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The cleaner shrimp *Lysmata amboinensis* adjusts its behaviour towards predatory versus non-predatory clients

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In cleaning mutualisms, small cleaner organisms remove ectoparasites and dead skin from larger clients. Because cheating by predatory clients can result in cleaner death, cleaners should assess the potential risk of interacting with a given client and adjust their behaviour accordingly. Cleaner shrimp are small marine crustaceans that interact with numerous client fish species, many of which are potential predators. We use *in situ* observations of cleaner–client interactions to show that the cleaner shrimp *Lysmata amboinensis* adjusts several behaviours when interacting with predatory versus non-predatory clients. Predatory clients were cleaned in a significantly lower proportion of interactions than non-predatory clients, and cleaners also exhibited a leg rocking behaviour—potentially signalling their identity or intent to clean—almost exclusively toward predatory clients. Incidence of leg rocking was positively correlated with client size, and laboratory experiments showed that it can be elicited by dark visual stimuli and decreases in illumination level. Thus, cleaners clean less frequently when predation risk is higher, and may use leg rocking as a signal advertising cleaning services and directed specifically at predators.

1. Introduction

Mutualisms—mutually beneficial interactions between species—are enigmatic, and understanding how cooperative interactions between genetically unrelated individuals arise and persist has remained challenging [1,2]. One mechanism that can contribute to the stability of mutualisms is retribution in response to cheating once it has occurred (e.g. partner switching [3,4], punishment [5]). However, in some cases, the costs borne by the cheated party are extremely high, so selection can be especially strong to favour assessment of potential risk before an interaction begins and modification of behaviour to avoid being cheated. Cleaning mutualisms are good systems for studying risk assessment, as they involve many clients that are potential predators of cleaners. Consequently, cleaners might assess the potential risks presented by clients and adjust their behaviour accordingly.

Cleaner shrimp are marine tropical crustaceans that live at cleaning stations and provide cleaning services to reef fish clients by removing ectoparasites [6]. Approximately 50% of client visits are by fishes whose diet include crustaceans similar in size to cleaners, and thus are potential predators (e.g. [7–10]). Yet, client fish predation on cleaner shrimp appears rare [11]. One hypothesis is that adjustment of behaviour by either partner contributes to the mutualism's stability by keeping cheating (table 1) low (as in mutualisms involving cleaner fish, e.g. [3,13,14]).

Cleaner shrimp–client fish interactions involve a suite of interacting behaviours by each party (e.g. [7,15,16]), so there are several ways in which

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Table 1. Summary of what is considered to be cooperating and cheating by each party in a cleaner shrimp–client fish interaction.

	cleaner shrimp	client fish
cooperate	eat ectoparasites or dead tissue	pose for cleaning and remain still throughout
cheat	eat healthy client tissue (potentially indicated by a sharp twitch or 'jolt,' thought to indicate a painful pinch [12]), to which clients may respond by retaliating	attack/chase shrimp and/or eat the cleaner shrimp

cleaners could strategically adjust their behaviour. First, cleaners could engage in fewer risky behaviours when risks are higher, such as not cleaning certain clients or cheating (table 1) potential predators (e.g. [10]). Cleaners could also increase behaviours that identify them as cleaners in the presence of potential predators, to maximize the chances of being identified as mutualistic partners rather than prey. For example, many cleaner shrimp signal to advertise cleaning services (e.g. [7,9,17]), and may signal more frequently or intensely to predatory clients than non-predatory clients (e.g. [9]). Studies of signalling between cleaners and clients (e.g. [7,9,17]) have focused thus far on visual signals, showing that cleaner shrimp–client mutualisms are at least in part visually mediated.

Here, we analysed video recordings of cleaner–client interactions in nature to show that the cleaner shrimp *Lysmata amboinensis* modifies several aspects of its behaviour in the presence of predatory versus non-predatory clients. We also used laboratory experiments to examine which visual factors underlie some of these behavioural changes.

