The interplay between satiation and temptation drives cleaner fish *Labroides dimidiatus* foraging behaviour and service quality towards client reef fish

Authors: Zegni Triki[1,2]*; Xiang-Yi Li Richter[1,2]; Ana Pinto[2]; Antoine Baud[2]; Sandra A. Binning[3]; Mélisande Aellen[2]; Yasmin Emery[2]; Virginie Staubli[2]; Nichola Raihani[4,5]; Redouan Bshary[2]

Author affiliation:

[1] Institute of Ecology and Evolution, University of Bern, Baltzerstrasse 6, 3012 Bern, Switzerland

[2] Institute of Biology, University of Neuchâtel, Emile-Argand 11, 2000 Neuchâtel, Switzerland

[3] Département de sciences biologiques, Université de Montréal, 1375 Ave. Thérèse- Lavoie-Roux, Montréal, Qc. Canada, H2V 0B3

[4] Department of Experimental Psychology, UCL, 26 Bedford Way, London, UK WC1H 0AP

[5]School of Psychology, University of Auckland, 23 Symonds St, Auckland, New Zealand.

Corresponding author: Zegni Triki, email: zegni.triki@gmail.com

Abstract

Supply and demand affect the values of goods exchanged in cooperative trades where high demand typically leads to a higher price. An exception has been described in the marine cleaning mutualism involving the cleaner fish *Labroides dimidiatus* and its variety of ‘client’ coral reef fishes. Cleaner fish feed on clients’ ectoparasites but prefer eating clients’ mucus instead, which constitutes cheating. Here, we provide field observations, followed by a set of laboratory experiments with real clients and Plexiglas feeding plates as surrogates for clients. In the field and in three experiments with real clients, we found that satiated cleaner fish were more cooperative, even though low hunger levels should make them less dependent on cleaning interactions. Similarly, the more abstract version of the experiments using Plexiglas plates offering two food types mimicking client ectoparasites and mucus showed that satiation led cleaner fish to feed more against their preferences – an indicator of cooperative behaviour. However, this outcome occurred only if the temptation to eat the preferred food was low. When the temptation to cheat was high, cleaners did so. We provide further general support to these findings with a game-theoretic model. Many mutualisms involve food as a commodity. Thus, identifying foraging decision rules will enhance our understanding of how individuals adjust to real-time market conditions rather than playing evolved strategies adapted to the average market conditions.

Keywords: cooperation, mutualism, decision-making, game-theory, cheating, wild fish.

Introduction

The values of goods or services exchanged in human economic markets follow the rules of supply and demand (Smith 1776). Typically, goods become more expensive when they are in high demand. Similar economic rules of supply and demand used to predict payoff distributions among cooperating humans also apply to other species within the framework of biological market theory and its emphasis on partner choice (Noë et al. 1991; Noë and Hammerstein 1995). Evolutionary models of biological market theory invariably predict that as demand goes up, so does the price (Noë and Hammerstein 1994; Johnstone and Bshary 2008; De Mazancourt and Schwartz 2010; Akçai et al. 2012; Grman et al. 2012; Schwartz and Hoeksema 1998). The models assume that individuals evolve to play optimal strategies when market conditions are generally stable across generations (Noë & Hammerstein 1994). In contrast, empirical studies manipulate current conditions to test how individuals flexibly adjust to changes in a market. For example, lycaenid butterfly larvae produce more attractive volatiles and offer more sugary food secretions to incite more ants to tend and protect them if current ant numbers are low (Leimar and Axén 1993; Axén et al. 1996). Similarly, vervet monkeys give more grooming to a group member that has been experimentally made the sole provider of high-quality food than if a second group member can also provide access (Fruteau et al. 2009). Various reviews on partner choice in cooperative interactions summarise the available evidence that individuals adjust their behaviour to current market conditions, see Jones et al. (2012), Barclay (2013) and Hammerstein and Noë (2016).

A notable exception to the market law of supply and demand has been described in the marine cleaning mutualism involving the cleaner fish *Labroides dimidiatus* and its client fishes (Triki et al. 2022). Clients offer a good – ectoparasites – to the cleaner fish, which provide a service to clients by removing these ectoparasites. These iterated interactions yield a net benefit to clients (Ros et al. 2011; Waldie et al. 2011, Demairé et al. 2020), but this is in part due to clients making cleaner fish eat against preference as the latter prefer eating the clients' mucus that protects scales and skin (Côté 2000, Grutter & Bshary 2003). Non-predatory clients can reduce the likelihood that cleaner fish eat their mucus by either punishing a cheating cleaner by chasing them, or by swimming off and seeking a different cleaner fish for their next cleaning interaction (Bshary & Grutter 2005). The ratio of parasite-to-mucus consumption by cleaner fish is thus a key variable describing their service quality (Bshary & Noë 2023). As mucus consumption often causes the occurrence of client 'jolts' (i.e. an abrupt whole-body movement or convulsion) in response to cleaner fish mouth contact (Bshary & Grutter 2002), jolt frequency is an easily observable correlate of cleaner fish service quality. According to the logic of the biological market theory, cleaner fish would cause clients to jolt less frequently when demand for cleaning services by clients is low, and higher jolt rates when the demand for cleaning is high. The ratio of cleaner fish to clients can cause shifts in client fish demand for cleaning services. This ratio may vary naturally due to demographic changes (mortality and recruitment) or environmental perturbations (Triki et al. 2018), and can also differ between habitats (Wismer et al. 2014; Triki et al. 2019). In a previous study which explicitly manipulated the cleaner-client ratio by reducing cleaner fish population to 50%, the demand for cleaning services increased without affecting client jolt rates (Triki et al. 2022). A game theoretic model developed to analyse cleaner-client interactions in the biological market context revealed that the link between supply-to-demand ratios and client jolt rates is indeed not straightforward in this cleaning mutualism system (Triki et al. 2022). Instead, the outcome depends on how the marginal benefits of mucus consumption over ectoparasite consumption change with increasing food abundance, in combination with how readily clients increase their tolerance levels to mucus consumption as a function of cleaner availability. If the marginal benefits decrease faster, slower, or at the same speed as the counteracting increase in client tolerance, resulting client jolt rates will be lower, higher, or unchanged, respectively (Triki et al. 2022).

