

## ARTICLES

# Client fish ectoparasite loads and cleaner shrimp *Urocaridella* sp. c hunger levels affect cleaning behaviour

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Cleaning is a classic example of mutualism and determining the factors that maintain the balance between the costs and benefits for mutualist partners can assist our understanding of how cleaning relationships are maintained. Optimal foraging theory suggests two factors that might help to maintain the relationship between cleaners and their clients: client ectoparasite load and cleaner hunger levels. The ecological relevance and importance of foraging by cleaner fish in marine systems has been demonstrated repeatedly, yet there is little information available on this behaviour in cleaner shrimp. To determine whether cleaner shrimp base their choice of client fish on food patch quality (i.e. client fish ectoparasite load) we offered the yellow-beaked cleaner shrimp *Urocaridella* sp. c a choice of parasitized and unparasitized rock cods, *Cephalopholis cyanostigma*. To determine whether cleaner shrimp hunger levels influence cleaning time, we manipulated hunger levels in *Urocaridella* sp. c and examined their behaviour towards parasitized client fish. Cleaner shrimp preferred parasitized to unparasitized client fish and food-deprived cleaner shrimp cleaned parasitized rock cods more frequently than satiated cleaner shrimp did. Therefore, variations in client fish ectoparasite load and cleaner shrimp hunger level are two factors that affect the balance in this mutualism. Finally, our results meet some of the assumptions of biological market theory, a framework used to understand cooperative interactions, and thus this framework is suggested for future studies on this cleaning system.

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Mutualisms are ubiquitous in ecological systems and their importance is well appreciated (Bronstein 2001). The question that often arises when studying these systems is how are the relationships maintained? Determining which factors maintain the balance between the costs and benefits for mutualist partners can assist in answering this question. One system that has been referred to as a classic example of a mutualism is the relationship between cleaners and their clients (Trivers 1971; Cushman & Beattie 1991). Cleaner organisms remove and eat ectoparasites and other material, such as mucus, scales and skin, from the body surfaces of other apparently cooperating animals, also known as clients (Feder 1966). The benefit to the cleaner is that it gains food, while the client benefits by having its parasites removed. Proximate cues that maintain the relationship are likely to be a cleaner's desire to clean and a client's desire to be cleaned. Two factors that might

influence a cleaner's desire to clean are its hunger levels and its client's ectoparasite loads. When a cleaner is hungry, the only way to obtain food is by actively searching or foraging. Cleaners are usually smaller than their clients (Feder 1966) and foraging may come at a cost, for example being eaten by a client. Therefore, there is likely to be a trade-off between the risk of being eaten (i.e. the cost of foraging) and the cost of not eating (i.e. starving).

Optimal foraging theory (OFT) has long been used as a framework to explain the costs and benefits of foraging in animals (Stephens & Krebs 1986) and foraging ideas have been used to describe cleaning associations in cleaners (Grutter 1995; Sikkel et al. 2000; Bshary & Grutter 2002b). Assuming there is no difference in food quality between patches, OFT suggests that a forager should choose the patch with the greatest amount of food to optimize its energy gain (Stephens & Krebs 1986). In accordance with this theory, cleaners should prefer clients that carry more ectoparasites (i.e. the more profitable food patch).

The benefits of foraging are likely to begin to outweigh the costs as an animal becomes hungry and it has been suggested that hunger is a proximate cue for cleaning

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behaviour in cleaners (Colin 1972; Côté & Molloy 2003). Since there is a trade-off between foraging and risk, we expect a positive correlation between hunger level and foraging, or willingness to clean. Therefore, a starved cleaner is more likely to engage in foraging behaviour and spend more time cleaning clients than a satiated cleaner.

