4.264$, $p < 0.001$) (Fig. 3). Similarly, the proportion of times a client species was swiped did not vary between locations ($t = -0.611$, df = 57, ns); however, the number of swipes per unit time did ($z = 3.073$, $p < 0.0025$), with 21 times more swipes taken from clients at Heron Island (Fig. 3). Again, the tendency for a client species to twitch did not vary between locations ($z = 0.017$, ns) but it did so when standardized for time, with client species from Heron Island twitching 2.8 times more per unit time than those at Lizard Island ($z = 3.038$, $p < 0.005$) (Fig. 3). The proportion of times that a client species fled from cleaners ($t = -0.462$, df = 57, ns) or chased cleaners ($t = -0.907$, df = 57, ns) did not differ between locations (Fig. 3).

Labroides dimidiatus spent 1.4 times more time inspecting fish at Heron Island than at Lizard Island ($z = 3.39$, $p < 0.001$) with a $\bar{x}$ (SE) of 796 (53) s/h at Heron Island and 557 (33) s/h at Lizard Island. The number of fish inspected by *L. dimidiatus* did not differ between locations ($z = 1.61$, ns) with cleaners inspecting 228 (18) fish/h at Heron Island and 194 (12) fish/h at Lizard Island. Thus the average individual cleaner at Heron Island spent an estimated 159 min inspecting 2736 fish/d while at Lizard Island it spent about 111 min inspecting 2328 fish/d.

Discussion

Interactions between the cleaner *Labroides dimidiatus* and its many clients differed over a distance of 1000 km. Our expectations regarding the comparative

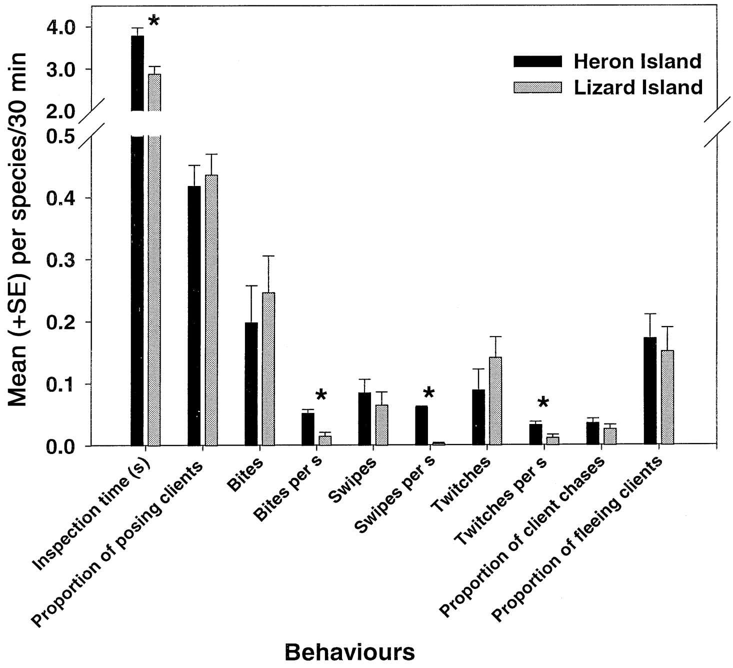

Fig. 3: Cleaning behaviours per client fish species at Heron Island and Lizard Island. Data are for 58 client species present at both sites

analyses across client species were not realized, but the differences we expected in between-site comparisons were generally supported by the data. The diet of cleaners also differs between these locations, with cleaners eating more parasitic gnathiid isopods at Lizard Island than at Heron Island (Grutter 1997b). Furthermore, clients are consistently infested with more gnathiids at Lizard Island than Heron Island (Grutter & Poulin 1998a). Of course, to determine the causes of geographical variation in behaviour, experimentation is necessary to rule out the influence of covarying factors. Nevertheless, our results suggest that variation in cleaning behaviour is linked to spatial variation in ectoparasite abundance.

Although *L. dimidiatus* cleaned similar numbers of fish at the two locations they spent more time inspecting fish at Heron Island than at Lizard Island. This suggests that the costs of foraging are higher at Heron Island. These geographical differences are unlikely to be caused by the confounding effect of different sampling times. Although we collected data from Heron and Lizard Islands in different years, we did so at the same time of year.

The swiping behaviour of cleaner fish differed geographically. Cleaners took, on average, 21 times more swipes per unit time per client species at Heron Island than at Lizard Island. At both locations, there was a trend for inspection time to decrease as swipe frequency increased. Swiping may therefore be perceived by the client as an aggressive behaviour, although its real function is unclear. Potts (1973a) mentioned a similar aggressive behaviour by a cleaner which attacked, with a ramming bite, the flank of potential competitors. The 'swiping' behaviour described here was similar but appeared in a different context. Lucas & Benkert (1983) described swiping behaviour in the planktivorous *Oligoplites saurus* that occasionally feeds on fish scales; they compared it to the feeding behaviour of true scale-feeders. Glasby & Kingsford (1994) described 'skimming behaviour' in the planktivorous fish *Atypichthys strigatus* which occasionally cleans other fish. In our case, since swiping involves the use of the cleaner's mouth, 'swiping' against the body surface of clients may involve feeding on mucus (see also Ward & Barlow 1967; Robertson 1973). Seven of the 10 species that received the most swipes at Heron Island were labrids and scarids; these are well known for their thick coat of mucus compared to other species (Gorlick 1980) that received few swipes. Fish mucus contains lipids that are energy rich (Lewis 1970) and some cleaners remove this food from clients (Gorlick 1980; Grutter 1997b; Sazima et al. 1998). If swiping is a method of feeding on mucus, the geographical differences in swiping behaviour may be due to geographical differences in parasite availability.