2. Methods

(a) Video observations

To record *in situ* cleaner–client interactions, we deployed cameras (Hero3+, GoPro Corporation, San Mateo CA, USA) at two cleaning stations on the Interuniversity Institute House Reef (Eilat, Israel; 29° 33′ N, 34° 57′ E) during Summer 2016. These two stations were the only stations located in a period of 12 days spent searching the research area. Deployments occurred daily at approximately 09.00 and 14.00 and lasted for 3–4 h. During filming, divers left the area. In total, we recorded 31.4 h of footage (16.7 and 14.7 h at each station).

Using the annotation program BORIS [18], we identified interactions in which cleaner and client were fully visible and clients were on screen longer than 5 s. We annotated all instances of eight focal behaviours through the end of the first cleaning interaction or up to 1 min if no cleaning occurred (table 2). Behavioural sequences within each interaction were confirmed by EMC. *Lysmata amboinensis* lives in associations of two individuals [22], and since usually only one shrimp was visible or cleaned in each interaction, annotations from only one shrimp were analysed per interaction. Client species (and in one sexually dimorphic case, sex), diet (predator or non-predator of crustaceans) and average total length (centimetre) were identified using fishbase.org [23].

(b) Sequential analysis

We reduced behavioural sequences to their component transitions using a two-column format in which the left-hand column represented an antecedent, and the right-hand the consequent, behaviour. We summarized transitions using an adjacency matrix [24], in which cells represent the number of occurrences for each transition between two behaviours across the dataset, using *igraph* [25]. To test whether certain transitions occurred more often than expected by chance, we permuted the right-hand column (as in [7,26,27]). This generated a distribution of expected transition frequencies for each behavioural pair if transitions occurred randomly, but with the relative frequency of each behaviour held constant. In adjacency matrices resulting from permuted data, we replaced temporally impossible transitions (e.g. behaviours before 'client enter' or after 'client exit') with zero and divided the matrix by the number of allowed transitions.

We then calculated a null distribution for each behavioural transition using adjacency matrices from 10 000 permutations. From the null distribution, we extracted the 99.89% quantile (the Bonferroni-corrected significance because 47 allowed transitions were tested in parallel, although results were qualitatively similar without correction) for each transition and compared these quantiles to the observed. Observed transitions that occurred more frequently than their respective 99.89% null quantile were considered to have occurred significantly more often than expected by chance. Behaviours and significant transitions between them were visualized as networks.

Networks were similar for the two cleaning stations, both for all clients together and for predatory and non-predatory clients separately (electronic supplementary material, figure S1). Thus, data from the two stations were combined during analysis.

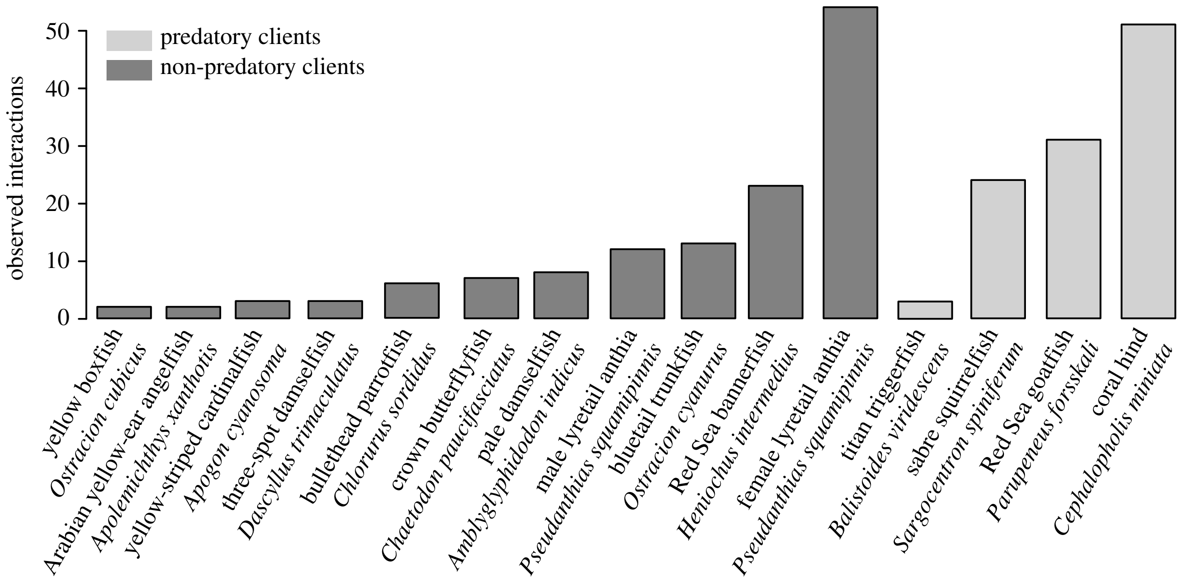
(c) Cleaner response to 'synthetic' clients