Cleaning interactions involving fish as the cleaners have been studied intensively and have demonstrated the ecological relevance and importance of cleaning in marine systems (reviewed by Losey et al. 1999; Côté 2001). Cleaning interactions where shrimp are the cleaners are also common, yet little is known about them (reviewed by Côté 2001). Cleaner shrimp in the wild eat ectoparasites and reduce ectoparasite loads on client fish under laboratory conditions (Becker & Grutter 2004). Little information, however, is available on what factors affect the foraging behaviour of cleaner shrimp.

The majority of studies on cleaner shrimp foraging behaviour have been observational and assumed that client fish have ectoparasites and that the cleaner shrimp removed them but did not look for ectoparasites (Limbaugh 1961; Limbaugh et al. 1961; Feder 1966; Holzberg 1971; Sargent & Wagenbach 1975; Criales & Corredor 1977; Corredor 1978; Moosleitner 1980; Patzner 1982; Jonasson 1987; Dreyer 1994). Only three studies have addressed the issue of client fish ectoparasites when examining cleaner shrimp cleaning behaviour. Bunkley-Williams & Williams (1998) observed cleaner shrimp remove juvenile cymothoid isopods from captive client fish and Becker & Grutter (2004) found fish ectoparasites in the guts of wild cleaner shrimp. Turnbull (1981) found one fish ectoparasite in the gut of a cleaner shrimp but dismissed this finding suggesting that it was due to chance. Turnbull also mapped the locations of client fish ectoparasites and found a relationship with the area on the body of client fish that cleaner shrimp foraged. The evidence provided from these three studies suggests that ectoparasites are important in the cleaning or foraging behaviour of cleaner shrimp. Manipulating fish ectoparasite loads, therefore, may provide important information on the relationship between cleaner shrimp and their client fish.

The influence of hunger on cleaning by shrimp has been examined only once: increased hunger levels affected the selectivity of a cleaning response by cleaner shrimp (Colin 1972). Hunger levels occur on a continuum between starving and satiated. By comparing these extremes we can determine whether hunger activates a cue that influences a cleaner shrimp's willingness to clean.

To examine the effect of cleaner shrimp hunger and client ectoparasite load on cleaning behaviour, we used the yellow-beaked cleaner shrimp (Coleman 1993) *Urocaridella* sp. c (Debelius 1999) and client fish *Cephalopholis cyanostigma* which are parasitized with monogenean flatworms of the *Benedenia* genus. These monogeneans are the most commonly found ectoparasite on this client fish (J. Becker, unpublished data). Monogeneans also do not generally leave their host (Llewellyn 1972), so cross contamination between hosts during laboratory experiments was unlikely. To examine whether food patch

quality (i.e. ectoparasite load) influences where a cleaner shrimp chooses to forage, we exposed cleaner shrimp to client fish with and without ectoparasitic monogeneans. To examine whether hunger levels influenced when a cleaner shrimp cleaned, we exposed food-deprived and satiated cleaner shrimp to a parasitized client fish and recorded their behaviour.

## METHODS

Client fish and cleaner shrimp were collected from reefs within the Lizard Island Group, Australia (23°27'S, 151°55'E). After capture by hook and line, fish were allowed to acclimate to captivity in groups of four, in holding tanks (100 cm diameter × 50 cm) for at least 7 days. Shrimp were collected by divers using hand nets and allowed to acclimate to captivity in four glass aquaria (50 × 50 cm and 70 cm high), 15 shrimp per aquarium. All experiments were conducted in a flow-through aquarium system at the Lizard Island Research Station.