Field observations support the hypothesis that swipes by cleaners are 'predatory'. At Heron Island, parrotfish were often observed to swim away from cleaners (C. Bansemer, pers. obs.). *Labroides dimidiatus* often moved rapidly into schools of scarids and then took swipes from the fish. This behaviour appeared more like that of the false cleaner *Aspidontus taeniatus* which mimics *L. dimidiatus* to tear away pieces of fins from unsuspecting clients (Wickler 1966; Kuwamura 1983). Our quantitative results, though, provide no compelling evidence that swiping by cleaners elicits negative responses in clients.

This is the first study to show that inspection time increases with client size (Poulin 1993; Grutter 1995; Grutter & Poulin 1998b). Previous studies assumed that a positive relationship between cleaning rate and fish size indicates a mutualistic relationship as larger fish, which are more likely to be heavily parasitized (Poulin & Rohde 1997; Grutter & Poulin 1998a), should seek cleaners more and be preferred by cleaners over less parasitized clients (Poulin 1993; Grutter & Poulin 1998b). However, the amount of mucus on clients probably also increases with the size of fish. It is possible that cleaners may feed longer on larger clients not only because they have more parasites but also because they provide more mucus.

At both locations, clients that posed more were inspected for longer periods than clients that posed less. Côté et al. (1998) also found that clients that posed were more likely to be cleaned, and were cleaned for longer periods. Posing therefore appears to facilitate cleaning interactions. Ectoparasite load usually increases with host size (Poulin & Rohde 1997; Grutter & Poulin 1998a). Posing tendency, however, was not correlated with fish size at either location, nor with gnathiid load, and more species posed at Lizard Island, where fish have more gnathiids, than at Heron Island. This was surprising as cleaners prefer infected clients and larger fish should provide cleaners with more food and thus be preferred. However, at Heron Island only, fish that posed more also received more bites, suggesting that clients that pose are cleaned better.

At both locations, twitching in clients increased with bites by cleaners. Losey (1979) suggested client twitches serve as warning signals. The current study suggests that client twitches are directly elicited by the bites taken by cleaners. This agrees with Sazima et al.'s (1998) observations that clients sometimes 'jerk' after being bitten by a cleaner. Pain is likely to be associated with the removal of ectoparasites or mucus and twitches may be the client's nonaggressive reaction to it. Surprisingly, at both Lizard and Heron Island, swiping behaviour was not related to clients chasing or fleeing from cleaners. Chasing and fleeing were also not related to inspection time, suggesting that cleaning bouts were not terminated sooner prior to chasing or fleeing from a cleaner. Similarly, chasing was not related to fish size at either location, suggesting that small client fish are as likely to respond aversively by chasing as large fish are. Thus cleaners may behave similarly towards all sizes of fish.

The above patterns suggest that the foraging behaviour of cleaners is affected by parasite availability. At Heron Island, gnathiid isopods make up 76% of the diet of cleaners (Grutter 1997b). More interestingly, the species most cleaned by cleaners was *Hemigymnus melapterus* which has the highest abundance of gnathiids of all teleosts at Heron Island (Grutter & Poulin 1998a). Their high frequency of cleaning was not due to their abundance as they were not the most abundant client species (C. Bansemer & A. Grutter, pers. obs.). Despite also having the most gnathiids at Lizard Island (Grutter & Poulin 1998b) and a similar density on the reef as at Heron Island (A. Grutter, pers. obs.), *H. melapterus* was not the most frequently cleaned fish at Lizard Island (ranked ninth out of 108 client species). This may be due to the fact that gnathiids are common on other fish at Lizard Island and therefore cleaners need not be as selective in their choice of clients.

Our results suggest that 'cheating' may occur in cleaning (Poulin & Vickery 1995; see also Weeks 2000) and that it can vary geographically. More information on the net outcomes of these interactions is needed to determine the evolutionary significance of this variation. It may relate to differences in the rewards of honesty: where honesty does not pay much, cheating may be favoured, as predicted by Poulin & Vickery's (1995) model. To understand the ecological role of cleaning behaviour on coral reefs we need to identify how cleaning behaviour is maintained when cheating is possible. Asymmetry in client cheating may occur as not all clients can cheat by eating cleaners. A recent study suggests that herbivorous surgeonfish, which cannot cheat by eating cleaners, use punishment to control cheating in cleaners (Bshary & Grutter, in review). More information is needed on how other clients control cheating in cleaners and how cleaners in turn avoid cheating in clients, particularly piscivorous clients.

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