Preliminary analysis of *in situ* interactions indicated that leg rocking may be a signal directed at predatory clients (see Results). To further examine what aspects of visual stimuli elicit leg rocking, we exposed shrimp ($n = 10$) in the laboratory to visual 'synthetic clients.' Shrimp were housed in individual aquaria (30 cm long × 20 cm high × 15 cm wide) at Duke University (Durham, NC) in artificial seawater (23–24°C, salinity 28–31 ppt) made from Instant Ocean (United PetGroup, Blacksburg, VA, USA). They were fed Crab Cuisine (Hikari®, CA, USA) the day before a trial. We used PowerPoint (Microsoft Corporation, Redmond, WA) on an iPad mini 2 (screen 16.5 × 12.5 cm; Apple, Inc., Cupertino, CA, USA) to display synthetic clients against the short side of the aquarium. Synthetic clients were black or white circles, triangles and rectangles which covered 50% of the screen and were displayed for 20 s on the same grey background.

We also created light and dark solid grey screens that caused identical changes in ambient sidewelling irradiance as white and black stimuli, respectively, as measured using a 200 µm fibre coupled with a USB2000 spectroradiometer (Ocean Optics Inc., Dunedin, FL) at 5 mm distance and perpendicular to the screen. We then performed trials in which the stimulus was a change from the background grey to either the darker or lighter shade for 20 s. All instances of leg rocking were annotated by an annotator blind to stimulus identity. We then calculated the proportion of trials in which each shrimp leg rocked to a given stimulus.

Stimuli were presented in random order ($n = 5$–10 trials per stimulus per individual). Between stimuli, 2 min of control grey background were displayed, from which we randomly extracted 20 s for analysis. Tanks were lit from overhead by an LED light panel (Fotodiox Pro LED 312-DS, Fotodiox Inc., IL, USA) held at a constant brightness.

