

Image scoring and cooperation in a cleaner fish mutualism

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Humans are highly social animals and often help unrelated individuals that may never reciprocate the altruist's favour^{1–5}. This apparent evolutionary puzzle may be explained by the altruist's gain in social image: image-scoring bystanders, also known as eavesdroppers, notice the altruistic act and therefore are more likely to help the altruist in the future^{5–7}. Such complex indirect reciprocity based on altruistic acts may evolve only after simple indirect reciprocity has been established, which requires two steps. First, image scoring evolves when bystanders gain personal benefits from information gathered, for example, by finding cooperative partners^{8–10}. Second, altruistic behaviour in the presence of such bystanders may evolve if altruists benefit from access to the bystanders. Here, we provide experimental evidence for both of the requirements in a cleaning mutualism involving the cleaner fish *Labroides dimidiatus*. These cleaners may cooperate and remove ectoparasites from clients or they may cheat by feeding on client mucus^{11,12}. As mucus may be preferred over typical client ectoparasites¹³, clients must make cleaners feed against their preference to obtain a cooperative service. We found that eavesdropping clients spent more time next to 'cooperative' than 'unknown cooperative level' cleaners, which shows that clients engage in image-scoring behaviour. Furthermore, trained cleaners learned to feed more cooperatively when in an 'image-scoring' than in a 'non-image-scoring' situation.

Early game theoretic models of indirect reciprocity based on image scoring assumed that every single act is altruistic and that image scoring is already present in a population, as is the strategy to help individuals that have been observed to help others^{5–7}. Thus, these models do not address why image scoring and helping should evolve in the first place.

Communication network theory¹⁴, however, provides a framework for indirect reciprocity based on image scoring. Image scoring, called eavesdropping in the communication literature¹⁵, involves collecting information on interactions between third parties where the information gained provides direct benefits to the bystander. This image-scoring behaviour in bystanders leads to changes in their behaviour, best documented in situations involving conflict, where individuals may adjust their fighting behaviour according to knowledge gained by observing their opponent^{16,17}. Thus, bystanders attribute an image score about fighting parameters to observed individuals. Eavesdropping in agonistic contexts has been documented across a wide range of animal taxa¹⁵. In the context of cooperation, image scoring may evolve if individuals differ consistently in the amount that they cooperate^{10,18}. Here, observers may select individuals as partners for cooperative tasks based on how cooperative they are in their current interaction. Once such egoistic image scoring/eavesdropping has evolved, interacting individuals are selected to adjust appropriately their behaviour according to the presence or absence of bystanders (termed "audience effects"¹⁹).

Therefore, in the context of cooperation, image-scoring observers would select for cooperative behaviour as an audience effect, as it would provide the altruist with access to a cooperating partner.

Altruism based on image scoring and indirect reciprocity may occur in symmetric games (prisoner's dilemma-type games) where both partners may cooperate or cheat. However, the game may also be asymmetric where only one class of players can choose between helping and cheating its partner, while the other class of players collects crucial information by image scoring. For example, males may use helping as a behavioural handicap while females are the eavesdroppers^{8–10}. In addition, many interspecific mutualisms consist of asymmetric investment by one player while the returns of the partner come as a by-product²⁰—cleaning mutualism is a typical example²¹.

The interactions between the cleaner fish *Labroides dimidiatus* and its client fishes are a well-known example of interspecific mutualism²². Cleaners may cooperate and remove ectoparasites from client fish, or they may cheat by feeding on client mucus^{11,12}, which they prefer over typical client ectoparasites¹³. Hence, there is a temptation for cleaners to cheat. Although a few piscivorous clients could cheat by attempting to eat the cleaner fish²², the vast majority of clients consist of species that do not predate on fish²³. Such clients have no means to exploit a cleaner fish, precluding tit-for-tat-like²⁴ control strategies. Instead, field observations suggest that image scoring is one of several alternative mechanisms²¹ used by clients to avoid exploitation by cheating cleaners. Client fish almost always invite a