### Food Availability Manipulation

To determine whether cleaner shrimp prefer parasitized to unparasitized client fish we exposed them to client fish with and without ectoparasites. We manipulated ectoparasite loads on the two client fish (matched for size) used per trial ( $N = 12$  trials) by first anaesthetizing each fish with clove oil (Munday & Wilson 1997). This anaesthetic does not effect monogenean consumption by *Urocaridella* sp. c (Becker & Grutter 2004). One client fish received a freshwater bath for 2 min which kills and removes most ectoparasites on fish (Becker & Grutter 2004). The other fish received a salt water bath to control for the effect of handling the client fish. Both client fish were then placed in the experimental aquarium (70 × 70 cm and 50 cm high) for 24 h to recover and acclimate to the new environment. At the same time, we placed a cleaner shrimp in the experimental tank to acclimate. It was housed in a fine-mesh (1 × 1 mm) chamber (10 × 10 cm and 15 cm high) to prevent it from interacting with the client fish before the experiment. The experimental aquarium had an opaque screen in the centre that separated the client fish from each other, in compartments (20 × 35 cm and 50 cm high), so they could not interact and potentially influence the behaviour of the cleaner shrimp (see tank design by Östlund-Nilsson 2001). Galvanized wire mesh (2.5 × 2.5 cm) separated the client fish from the cleaner shrimp along a 'choice' compartment (15 × 70 cm) that spanned the two compartments housing the client fish. This allowed cleaner shrimp to reach both client fish via the wire mesh but did not allow the client fish to reach the cleaner shrimp or each other. A layer of sand 2 cm thick was placed in the bottom of the tank and PVC pipes (diameter 5 cm, length 12 cm) were provided as shelter for the cleaner shrimp and client fish during the experiment. We started the experiment by releasing the cleaner shrimp from its mesh compartment in the centre of the choice compartment. We recorded how long the cleaner shrimp spent in

physical contact with each client fish during 15-min observations at six times of day (0600–0700; 0830–0930; 1100–1200; 1300–1400; 1530–1630; 1800–1900 hours) for 2 days after the release of the cleaner shrimp. Observations were not conducted between 1900 and 0600 hours as cleaner shrimp did not clean during this time (J. Becker, personal observation). Physical contact was assumed to be a measure of the cleaning activity of the cleaner shrimp, as initial observations showed that cleaner shrimp clean client fish while crawling around the surface of the client fish. We used a univariate repeated measures ANOVA to examine the effect of parasite presence or absence on the cleaning duration of cleaner shrimp over 48 h with time interval being the repeated measure.

### Hunger Manipulation

To address the assumption that hunger influences cleaning time, we manipulated hunger levels in individual cleaner shrimp so that food-deprived and a satiated cleaner shrimp were exposed to a client fish. Before each trial ( $N = 16$  trials), one client fish and two cleaner shrimp were acclimated in the experimental tank (50 cm  $\times$  50 and 70 cm high) for 3 days. During this period, cleaner shrimp were housed in fine-mesh chambers to prevent shrimp and client fish from physically interacting with each other. One cleaner shrimp was fed daily to satiation with pieces of prawn (0.5 cm<sup>3</sup>) and the other was not fed. Each cleaner shrimp was individually marked with nail polish (Express Finish, Maybelline LLC, Distributor, New York, U.S.A.) so that we could recognize them. Both cleaner shrimp were released from their mesh nets at the same time and observed for seven 10-min blocks over 100 min. Recording time intervals began at 0, 10, 20, 30, 40, 50, 70, 90 min after release. The two cleaner shrimp were observed separately by two observers (one observer for the food-deprived cleaner shrimp and one observer for the satiated cleaner shrimp) and the time each cleaner shrimp spent in physical contact with the client fish was recorded. The nail polish colour codes used to identify each cleaner shrimp were allocated such that there were an equal number of colour codes used for all combinations of observer and cleaner shrimp treatment (i.e. food deprived or satiated). Different cleaner shrimp were used in all trials ( $N = 16$ ). We used a univariate repeated measures ANOVA to examine the effect of hunger level, colour code and observer on the time the cleaner shrimp spent cleaning the client fish over a 100-min period with the seven 10-min time intervals being the repeated measure.

Statistica version 6 (StatSoft Inc., Tulsa, OK, U.S.A.) was used for all statistical analyses.