The biological market model put forward by Triki et al. (2022) was not explicit about the mechanisms underlying cleaner fish decision-making during cleaning interactions. However, there is an obvious candidate mechanism that links variation in food abundance to cleaner fish adjustment of service quality: satiation levels. If cleaner fish are rare, each individual cleaner fish faces high demand for cleaning services from clients. During the population density manipulation experiment (Triki et al. 2022), the 50% remaining cleaner fish did not change the frequency and duration of cleaning interactions in response, which means that clients had on average fewer cleaning interactions. In fact, client fishes from cleaning stations where cleaner fish were removed recorded lower haematocrit levels, an indicator of anaemia caused by hematophagous ectoparasites (Demairé et al. 2020). This suggests that clients harboured more ectoparasites, allowing cleaner fish to forage more efficiently, and hence reach higher levels of satiation. Importantly, the scenario delineated above lacks straightforward empirical validation of two assumptions, namely an increased ectoparasite load in clients and the increased foraging efficiency of cleaners. Importantly, however, it makes the prediction that cleaner fish adjust their service quality, indicated by client's jolt rates, to their own satiation levels. If that were the case, cleaner fish should not only adjust their service quality to long-term changes in cleaner-to-client ratios but also in response to short-term fluctuations in satiation levels.

In order to develop predictions on how satiation levels affect service quality in the short-term, we can consider the long-term predictions from the biological market model proposed by Triki et al. (2022). The main difference between short-term and long-term variation in cleaner satiation levels is that the latter is caused by changes in cleaner-to-client ratios, while the former is due to a mixture of the service quality provided and chance fluctuations in client visitation of the cleaning station. For example, several high-quality clients seeking cleaning services in short succession will cause the interacting cleaner fish to be temporarily more satiated than average. In this state, the cleaner fish is less immediately dependent on cleaning interactions with clients and might, therefore, be less willing to clean for the next few interactions, which may lead to cleaner fish demanding a higher 'price' by increasing their mucus feeding rates, i.e., cheating rates. Conversely, as any benefits of foraging decrease with increased levels of satiation, the marginal benefits of mucus consumption also decrease when cleaner fish are more satiated. Most importantly, this decrease in the temptation to eat mucus is not compensated by clients being less likely to respond aggressively or with fleeing. Instead, the clients will respond to cleaner mucus feeding with probabilities that correspond to current overall market conditions rather than to the cleaner's momentary satiation level. As long as clients still punish or switch cleaner fish partners, the model's logic converges with optimal foraging theory and its focus on trade-offs between foraging and risk (Milinski and Heller 1978; Cuthill and Houston 1997): satiated cleaner fish should become risk averse and hence reduce their cheating rates.

Here, we investigated how short-term fluctuation in cleaner fish satiation levels affected their service quality in four different parts. First, we used field observation data to test whether interacting first with large client fish – a correlate for a temporarily increased food intake and thus increased satiation – affected cleaner fish service quality in the following cleaning interactions. Cleaner service quality was measured by recording client jolt rate (Bshary & Grutter 2002) in subsequent interactions. Second, we conducted a set of laboratory experiments wherein we exposed satiated and hungry cleaner fish to real client fishes and quantified the client jolt rates, as a measure for cleaner fish service quality. Third, in another set of laboratory experiments we used Plexiglas plates with food as surrogates for real client fish. In the set-up, we varied the cleaner fishes' satiation levels and presented them with Plexiglas plates offering fish flake mixture items and prawn items to mimic client's ectoparasites and mucus, respectively. Each plate was attached to a lever so that the experimenter could remove it as soon as a cleaner fish ate a prawn item, i.e., mimicking a client fish swimming away after a cheating event. The experiment thus measured the cleaner fish's willingness to feed against their preference and eat more flakes, which corresponds to eating ectoparasites rather than mucus in nature. This experimental system has been successfully used in the past and seemingly captures key features of real cleaner-client cleaning interactions (Bshary and Grutter 2005, 2006; Pinto et al. 2011; Salwiczek et al. 2012; Gingins et al. 2013). We could therefore evaluate how the baseline willingness to feed against preference affected adjustments of food choices when satiated. Fourth, we developed a game theoretical model to analyse how variation in the temptation to cheat by eating according to preference may interact with satiation levels in causing changes in cooperation levels.

Methods

Part 1: Field observations

Field observations on natural cleaner-client interactions collected from May to July 1998 and 1999 at Ras Mohammed National Park, in Egypt (see Bshary et al. 2011) were reanalysed here for current purposes. Bshary et al. followed and observed 16 individual adult cleaner fish on the reef for a duration of 3 to 4h per cleaner fish, during which they recorded all instances of cleaner-client fish cleaning interactions. Cleaners spend about 20% of their time interacting with clients (Barbu et al. 2011), and hardly ever ignore 'visitor' clients, i.e. typically large species with access to several cleaning stations (Bshary 2002). Thus, visitors are not always available, and their appearance is subject to random variation. For every cleaner-client interaction, Bshary et al. (2011) recorded the client fish species, the duration of the interaction, and the number of client fish body jolts. Bshary et al. transcribed the field observation data in a format of sequences of cleaner-client interactions. This helped us to reconstruct sequences of interactions with large visitor clients as a correlate for a temporarily increased demand for cleaning that is based on random fluctuations. As large clients are also more profitable because parasite load correlates with body size (Grutter 1994), these strings of interactions naturally lead to higher feeding rates by the cleaner fish. A sequence containing high feeding rates had at least three consecutive cleaning interactions with visitors for a minimum total duration of 60s. We first identified all of the high feeding sequences from these field observations, and then manually extracted all situations when the following interaction occurred with a non-predatory resident client. Strings of interactions and follow-up interactions that included (resident) predatory clients were deliberately excluded as cleaner fish tend to improve their service quality and reduce their biting frequency towards predator clients (see Bshary et al. 2011). Thus, including such interactions could have biased the data.

The aim here was to test whether cleaner fish satiation level affected service quality (inferred from client jolt rates). To do so, we attributed the status "satiated" to cleaner fish interacting with residents immediately after having a high feeding sequence; and the status "hungry" to cleaner fish interacting with residents without such a recent high feeding sequence. To simplify the analysis, we averaged the observation values for jolt rate per client species and the cleaner fish status. This yielded a matched design with 17 resident client species, where we had a value for a given species when interacting with satiated cleaner fish and when interacting with hungry cleaner fish.