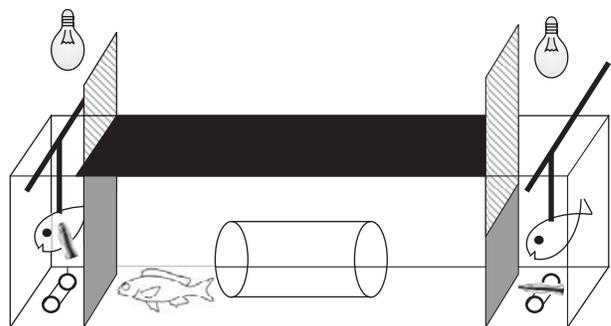


Figure 1 | Experimental set-up to test for image scoring. Aquarium (95 × 36 × 36 cm) with a black cloth over the middle and 40-W incandescent lights over the side compartments, enhancing the one-way mirrors, which allowed the client in the middle to see the cleaner fish and client model in the side compartments. Pipes served as shelters for fish. Cooperative cleaners foraged on prawn (0.002 g) smeared on the model, whereas unknown cooperation level cleaners swam around freely. The time the client spent next to each cleaner with its entire body out of the shelter was recorded. Hatched area indicates opaque sliding covers.

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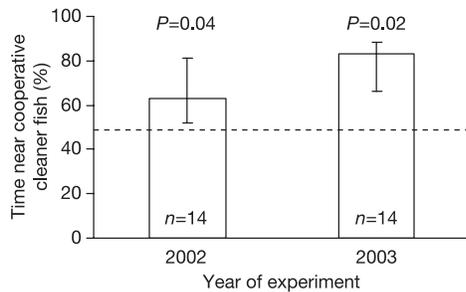


Figure 2 | Client fish conduct image scoring. The percentage of time a client fish spent near the cooperative cleaner fish compared to 50% (50% being the amount of time expected if the behaviour was random (dashed line)). Clients could also approach an unknown cooperation level cleaner. The same experiment was conducted in consecutive years. Median and interquartiles are given.

cleaner's inspection if they witnessed that the cleaner's last interaction ended without conflict, invite less if they do not have such knowledge, and invite the least if the last interaction ended with conflict^{25,26}. Furthermore, cleaner fish are more cooperative in the presence of bystanders than when they are alone with one client²⁶. These results are consistent with the hypothesis that image scoring by client fish is a selfish act used to find a cooperative cleaner or to avoid a cheating cleaner, resulting in (more) cooperative behaviour in cleaners in the presence of bystanders. Here, we test this hypothesis experimentally.

To test whether client fish engage in image-scoring behaviour, we offered a client fish the choice of interacting with two cleaner fish (Fig. 1): one cleaner appeared to behave 'cooperatively' with a model of a client whereas the other did not interact with the model (that is, it had an 'unknown cooperative level'). Client fish spent significantly more than 50% of their time near the cooperative than near the unknown cooperative level cleaner (Fig. 2). This experiment was done twice in consecutive years and both results were significant (one sample Wilcoxon signed rank-sum test with $H_0 = 50\%$: 2002, $n = 14$, $T = 18.5$, $P = 0.04$; 2003, $n = 14$, $T = 16$, $P = 0.02$).

The second experiment, which tested whether cleaner fish foraging behaviour differed in an image-scoring situation compared with a non-image-scoring situation, was based on the following logic: because cleaners may prefer client mucus over ectoparasites¹³, they must feed against their preference (that is, not cheat) during a current interaction to gain access to an observing client. After previous experiments on partner control mechanisms in cleaning mutualism²⁷, we replaced clients, mucus and parasites with plates on levers, and by presenting preferred prawn and less-preferred fish flakes on the plates, respectively (Fig. 3). The levers allowed us to control the plates' response to cleaner fish foraging behaviour according to predetermined rules. As a baseline, all cleaners were offered only one plate (single plate) (Fig. 3a). Furthermore, cleaners were tested in one of two scenarios involving two plates presented simultaneously. In the control no-image-scoring scenario, each plate remained in the aquarium until the cleaner ate one prawn item off it (Fig. 3b). In the experimental image-scoring scenario, the removal of one plate when a cleaner fish fed on prawn led to the immediate removal of the second plate (so the cleaner could not eat anything from the latter) (Fig. 3c). Thus, in the image-scoring scenario, cleaners could eat only the two flake items (FF) on the first plate to then access the second plate, ignoring the two remaining prawn items on the first plate (Fig. 3c). On all other plates, they could eat two flakes and then a prawn item (FFP) for maximal foraging success. Therefore, to maximize their food intake, we predicted that cleaners should eat more against their preference (a ratio of flake items eaten to total items eaten) while interacting with the first plate in the image-scoring scenario than while feeding from any other plate. Comparing the single-plate situation against the two-plate situation tested the