(*a*) observed interactions per client species



(*b*) predatory clients

(*c*) non-predatory clients

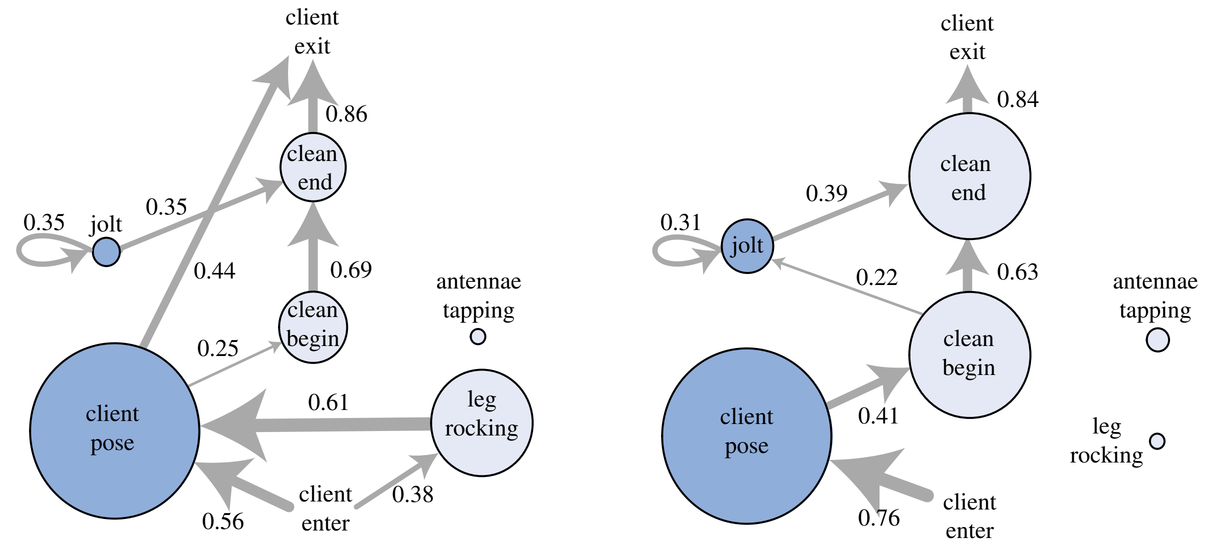


Figure 1. (*a*) Number of interactions with predatory and non-predatory clients. (*b*,*c*) Network diagrams of significant behavioural transitions between cleaner shrimp (light) and client fish (dark) behaviours in interactions with predatory (*b*) and non-predatory (*c*) clients. Circles (behaviours) are scaled to represent number of occurrences of a given behaviour. Numbers and arrow thickness represent the probability of progressing between behaviours. (Online version in colour.)

Table 2. Focal client and cleaner behaviours.

	behaviour	description
client	client enter/exit	client fish enters the camera's field of view (interaction begins)/exits the camera's field of view (interaction ends)
	pose	client fish stops forward motion near a cleaning station, resting on or near the substrate; often accompanied by a flaring of the opercula and/or fins
	jolt	sudden twitching movement, potentially indicative of cleaner cheating (as in cleaner fish [12], though for a divergent opinion in cleaner shrimp, see [19,20])
cleaner	leg rocking	rapid back and forth rocking of the white front pair of legs; sometimes accompanied by 'lashing' (e.g. [21]) of the antennae
	antennae tapping	tapping of the antennae on the client's body; the cleaner and client are otherwise not in physical contact with one another
	clean begin/end	begin/end physical contact between cleaner and client; distinct from antennae tapping