Part 2: Interactions with real client fish (Laboratory Experiments 1-3)

We conducted laboratory-based experiments in 2010, 2017 and 2018 at the Lizard Island Research Station, Great Barrier Reef, Australia. Using barrier nets and hand nets, we collected female cleaner fish (*L. dimidiatus*), staghorn damsels (*Amblyglyphidodon curacao*), monocle bream (*Scolopsis bilineatus*), and striated surgeonfish (*Ctenochaetus striatus*) from the surrounding reefs of Lizard Island and transported them to the lab facilities on the island. In captivity, we housed fishes in individual aquaria (minimum size: 69 x 25 x 30 cm) with PVC tubes of various sizes as shelters. All aquaria had continuous flow of water and air filters. We fed the cleaner fish daily with mashed prawn spread on Plexiglas plates that served as surrogates for client fish. Client fishes each had their own diet: we fed the *A. curacao* daily with commercial fish flakes, *S. bilineatus* with diced prawn, and *C. striatus* with a mixture of flakes and prawn smeared on Plexiglas plates. At the end of the lab experiments, we released all caught fishes back at their respective sites of capture.

All fish we used in these experiments were adults. In all experiments, a cleaner fish and a client fish could interact with each other for ten minutes in Experiment 1 and for 15 min in Experiment 2. We video-recorded these interactions. In the 'satiation' condition, cleaner fish were allowed to feed on food plates five minutes prior to interacting with clients; whereas in the 'hungry' treatment, cleaner fish had been fed last the previous afternoon prior to the interaction with the client. Every cleaner fish experienced both "satiation" and "hungry" treatments, while we ensured a counterbalanced design to control for potential treatment order bias. Researchers who analysed the videos were blinded to the condition of the cleaner fish. In each video, we measured the total duration(s) of the cleaning interactions and the number of client fish body jolts in contact with a cleaner fish mouth (Bshary 2001).

Experiment 1 (2010)

Experiment 1 was conducted in July 2010 and involved 16 cleaner fish, 16 *A. curacao*, 16 *S. bilineatus*, and 16 *C. striatus*. Each cleaner fish was paired with three different client reef fishes (one individual of each species). For each treatment (hungry or satiated), we tested every cleaner fish twice a day (morning and afternoon session) with the same client fish partner, with each testing session lasting 10 minutes (i.e. 20 minutes in total per day). Experiments were therefore conducted over six consecutive days. We counterbalanced the order of which species a cleaner fish interacted with as well as the treatment order among our 16 cleaner fish test subjects to account for any sequence effects in experience and client ectoparasite loads.

Experiment 2 (2017)

Experiment 2 was conducted in July 2017. We tested 20 cleaner fish with 20 *C. striatus*. Each cleaner fish had its own *C. striatus* partner. In Experiment 2, cleaner fish interacted twice with the client partner (once for the hungry treatment and once for the satiated treatment) for 15 minutes in each session. Treatment order was counter-balanced as for Experiment 1.

Experiment 3 (2018)

Experiment 3 was conducted in July 2018. We tested 20 cleaner fish with 20 *C. striatus*. The methods followed the same procedure as in Experiment 2.

Part 3: Interactions with Plexiglas plates as surrogates for real client fish (laboratory Experiments 4-7)

The aim of the experiments with Plexiglas plates was to test adult cleaner fish for their foraging decisions when hungry vs satiated. In contrast to interactions with clients, where jolts are a correlate of cleaner fishes eating mucus (Bshary & Grutter 2002), the experimenters can see for each foraging decision precisely what the cleaner chose to eat. The plates offered prawn items and flake items. We know from previous studies that cleaner fish prefer prawn over flakes (Bshary and Grutter 2005). Therefore, eating a less preferred flake item is a proxy for choosing to eat an ectoparasite, which constitutes cooperating. In contrast, eating a preferred prawn item is a proxy for choosing to eat client fish mucus, which constitutes cheating.

Prior to starting the tests, we trained cleaner fish subjects that foraging against their preferences increases food intake. The training plates contained 12 flake items and two prawn items. Cleaner fish could freely forage on flake items, but we withdrew the plate upon the consumption of a prawn item. The plate was returned within a minute, and the cleaner could forage again until it ate the second prawn item, leading to the removal of the plate until the next trial. In total, we ran six training trials over two days. All cleaner fish experienced eating first flake items before eating a prawn item and hence could learn about the diverging consequences of food type choices.

In total, we conducted the experiment four times: Experiment 4 in June 2004, Experiment 5 in July 2017, Experiments 6 and 7 between February and July 2018. In all of these experiments, tests and manipulations occurred during daytime hours between 8:00 and 17:00. Test trials invariably consisted of presenting a plate with three flake and three prawn items on it, where the cleaner eating a prawn item led to the immediate removal of the plate. The plates were 12 x 7 cm in size, except for experiment 6 (where they were 9 x 9 cm). At the end of the trials, we calculated separately for the two treatments the feeding against the preference ratio by dividing the sum of flake items by the sum of prawn items consumed during the trials. Another similarity between the four experiments was that cleaner fish experienced testing days where they could eat extra flake items before each trial to create the ‘satiated’ treatment, and testing days without extra food to create the ‘hungry’ treatment. The order of treatments was counterbalanced across cleaner fish within each experiment. Intertrial intervals were about 30 min.

In Experiment 4, we tested 16 adult cleaner fish. We had 14 test trials over two days with seven trials per treatment and day. In Experiment 5, we tested 18 adult cleaner fish. We ran 20 test trials over two days, with ten trials per treatment and day. In Experiment 6, we tested 18 adult cleaner fish, and we performed in total 16 test trials per fish over two days. Lastly, in Experiment 7, we tested 20 adult cleaner fish. In contrast to Experiments 4-6, we manipulated the concentration of flakes in the flake-prawn mixture. Previously, a rough estimation was that we prepared this mixture as one third volume of fish flakes mixed with two thirds volume of prawn. Furthermore, the flake brands made available through the research station changed between years (with no tracking of brand names), and it appeared from the results of the first three experiments that this may have affected the cleaner fish’s baseline willingness to feed against preference. Previous research has shown that flake concentration affects feeding against preference, with cleaner fish less willing to eat flake mixture items containing high flake concentration (Gingins et al. 2014). This baseline willingness, in turn, may affect how cleaner fish adjust feeding against preference as a function of satiation levels. Therefore, in Experiment 7, we tested whether the flake content in the flake mixture had any effect on cleaner fish foraging decisions when hungry compared to when satiated. We weighed prawn and flakes to the nearest mg to produce two precise sets of flake-prawn mixtures. One mixture contained 10% flake and 90% prawn while the other contained 40% flake and 60% prawn. We tested the fish over four days with 10 test trials per fish and per day. Each fish faced ten trials per satiation level treatment (hungry vs satiated) and flake content in the flake mixture (10 vs 40%). We counterbalanced the treatment order among the tested fish.