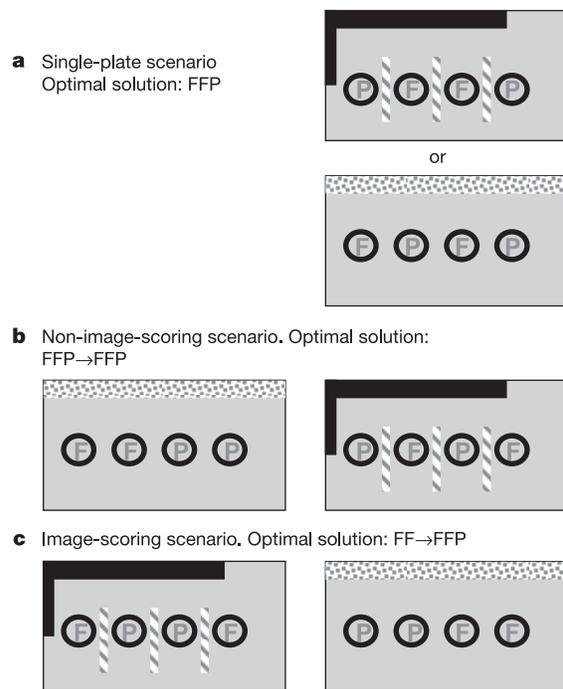


Figure 3 | Experimental set-up to test for indirect reciprocity. Optimal feeding solutions in a foraging experiment where eating fish flakes (F) was allowed whereas eating prawn (P) resulted in immediate termination of an interaction due to plate removal. **a**, Single-plate situation. **b**, Two plates are removed independently when the cleaner fish eats a prawn item. **c**, Two-plate situation where eating prawn on one leads to the removal of both plates. Half of the cleaners were tested in **a** and **b**, the other half in **a** and **c**. Plates were coloured in two ways to allow discrimination: hatched area, pink; stippled area, beige.

alternative hypothesis that cleaner fish may be more cooperative when more food is available, independently of any image-scoring behaviour of clients.

Within treatment groups, we found that in the image-scoring scenario, cleaners fed significantly more against their preference when interacting with the first plate in the two-plate situation than when interacting with the second plate or in the single-plate situation (Friedman test, $n = 12$, $\chi^2_2 = 12.5$, $P = 0.002$, post-hoc multiple comparisons $P < 0.01$) (Fig. 4). In the non-image-scoring scenario, the foraging behaviour of cleaners on all three plates did not differ significantly (Friedman test, $n = 12$, $\chi^2_2 = 1.3$, $P > 0.05$) (Fig. 4). Between treatment groups, cleaners ate significantly more against their preference on the first plate in the image-scoring scenario than on the first plate in the non-image-scoring (control) scenario (Mann–Whitney U -test, $m = 12$, $n = 12$, $Z = 3.15$, $P = 0.002$; Fig. 4). Although cleaners did not always eat items in the sequence that would maximize their food intake, they still also ate against their preference (their preference being prawn²⁷) in all situations (Fig. 4). In the image-scoring scenario, all cleaners sometimes ate only flakes from the first plates (between 2–12 out of 20 trials, median = 7 trials), which allowed them to access the second plate. This happened significantly less often in the no-image-scoring scenario (between 0–4 out of 20 trials, median = 1.5 trials) where the second plate could still be accessed (Mann–Whitney U -test, $m = 12$, $n = 12$, $Z = 3.61$, $P < 0.001$).

Our results show that both requirements for simple indirect reciprocity—image scoring by clients and an increased level of cooperation by cleaners in the presence of image-scoring clients—exist in a cleaning mutualism. Our experimental results confirm interpretations based on field observations^{25,26}. Under natural conditions, cleaners feed against their preference (that is, eat ectoparasites rather than client mucus) to reduce the risk of conflict with their

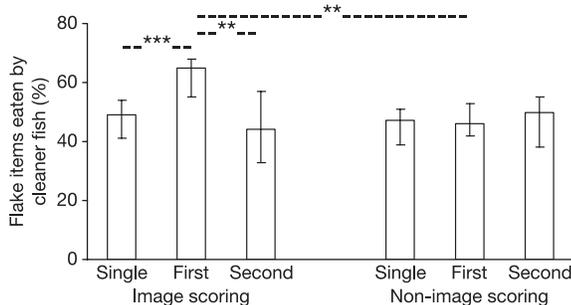


Figure 4 | Indirect reciprocity because of image scoring. Percentage of flake items eaten relative to all items eaten (flake and prawn) in 20 rounds. Twelve fish were tested with single plates and two plates in the image-scoring scenario, and twelve fish were tested with single plates and two plates in the non-image-scoring scenario. Each cleaner contributed one mean value to the single-, first- and second-plate situations. Double asterisk, $P < 0.01$; triple asterisk, $P < 0.001$ in post-hoc comparisons. Median and interquartiles are given.