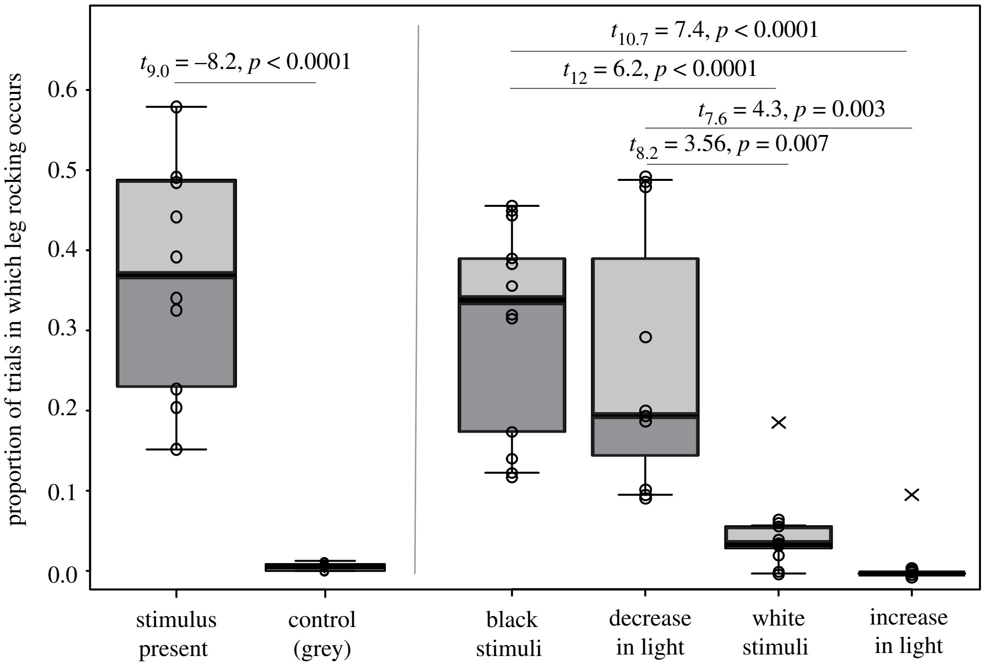


Figure 2. Leg rocking responses to visual stimuli. Boxes show the mean (line), quartiles (box) and minimum and maximum (whiskers). Points show the mean proportion for a single individual (outliers (x's) are from one individual). Points are jittered vertically for clarity. Significant differences are labelled with bars and statistics from *t*-tests (equal variances) or Welch's *t*-tests (unequal variances). The Bonferroni-corrected $\alpha = 0.008$.

3. Results

(a) Interactions with predatory versus non-predatory clients

We analysed behavioural sequences from 241 interactions ($n = 119$ and 122 at Stations 1 and 2, respectively) with 14 client fish species (range 2–50 interactions/client species). Visits from four predatory client species constituted 42% and 46% of visits at Stations 1 and 2, respectively (figure 1*a*; electronic supplementary material, figure S2). Interactions with predatory (figure 1*b*) versus non-predatory (figure 1*c*) clients differed in several ways.

First, predatory clients were cleaned in a significantly lower proportion of interactions (mean ± s.d. = 0.28 ± 0.08) than non-predatory clients (0.51 ± 0.43; $t_{9.57} = 2.5$, $p = 0.03$). Among clients who adopted cleaning solicitation poses, 25% of predatory clients were cleaned compared to 41% of non-predatory clients. Additionally, 44% of predatory clients who posed exited without being cleaned, in contrast to 25% of non-predatory clients (and there was no significant connection between pose and exit for non-predatory clients).

Second, cleaners leg rocked in a significantly higher proportion of interactions with predatory (0.51 ± 0.39) versus non-predatory clients (0.12 ± 0.21; $t_{12} = -2.39$, $p = 0.03$; figure 1), usually directly after a predatory client approached the cleaning station.

Third, jolting occurred in a lower proportion of interactions with predatory (0.10 ± 0.10) than non-predatory clients (0.22 ± 0.23), but not significantly so ($t_{12} = 0.55$, $p = 0.59$). Non-predatory clients jolted more times per interaction (range: 0–3 jolts/interaction, mean ± s.d.: 0.50 ± 0.88) than predatory clients (range: 0–0.3, mean ± s.d.: 0.15 ± 0.16), but again the difference was not statistically significant ($t_{11.5} = 1.29$, $p = 0.22$).

To examine what drives behavioural differences between predatory and non-predatory clients, we constructed behavioural networks for clients based on size, dividing them into 'large' (greater than 20 cm, $n = 7$) and 'small' (less than 20 cm, $n = 8$) categories centred roughly around the mean client size. Predatory clients were on average larger (46.8 ± 20.6 cm) than non-predatory (18.4 ± 12.8 cm) clients, but not significantly so ($t_{3.8} = -2.56$, $p = 0.07$). Overall, behavioural networks for large and small clients closely matched those for predatory and non-predatory clients, respectively (electronic supplementary material, figure S3), suggesting that cleaners assess client size in determining whether to treat them as predatory or non-predatory.

(b) Is leg rocking a signal directed at predatory clients?

Leg rocking was followed by cleaning at some point in a behavioural sequence in 45% of interactions with predatory clients, but only 5% of interactions with non-predatory clients, suggesting it may be a signal directed specifically at predatory clients. Linear models (fitted using *lm* in R [28] and excluding the Titan triggerfish, an outlier identified using Cook's distance [29]) showed that the proportion of interactions in which leg rocking occurred correlated significantly and positively with client species size ($F_{12} = 9.84$, $R^2 = 0.40$, $p = 0.009$). This positive relationship held—but was not statistically significant—for both predatory ($F_2 = 2.68$, $R^2 = 0.45$, $p = 0.20$) and non-predatory ($F_9 = 2.35$, $R^2 = 0.16$, $p = 0.15$) clients separately.