Statistical analyses

We used the open source software R Version 3.6.3 (R Core Team 2020) to run the statistical analyses and generate the figures. Given that we had multiple experiments, that were run in different time periods and by different researchers, we opted for analysing every dataset generated from these experiments separately.

Part 1. For field observations, we used a linear mixed effect model (package: `LMER,` (Kuznetsova et al. 2017)) with the frequency of jolt rate as the response variable, cleaner satiation state (hungry vs satiated) as a fixed factor, and client species as a random factor.

Part 2. For Experiments 1-3 (with client fish), we analysed client fish jolt rate as the number of jolts per 1s of interaction as the response variable. For Experiment 1, the statistical model had satiation treatment (hungry vs satiated), client species (*A. curacao*, *S. bilineatus*, *C. striatus*) and their interaction term as fixed factors. In Experiment 1, we had cleaner fish identity and the test session (morning or afternoon) as random factors. For Experiments 2 and 3, we included satiation treatment as fixed factor and cleaner identity as random factor. In Experiment 1 and 3, we fitted Generalized Linear Mixed Models using Template Model Builder (`glmmTMB` in R language, (Magnusson et al. 2017)) for beta distribution (values between 0 and 1) due to zero-inflated data, while we fitted an LMER model for data from Experiment 2.

Part 3. For Experiments 4-7 (Plexiglas plates), we also fitted `LMER` models with flake to prawn ratio as the response variable, satiation treatment (hungry vs satiated) as a fixed factor, and cleaner identity as a random factor. Additionally, in Experiment 7, we had another factor which was the fish flake concentration in the flake mixture. Therefore, we had flake content (10 vs 40 %) as another fixed factor in the model for this dataset, as well as the interaction term between flake content and satiation treatment.

For post hoc analyses, we ran `emmeans` functions in R language (Lenth and Lenth 2018). All model assumptions were met. In some cases, we included data transformation, such as square root (for field data, part1) or log-transformation (for Plexiglas plate experiments, part3), to meet normality and homogeneity of variance assumptions. We provide a detailed step-by-step R code along with the data for further information.

Part 4: Game theoretic model

We extended the existing theoretical model described in Triki et al. (2022) to help explain the effect of the quality of different food types on cleaner fish service quality as a function of satiation levels. The previous model explored how cleaner fish should adjust service quality (the ratio between parasite removal acts and mucus feeding acts) when an increased demand for cleaning by clients causes an increase in the cleaner's overall access to food and hence a constant increase in satiation levels. The model showed that the adjustment depends on how clients adjust their probability to punish a cleaner for a cheating act as a function of increased parasite load. In general, increased parasite load should make clients more tolerant, but the exact function may vary between species for various reasons (e.g. differences in manoeuvrability; Roche et al. 2021, or punishment being co-opted by intraspecific aggressiveness; Soares et al. 2019). As a consequence, the model predicts that satiated cleaner fish may behave more cooperatively towards more 'cautious' client species and more exploitative towards more 'easy-going' client species (Triki et al. 2022). Here, we apply this logic to analyse how short-term variation in satiation may affect the cleaner fish's willingness to feed against preference as a function of the temptation to cheat. The level of temptation is how much cleaner fish prefer a client species' mucus over ectoparasites, or in the plate experiments, it is how much cleaner fish prefer the prawn items over the flake items.

The model description is formulated based on the plate experiments. The cheating rate (r) is determined by balancing the benefit of gaining nutrition through eating a prawn item and the cost imposed by the experimenter by withdrawing the Plexiglas plate.

$$\dot{r} = B(x) - C(r, x), \qquad (1)$$

where the benefit function $B(x)$ is an S-shaped decreasing function of food intake x. The shape of the benefit function is controlled by a parameter γ, which represents the quality of the food.

$$B(x) = 1 - e^{-10e^{-\gamma x}} \qquad (2)$$

The larger the γ, the better the food quality, the faster the benefit of cheating decreases with the accumulated quantity of food intake.

The cost function takes the form

$$C(r, x) = r\left(1 - e^{-10e^{-10x}}\right), \qquad (3)$$

which is also an S-shaped function that decreases with the cumulated food intake of the cleaner fish x, as the marginal benefit of cheating decreases with the level of satiation, and it is proportional to the cheating rate r, because the experimenter withdraws the Plexiglass plate every time the cleaner eats a prawn item. The equilibrium cheating rate r^* can be calculated by setting $\dot{r} = 0$.

Results

Part 1: Field observations

Resident clients jolted less frequently if the cleaner fish had previously experienced a high feeding sequence of cleaning interactions with visitor clients (LMER: cleaner state (hungry vs satiated): X^2 = 29.84, estimate [low, high 95% Confidence Interval] = -0.117 [-0.16, -0.07],N = 34, p < 0.0001, marginal-R2 = 0.20, conditional- R2 = 0.77, Fig. 1).

Part 2: Interactions with real client fish (Experiments 1-3)

In all three experiments, we found a statistically significant main effect of satiation treatment on client fish body jolt rate, where client fish jolted less frequently when interacting with satiated cleaner fish compared to when interacting with hungry cleaner fish (glmmTMB and LMER: $p < 0.05$, see detailed statistics in Table 1, Fig. 2). In Experiment 1, where we had three different client species tested with cleaner fish, the posthoc test indicated that the effect was more evident in *C. striatus* (emmeans estimate = 0.679, t-ratio = 2.728, p = 0.007) and *S.*

bilineatus (emmeans estimate = 0.815, t-ratio = 3.199, p = 0.002) but not in *A. curacao* (emmeans estimate = 0.097, t-ratio = 0.218, p = 0.828) (Fig. 2a).