### Ethical Note

We caught wild cleaner shrimp and client fish from reefs near Lizard Island under a permit from the Great Barrier Reef Marine Park Authority. All aquaria in which animals were kept had a direct influx of sea water and thus water temperature closely matched sea water temperature. Animals were fed on a daily basis (cleaner shrimp: mashed

prawns; client fish: pilchards (1.5 cm<sup>3</sup>, two pieces per individual) and prawn), unless in accordance with experimental procedures. Client fish always consumed the food they were offered within 24 h after capture. Each holding task containing fish was observed for 5-min periods three times a day (at ca. 0600, 1200 and 1800 hours) for any antagonistic interactions between fish or related injuries. If antagonistic interactions between fish appeared to place any fish in danger of injury, they were separated immediately. Eight fish needed to be transferred into a different holding task and one was transferred a second time. Individuals did not appear to be wounded or unhealthy after the experiments and fed normally. Client fish and cleaner shrimp were kept for a maximum of 4 weeks and then released at the capture sites. The University of Queensland Animal Ethics Committee approved all experiments.

## RESULTS

### Food Availability Manipulation

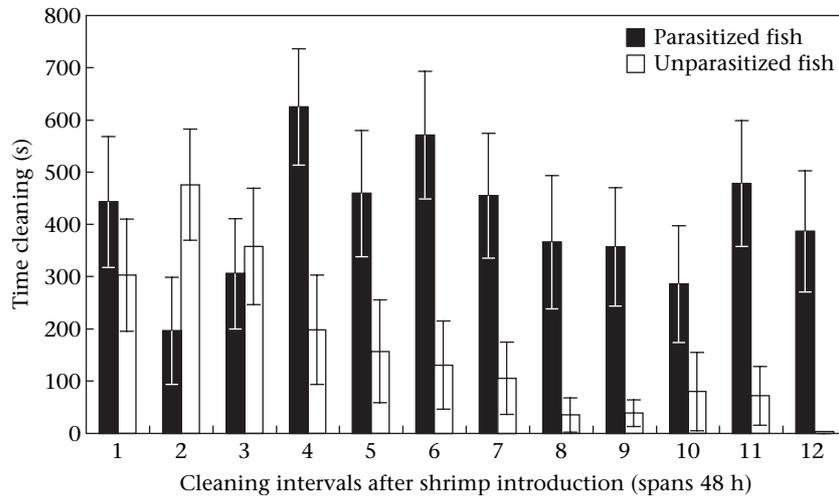
There was a significant interaction between the effect of parasite load and time interval on the time that cleaner shrimp spent cleaning individual client fish (Table 1). This was due to cleaner shrimp spending approximately equal times on client fish during the first three intervals and thus making no distinct choice of client fish (Fig. 1). After the three intervals, however, cleaner shrimp spent most of their time cleaning parasitized client fish (Fig. 1).

### Hunger Manipulation

There was a significant effect of hunger level on the time that cleaner shrimp spent cleaning client fish and this effect did not change over time (Table 2). In the full model there was no significant effect of colour code of cleaner shrimp ( $P = 0.285$ ) or of observer ( $P = 0.458$ ) on the time cleaner shrimp spent cleaning and all interactions among factors were highly nonsignificant ( $P = 0.820$ ), hence we omitted the factors colour and observer from the final analysis. The significant effect of hunger was due to the difference in time spent cleaning between the food-deprived and satiated shrimp for all time intervals except the last 10 min of the 100-min block when time spent cleaning appeared similar for both

**Table 1.** Univariate repeated measures analysis of variance testing for an effect of parasite presence or absence on the time cleaner shrimp *Urocaridella* sp. c spent cleaning the client fish *Cephalopholis cyanostigma* during 12 intervals over 48 h

Effect	Sums of squares	F	df	P
Parasite presence or absence (P)	4 430 024	9.0586	1	0.007
Residuals	10 758 845		22	
Time interval (T)		1.6763	11	0.079
P $\times$ T		3.2498	11	<0.001
Residuals	21 136 078		242	



**Figure 1.** The mean time  $\pm$  SE that cleaner shrimp spent cleaning parasitized and unparasitized fish during 15-min observation periods spread over a 48-h period. Only the time that cleaner shrimp were active was considered (the night was excluded).

cleaner shrimp (Fig. 2). Over the 100-min interval, on average, food-deprived cleaner shrimp spent 1.9 times longer cleaning parasitized client fish than satiated cleaner shrimp did.