Although cleaners leg rock more frequently to larger clients, which are more likely to be predatory, their low acuity vision [30] suggests they likely use visual cues other than fine-scale size assessment to decide to leg rock. In support of this, in the laboratory, we found that cleaners leg rock to visual stimuli in a significantly higher proportion of trials than to a grey background, and more often to black than white stimuli (statistics in figure 2). However, the increased response to black stimuli was almost entirely explained by the decrease in illumination that occurs when dark stimuli appear. Specifically, leg rocking occurred in a similar proportion of trials in response to dark stimuli and decreases in illumination, both of which were significantly higher than the proportion of trials in which leg rocking occurred to white stimuli or an increase in illumination (statistics in figure 2).

4. Discussion

Although many mutualisms involve tight coevolution between a pair of partner species (e.g. [31,32]), cleaning mutualisms are 'diffuse,' meaning two multi-species partner classes interact in a loosely associated network [33]. Diffuse mutualisms are thought to play a key role in the structure and diversity of ecosystems [34] by allowing numerous species to access a shared mutualist, with fitness consequences for both parties [33,35]. How diffuse mutualisms persist despite the unequal risks imposed by different partners, e.g. predatory versus non-predatory partners, however, is an evolutionary puzzle. Our finding that *Lysmata amboinensis* alters its behaviour in the presence of potentially predatory clients has implications for our understanding of how diffuse mutualisms remain stable.

We found that predatory clients were cleaned in a significantly lower proportion of interactions than non-predatory clients, suggesting that mutualistic services are more available to clients that pose less predation risk. Second, cleaners leg rocked almost exclusively to predatory clients and were more likely to clean predatory clients after leg rocking, as compared to non-predatory clients. Thus, leg rocking may serve as a signal directed specifically at predatory clients, a response that appears to be at least partially mediated by reductions in light that occur with the approach of usually larger predatory clients. Because signals represent a mechanism by which mutualistic partners can determine when, how, and with whom to interact, partners can potentially exert strong selection pressure on one another's signals [36], and signals may be crucial for mutualisms to arise and persist.

Lastly, we observed trends, but no significant differences, in jolting between predatory and non-predatory clients. Thus, if jolting corresponds to cleaner cheating, our results do not support the prediction that cleaners cheat predatory clients less often than non-predatory clients (e.g. [3,5]).

Overall, *Lysmata amboinensis* now joins two other Red Sea cleaner species which also exhibit strategic behavioural adjustment (the shrimp *Ancylomenes longicarpus* [10] and the wrasse *Labroides dimidiatus*, e.g. [37–40]). The presence of similar behavioural strategies among distantly related cleaners suggests that selection is driving convergent behavioural evolution in the Red Sea. By contrast, there is no evidence for behavioural adjustment in two Caribbean cleaners (the shrimp *Ancylomenes pedersoni* and *Elacatinus* cleaner gobies, reviewed in [19]). Thus, our study lends support to the hypothesis that cleaning behaviour in these ocean basins has followed independent evolutionary trajectories.

Ethics. All fieldwork described in this article was performed with the permission of the Israeli Nature and Parks Authority. All fieldwork was conducted within the reef area operated by the Interuniversity Institute and thus did not require a specific permit number, only permission to deploy cameras.

Data accessibility. Raw behavioural sequence data from *in situ* behavioural observations are available as electronic supplementary material, in the two-column format described in Methods (see file 'Electronic_Supp_two column behavior.csv').

Authors' contributions. E.C. conceived of and designed the study, carried out fieldwork, checked video annotations, obtained funding for fieldwork, assisted with laboratory experiments, carried out statistical analyses and wrote the manuscript. C.C. watched and annotated all videos, secured funding for laboratory experiments, carried out laboratory experiments and critically revised the manuscript. S.J. helped design the experiment, provided space and resources for laboratory experiments, assisted in securing funding and critically reviewed the manuscript. All authors gave final approval for publication and agree to be held accountable for the work performed therein.

Competing interests. We declare we have no competing interests.

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