Part 3: Interactions with Plexiglas plates as surrogates for client fish (Experiments 4-7)

Experiments 4-7 did not yield consistent effects of cleaner fish satiation state on their rates of feeding against preferences (see detailed statistics in Table 2, Fig. 3). For instance, in Experiment 4, cleaner fish fed significantly more against their preferences when satiated than when they were hungry (LMER: $p < 0.05$, Fig. 5a), which agrees with the previous results with real clients. However, we had the opposite effects in Experiment 5, where we had less eating against preference when satiated (LMER: $p < 0.001$, Fig. 3b), and no apparent effect of satiation treatment in Experiment 6 (LMER: $p > 0.05$, Fig. 3c).

When we manipulated the mixture's flake content in Experiment 7, we found that cleaner fish presented with the 40% concentrated flakes scored lower flake-prawn ratios than when presented with the 10% flake mixture (LMER: $p < 0.001$, Fig. 3d). This effect was driven by a significant interaction effect of flake content and satiation treatment (LMER: $p < 0.01$, Fig. 3d). With posthoc tests, we compared the hungry vs satiated treatment under the 40% flake content condition, and we found that cleaner fish ate more significantly against their preferences when hungry than satiated (emmeans: estimate = 0.273, t-ratio = 3.214, p = 0.002). In the 10% flake content condition, there were no significant differences in feeding against preference between hungry vs satiated cleaner fish (emmeans: estimate = -0.051, t-ratio = - 0.602, p = 0.549). Furthermore, we also compared how the flake content condition affected feeding against preferences within the hungry treatment and satiated treatment. The flake content condition affected cleaner fish feeding against preference rates when they were satiated (emmeans: estimate = 0.398, t-ratio = 4.679, p <0.0001) but not when hungry (emmeans: estimate = 0.073, t-ratio = 0.863, p = 0.392) (Fig. 3d).

Part 4: Game theoretical model

Our game-theoretic model can explain the results of the experiments with Plexiglas plates. In the model, the equilibrium cheating rate can be calculated with a closed-form expression

$$r^* = \frac{1 - e^{-10e^{-\gamma x}}}{1 - e^{-10e^{-10x}}}. \tag{4}$$

Varying the parameter γ in the benefit function changes how fast the benefit of cheating decreases with food intake (Fig. 4a). When the decline of cheating benefit is very slow (corresponding to the low quality of alternative food compared to the preferred prawn), the equilibrium cheating rate increases as food intake increases (Fig. 4b, blue and orange lines), mirroring the results of the second part of Experiment 7 with cleaner fish being less cooperative when satiated than when hungry when the flake-to-prawn ratio was high. In contrast, when the decline of cheating benefit becomes steeper (corresponding to better quality of the alternative food), the equilibrium cheating rate decreases as food intake increases (Fig. 4b, red and purple lines), mirroring the results of Experiment 4 and 7 with cleaner fish eating more often against their preference when satiated than when hungry when the flake-to-prawn ratio in the alternative food was low.

Discussion

We asked whether satiation affects service quality in cleaner fish, under the assumption that satiation levels may provide a proximate mechanism for why adjustments to levels of cooperation occur in response to short-term changes in biological market conditions. Both field data and lab experiments involving real clients consistently show that clients jolt less when cleaner fish are satiated (i.e. cleaner fish cheat less when not hungry). The exception to this trend was when clients were damselfish. This species jolted less frequently than other species to begin with in our experiment (see Fig. 2a). The experiments involving plates as well as the game-theoretic model added another dimension to the results on real interactions, showing that satiation may have both positive or negative effects on cooperation levels, depending on the cleaner fish's temptation to cheat. These results provide key insights into how animals may use basic proximate mechanisms to flexibly adjust to short-term and long-term changes in supply-to-demand ratio, potentially in ways that defy the human market law.

Interactions with real client fish

Short-term variation in satiation levels occur largely due to stochastic variation in local demand for cleaning without any changes in cleaner-to-client ratios. The stochastic variation is due to independent decisions by individual clients on when to visit a particular cleaning station. After a short-term increase in visitation rates, cleaner fish are temporarily more satiated. The results show that being satiated leads to cleaner fish causing less jolts per time unit. Thus, they demand a lower 'price' rather than increasing rates of mucus feeding. This result may be predicted when we apply optimal foraging theory (Cuthill and Houston 1997) and the logic of variable investment in repeated games (Johnstone and Bshary 2007) to our study system. As long as the marginal benefits of cheating are low when cleaner fish are in a satiated state and high when in a non-satiated state, satiation should lead to relatively higher levels of cooperation. Indeed, despite the variation in client body size and home range, the effect of satiation on client jolt rate was rather consistent in our experiments. Importantly, when we consider short-term fluctuations in cleaner satiation levels, being more cooperative when satiated increases payoffs in the near future because a good service positively affects the next interaction with the very same client 10-40 min later (Bshary & Würth 2001; Soares et al. 2013), i.e. when the cleaner fish's satiation level is most likely back to average. In other words, cleaner fish in a satiated state at least partly invest in relationships with their clients and reap the benefits in the future.

Given that satiation levels affect the cleaner fish's level of cooperation in the short-term, it seems likely that satiation levels also influence the cleaner fish's adjustments to long-term changes in cleaner-to-client ratios. With satiation as a mechanism, an increase in client demand for cleaning services (high client to cleaner ratio, high ectoparasite loads) would hence cause cleaner fish to provide better service. Conversely, a decrease in client demand (low client to cleaner ratio, low ectoparasite loads) would cause cleaner fish to lower their service quality. Satiation effects would thus oppose market effects. In contrast, client responsiveness to being cheated, another major factor affecting cleaner cooperation (Bshary & Grutter 2002; Roche et al. 2021), is expected to change according to market effects: clients should be more tolerant if demand for cleaning is high, and less tolerant if demand for cleaning is low (Triki et al. 2022). The relative effect sizes of these two opposing forces will hence decide how changes in the supply-to-demand ratio will affect cleaner fish's cooperation (Triki et al. 2022).