## DISCUSSION

Our hypothesis that food patch quality influences where a cleaner shrimp forages, or cleans, was supported by the fact that when given a choice, cleaner shrimp spent more time with parasitized than unparasitized client fish. This suggests that client ectoparasite loads may be one variable used by cleaner shrimp as a measure of food patch quality. A relationship between cleaning and client ectoparasite load has also been demonstrated for cleaner fish (Gorlick 1984; Grutter 1995; Arnal & Morand 2001; Arnal et al. 2001; Bansemmer et al. 2002; Bshary & Grutter 2002b). Gorlick (1984), using a similar choice experiment to that used in this study, found that the cleaner fish *Labroides phthirophagus* spent more time with client fish with ectoparasites than with clients that were ectoparasite free. Bshary & Grutter (2002b) also showed in the laboratory that the cleaner fish *L. dimidiatus* foraged more frequently on a section of the body of a client fish with ectoparasites than on the section where the ectoparasites had been removed (Bshary & Grutter 2002b). Our study suggests

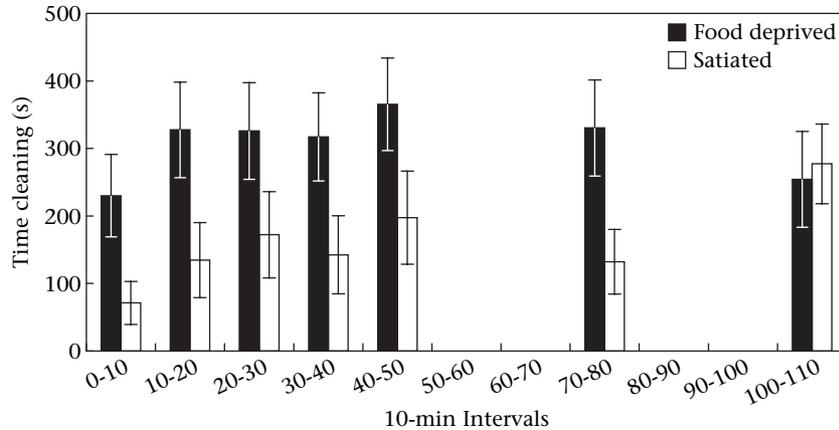
that cleaner shrimp, like cleaner fish, prefer particular client species and this preference may be related to patch quality (i.e. client ectoparasite loads).

Cleaner shrimp did not choose between parasitized and unparasitized client fish immediately, but rather did so only after the third cleaning interval from when they were first exposed to client fish. Before this the cleaner shrimp swam between the parasitized and unparasitized client fish several times, which suggests that the cleaner shrimp assessed each client fish for ectoparasites, possibly by close visual inspection or by physical contact. After this apparent initial 'evaluation', cleaning interactions with unparasitized client fish quickly subsided and the time spent with parasitized client fish increased. Possibly, cleaner shrimp need an initial period of evaluation to provide them with the necessary information to choose a client fish that will benefit the cleaner shrimp the most. A similar period of 'recognition' or 'evaluation' of good resources has also been suggested for other species of decapods when foraging (Elner & Hughes 1978; Jubb et al. 1983). Alternatively, the parasitized client fish, once aware that a cleaner shrimp was present, might have been producing signals that activated a cleaning response in the cleaner shrimp. Signals produced by clients that may activate a cleaning response in cleaner fish include client size, loyalty and diet preference (Bshary 2001). It is not yet known whether cleaner shrimp possess the same cognitive abilities as cleaner fish (Bshary et al. 2002); therefore, examining a cleaner shrimp's response to client signals is the obvious next step in testing this theory.

That food-deprived cleaner shrimp spent more time cleaning client fish than satiated cleaner shrimp did supports our hypothesis that increased hunger levels increase a cleaner shrimp's willingness to clean. This agrees with OFT because the need to obtain food when a cleaner shrimp is food deprived is likely to override the relative potential costs of foraging. The satiated cleaner shrimp, in contrast, engaged very little in cleaning activities with client fish. Therefore, satiated cleaner shrimp probably had time that could have been devoted

**Table 2.** Univariate repeated measures analysis of variance testing for an effect of hunger level (food deprived or satiated) on the time the cleaner shrimp *Urocaridella* sp. c spent cleaning the client fish *Cephalopholis cyanostygma* over seven 10-min intervals

Effect	Sums of squares	F	df	P
Cleaner shrimp state (S)	1 196 910	4.5003	1	0.042
Residuals	7 978 938		30	
Time (T)	334 478	1.9246	6	0.079
S $\times$ T	279 487	1.6082	6	0.147
Residuals	5 213 673		180	



**Figure 2.** The mean percentage of time  $\pm$  SE that cleaner shrimp, food deprived or satiated, spent with a parasitized fish over a 100-min period.

to other activities as well as reducing the probability of being predated on by clients. Similar results were found for the cleaner shrimp *Periclimenes pedersoni* (Colin 1972). This species of cleaner shrimp showed cleaning behaviours towards anaesthetized fish, paper fish models, paper fish shapes and paper rectangles, but when satiated with food did not show any cleaning behaviour towards model clients (Colin 1972). These results are also consistent with the idea posed for cleaner fish, that hunger is a proximate cue for cleaning behaviour (Côté & Molloy 2003).

There was little difference in the cleaning rates of food-deprived and satiated cleaner shrimp in the final observation period (100–110 min), with satiated cleaner shrimp increasing their cleaning rates to levels similar to those of the food-deprived cleaner shrimp. Possibly, by the final observation, the satiated cleaner shrimp had digested their food and had therefore initiated cleaning because they may have become hungry. In contrast, food-deprived cleaner shrimp may not have varied their cleaning rates over the 100 min of the experiment because it may take longer than that for a cleaner shrimp to become satiated in such a situation. To resolve these questions, more information is needed on the rate of digestion in cleaner shrimp and on rate of food intake required to satiate a cleaner shrimp. Alternatively, other cues produced by the client fish, such as those mentioned above, may have activated a cleaning response in the satiated cleaner just before the final observation period.

Our findings provide support for other models that are used to examine asymmetries in cooperative interactions. For example, our findings meet two of the four assumptions of biological market theory, a framework that has been recently used to describe the interactions involving the cleaner fish *L. dimidiatus* (Bshary & Grutter 2002a, b; Bshary & Schaffer 2002). Here, we show that two of the four criteria of a biological market are satisfied (Noë 2001). These are that partner choice by cleaner shrimp was based on the value of the commodity on offer (i.e. ectoparasite load) and that supply and demand (i.e. ectoparasite load and cleaner shrimp hunger levels) controlled the commodity value. Further experiments, examining the final two assumptions of market theory, are needed to

determine the applicability of biological market theory to the cleaner shrimp–client fish mutualism. These assumptions are that there should be competition among the more common traders for access to the less common traders and that the commodities (ectoparasite load and cleaning services) on offer can be advertised (Noë 2001).

The findings from this study that patch quality and hunger influence the cleaning behaviour of cleaner shrimp, with cleaning representing a form of foraging behaviour, agree with the predictions of OFT, that is, that an animal will forage in a manner that minimizes the metabolic energy expended, for example, by foraging on a high-quality food patch and foraging only when personal energy balance is in deficit. With this new knowledge that variations in client fish ectoparasite load and cleaner shrimp hunger level are two factors that affect the balance of trade in this mutualism we can begin to understand how this relationship is maintained.

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