Plexiglas plate (as surrogate for client fish) experiments and game theoretical model

In contrast to the data involving real clients, we found evidence that cleaner fish willingness to eat against preference in the Plexiglas plate experiments both increased or decreased as a function of satiation levels. Experiment 7 provided crucial insights regarding the mechanism leading to such variable results. Apparently, if the preference for prawn vs flakes is weak, satiated cleaner fish become more willing to eat flakes against their preference. In contrast, if the preference for prawn is strong because flake concentration is high and/or the flake mixture is particularly distasteful for cleaner fish, satiated cleaner fish become less willing to eat against preference. This interpretation is supported by the game theoretical model. In interactions with real clients, the logic would be reversed as the less preferred food (ectoparasites) would be similar in taste across species, while the quality of the preferred food (mucus) is known to vary between species (Arnal et al. 2001; Roche et al. 2021) and cleaners show preferences (Grutter & Bshary 2004). Both results and model open up new avenues for experiments involving real clients. The working hypothesis to be tested is that cleaner fish adjust service quality when satiated to client species properties. The prediction would be that client species for which a cleaner's temptation to eat mucus is high (client has large quantities of high-quality mucus and few ectoparasites) should jolt relatively more frequently, while client species for which a cleaner's temptation to eat mucus is low (client has small quantities of low-quality mucus and many ectoparasites) should jolt relatively less frequently compared to other species.

Satiation and feeding against preference

Another interesting research avenue is to use a comparative approach to test whether the motivational apparatus of cleaner fish has evolved specifically as an adaptation to the ecological challenges inherent in cleaning interactions (Kamil and Mauldin 1988; Shettleworth 1993). The challenge to eat against preference in order to increase own food intake is probably rare in nature. Therefore, we predict that other non-cleaning species would find it difficult to eat against preference in the first place, and even more so when satiated. A well-studied related phenomenon is called sensory-specific satiety also known as the 'dessert effect' (Rolls et al. 1981) which consists of a decrease in pleasure with continuous consumption of the same food or flavour compared with an unconsumed food or flavour (Havermans et al. 2009; Ostojić et al. 2013). In the cleaner fish case, the preference for one type of food is a given rather than the consequence of recent lack of consumption. Keeping the analogy to the dessert effect, satiated animals should tend to focus on preferred food, which in the case of cleaner fish would mean eating mucus or prawn (Grutter & Bshary 2003; Bshary & Grutter 2005). We predict that a reversal of this tendency allows cleaner fish to functionally invest into future relationships with clients when satiated. The evolution of such a motivational mechanism to adjust to short-term and long-term variation in supply-to-demand ratios contrasts with the way humans supposedly adjust to market conditions. Indeed, humans certainly have the cognitive abilities to monitor market developments and to plan for the future, a capacity that non-human animals (and plants and microbes) typically lack (Tulving 2005; but see Raby et al. 2007).

Conclusions/outlook

Our results highlight the importance of studying the mechanisms underlying decision making to enhance our understanding of biological markets. The effects of satiation levels should be studied in a wide variety of mutualisms, as food is a common commodity traded (Bronstein 1994; Pierce et al. 2002; Bronstein et al. 2006; Kiers et al. 2011). Cleaning mutualism is just one form of a so-called protection mutualism, where one class of partner species trades the protection of the other class of partner species against food (Bronstein 1994). In such protection mutualisms, a high demand for protection positively affects the food availability for the protectors (Axén et al. 1996). As a consequence, protectors may use their food intake rates and/or resulting satiation levels as a basis for flexible adjustment of service quality. The current study and the study by Triki et al. (2022) show that cleaner fish do not behave as predicted by the market law of supply and demand, where one would expect that low demand for protection leads to hungry protectors, which in turn should provide a better service than satiated protectors do. The arising question then is whether other protector species show similar patterns or whether they adjust protection as predicted by biological market theory. The potentially unique feature of the *Labroides* cleaning mutualism is the conflict between protector and food provider over what the protector should eat. This conflict of interest may affect service quality in opposite ways than expected by the market law (Bshary & Noë 2023). The effects of other ecological settings on protection quality have not been studied, but they could yield other interesting dynamics. For example, ant species could in principle adjust to high demand for protection by bringing more food to the colony for a faster colony growth. This option means that the benefits for ants are a linear function of food availability, rather than an asymptotic function of diminishing returns when an individual forages for itself. How such a linear benefit function affects the level of protection provided by ants, and what role individual satiation may play in decision-making, offers another option for future research.

Ethics note:

Experiments described in this manuscript received ethical approval from the University of Queensland and the Animal Ethics Committee of the Queensland government (DAF) (permit numbers: CA 2017/05/1061; CA 2018/01/1155 and CA 2018/06/1195).

Data and code accessibility: Source data are archived at Figshare data repository, and will be made accessible upon peer-reviewed publication (Triki et al. 2023) (https://doi.org/10.6084/m9.figshare.19778545).

Acknowledgements

We thank the Lizard Island Research Station staff for their continuous support and friendship. We are very grateful to Alex Vail and Dominique Roche for their help with catching the fish. Funding was provided by the Swiss Science Foundation (grant 188240 and 199286 to ZT, 153067, 135707, 173334 and 192673 to RB; 180145 and 211549 to XYLR) and the University of Neuchatel Égalité des chances grant to SAB. A preprint version of this article is available on EcoEvoRxiv (Triki et al. 2023).

Conflict of interest: The authors declare no conflict of interest.

Author contribution: RB conceived the study, all authors collected the data. ZT compiled data from all experiments, ran the statistical analyses and generated the figures. XYLR generated the theoretical model. ZT and RB wrote the paper with input from all authors.

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Table 1. Summary table of the statical outcomes from Experiments 1-3 with real client fish. Indicated in bold are statically significant *p*-values (alpha ≤ 0.05).

Fitted model	***N***	**Model / distribution**	***Chi square (X^2)***	***P*-value**	**Marginal-R^2 / Conditional-R^2**
Experiment 1 (year 2010)					
Satiation treatment	16	GlmmTMB / beta	**13.887**	**< 0.001**	**0.18 / 0.36**
Client species			3.983	0.136	
Satiation treatment x Client species			2.002	0.367	
Experiment 2 (year 2017)					
Satiation treatment	20	LMER / Gaussian	**8.313**	**0.004**	**0.10 / 0.62**
Experiment 3 (year 2018)					
Satiation treatment	19	GlmmTMB / beta	**3.890**	**0.049**	**0.17 / 0.85**

Table 2. Summary table of the statical outcomes from laboratory experiments with Plexiglas plates as surrogates for client fish. Indicated in bold are statically significant *p*-values (alpha ≤ 0.05). All statistical models were LMER.

Fitted model	***N***	***Chi square (X^2)***	***P*-value**	**Marginal-R^2 / Conditional-R^2**
Experiment 4 (year 2004)				
Satiation treatment	16	**6.445**	**0.011**	**0.12 / 0.43**
Experiment 5 (year 2017)				
Satiation treatment	18	**20.812**	**< 0.001**	**0.17 / 0.71**
Experiment 6 (year 2018)				
Satiation treatment	18	1.397	0.237	0.04 / 0.04
Experiment 7 (year 2018)				
Satiation treatment	40	3.412	0.065	**0.23 / 0.30**
Flake content		**15.356**	**< 0.001**	
Satiation treatment x Flake content		**7.282**	**0.007**	

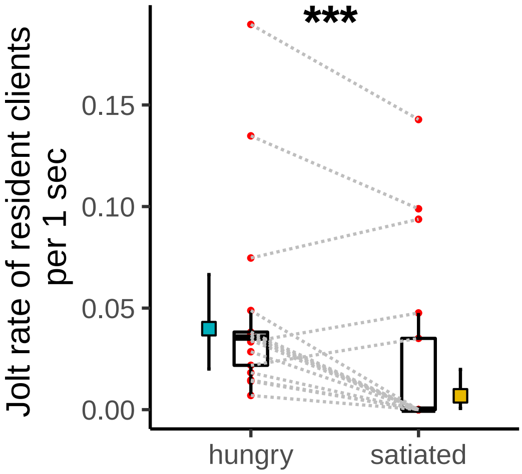

Figure 1. Jolt rates of 17 resident client species during natural cleaning interactions with hungry and satiated cleaner fish. The plot shows estimated means and 95% CI of model marginal effects with boxplots of median and interquartile of raw data, and the actual data points. Dashed lines connect data points of the same client species. *** LMER; $p < 0.001$.

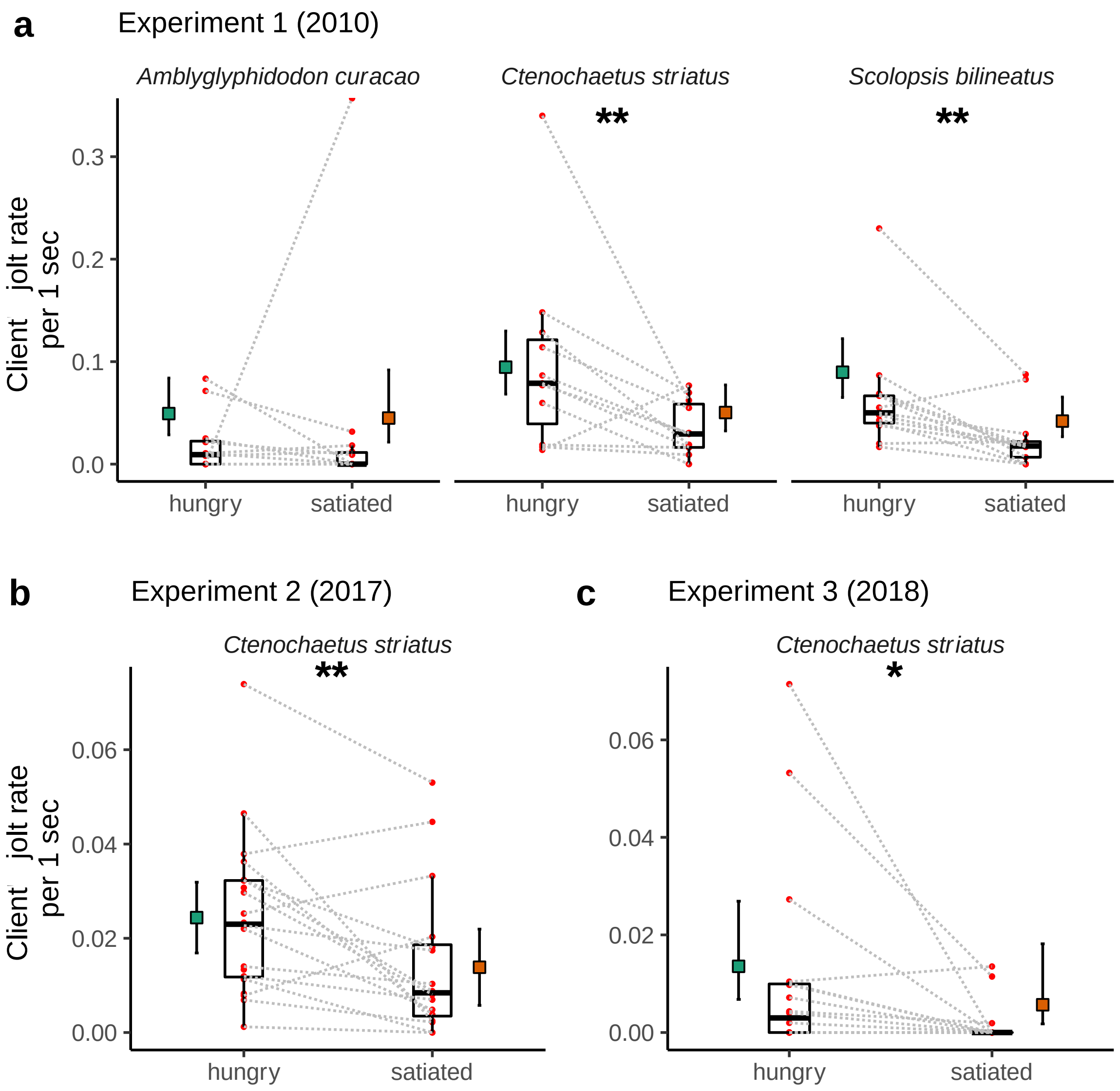

Figure 2. Client fish body jolt rates during cleaning interactions with cleaner fish in laboratory settings (Experiments 1-3). (a) to (c) show estimated means and 95% CI of models marginal effects, boxplots of median and interquartile of raw data, and the actual data points. Dashed lines connect data points from the same cleaner-client pair (client species: Staghorn damsels *A. curacao*, monocle bream *S. bilineatus*, and striated surgeonfish *C. striatus*). (a) Pairwise emmeans posthoc test ** $p < 0.01$; (b) **LMER; $p < 0.01$; (c) * GlmmTMB; $p < 0.05$**.**

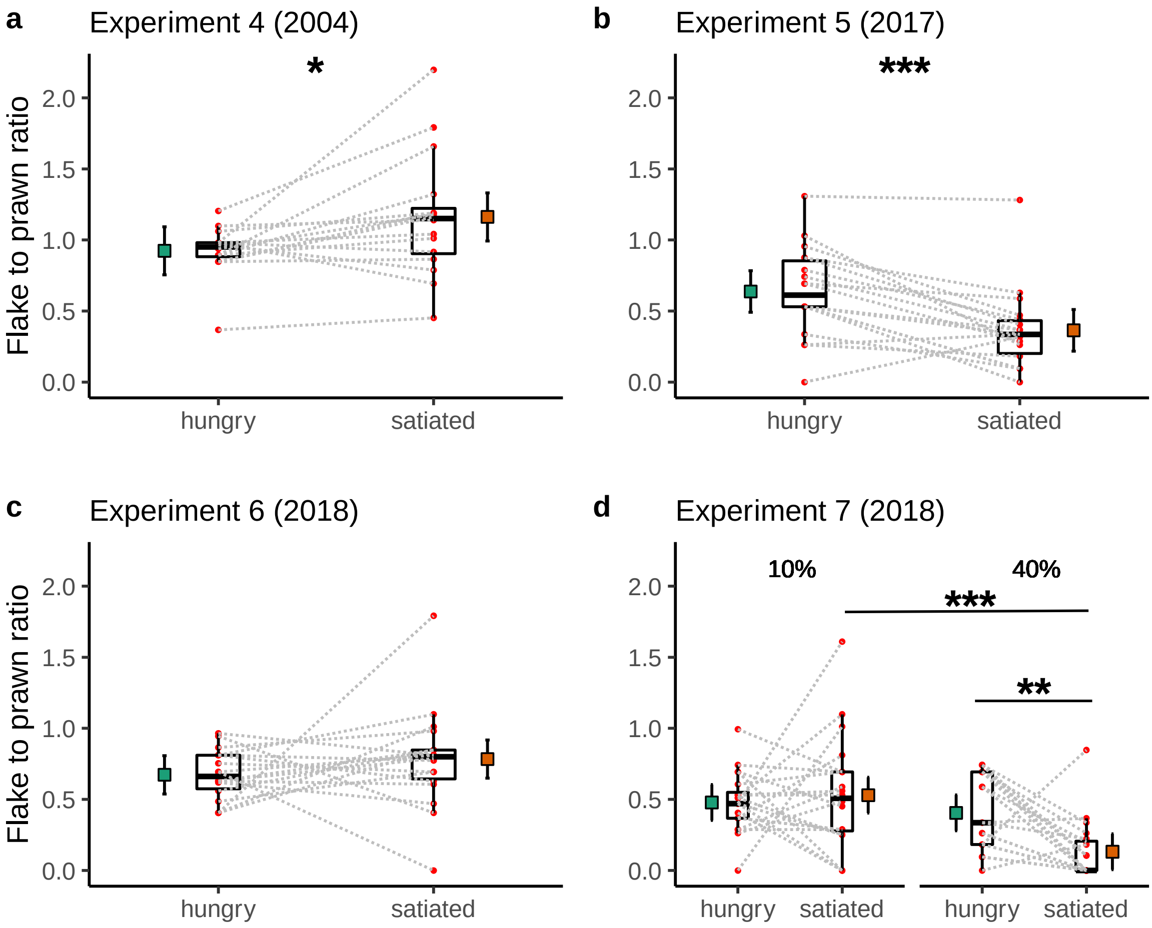

Figure 3. Cleaner fish feeding against preferences as a function of satiation state in four experiments with Plexiglas plates (Experiments 4-7). (a) to (d) show estimated means and 95% CI of models marginal effects, boxplots of median and interquartile of raw data, and the actual data points. Dashed lines connect data points from the same cleaner fish. (d) Experiment 7 had a two-by-two factorial experimental design with two levels of satiation state (hungry vs satiated) and two treatments of flake content (10% vs 40%). (a) *LMER; $p < 0.05$; (b) *** LMER; $p < 0.001$; (d) Pairwise emmeans posthoc test ** $p < 0.01$, *** $p < 0.001$.

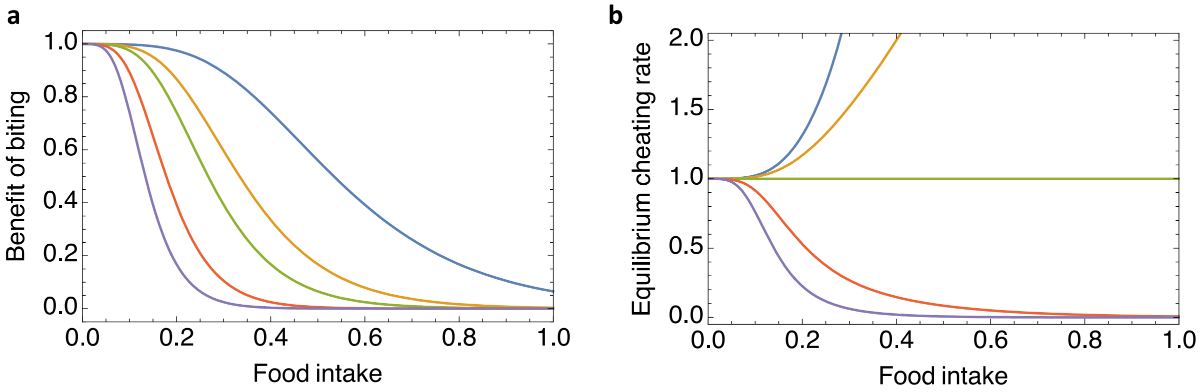

Figure 4. (a) An illustration of the benefit function, where the benefit of biting decreases with the quantity of food intake. Lines of different colours correspond to different food quality represented by different γ values, which were set to 5 (representing poorest quality), 8, 10, 15, and 20 (representing highest quality) from right to left. (b) The equilibrium cheating rate can either decrease or increase with food intake, depending on the quality of the alternative food, represented by the parameter γ in the benefit function. The values of γ for the blue, orange, green, red, and purplue curves are 5, 8, 10, 15, and 20, respectively.