current client in order to gain access to nearby observing clients²⁵. Although eavesdropping in communication networks may promote increased levels of aggression in the context of animal conflict^{15–17,28}, our data on cleaning mutualism show that eavesdropping may also result in increased levels of cooperation. In our system, indirect reciprocity based on image-scoring clients probably requires only relatively simple cognitive processes. Clients do not have to remember observed interactions as they react immediately to what they observe. Cleaners have over 2,000 client interactions per day¹¹ and therefore constantly receive feedback about the consequences of their actions, allowing them to associate their behaviour with foraging success. It will be a challenge to find more complex forms of indirect reciprocity and image scoring⁵—in particular the purely altruistic system that humans are capable of playing²—in other animals.

METHODS

For additional information, see Supplementary Information

Image-scoring behaviour in client fish. Trials were done in an experimental aquarium with three compartments, separated from each other by one-way mirrors. The mirrors allowed viewing into the side compartments from the middle one (Fig. 1). We placed two client models in the side compartments that each held a cleaner fish, *Labroides dimidiatus*. To create differences between the inspection behaviour of the two cleaner fish with their model, only one model had mashed prawn (0.004 g) spread on it. The model with food was placed in the compartment holding cleaner fish trained to feed off the model, whereas the model without food was placed in the compartment holding cleaner fish familiar to a model having no food on it. Therefore, the former cleaner would interact more with the model (cooperative cleaner) than the latter (unknown cooperation level cleaner). This method worked, as 27 out of 28 cleaners with a model with prawn on it interacted longer with the model than their 'partner' cleaner on the other side. Cooperative cleaners interacted on average for 250 s with the model (range 20–550 s), about 12.5 times longer than cleaners with a model without food (average 20 s, range 0–130 s). To control for the presence of food, an equal amount of prawn was placed in the other cleaner's compartment, but it dropped to the bottom where it was ignored by the cleaners. Food on the model was on the side facing the client *Scolopsis bilineatus* in the middle compartment. Opaque barriers covering the mirrors were removed as soon as both models were in place and fish behaviour recorded for 10 min. We recorded the amount of time the client spent in a designated area near each cleaner (Fig. 1) and the time each cleaner spent interacting with the model, estimated by a scan sample at 10-s intervals. Trials were scheduled so that cooperative cleaners were at each side of the aquaria in 50% of trials to account for any preference of the client for a particular side. Clients spent on average 320 s (range 86–599 s) of their time near either cleaner fish (that is, with their full body out of the shelter to either side).

Cleaner fish indirect reciprocity experiment. The experimental set-up allowed us (1) to offer two types of food as distinct items visible to the experimenter, hence enabling us to see exactly what item a cleaner fish ate with each bite; (2) to remove a plate immediately when a cleaner ate a preferred food item; and (3) to

offer two plates simultaneously and manipulate the presence of the second plate according to the cleaner's foraging behaviour.

First learning phase. Following methods described in ref. 13, we trained cleaners that eating less-preferred fish flakes was allowed whereas eating preferred prawn led to the immediate removal of a plate. Plate removal was done using a lever attached to the plate. A total of six learning trials was done every 2 h, four trials per day.

Second learning phase and experiment. We conducted six rounds of the experiment without scoring the cleaners' behaviour, followed by 20 experimental rounds. We used two different-looking plates (10 × 6 cm) (Fig. 3). Each round consisted of two trials 30 min apart, one with two plates present and one with a single plate present. The following round started 60 min later, so the experiment was spread over 3 days. Twelve cleaners were used for each of the control and experimental groups. The key difference between the experimental and the control group occurred in the two-plate situation: the control cleaners (non-image-scoring scenario) could eat from the first plate until they ate a prawn item, after which the plate was removed, and then move on to the second plate until they ate a prawn item, after which the second plate was removed (Fig. 3b). Thus, the second bystander plate did not form an image of the cleaner's behaviour. The experimental (image-scoring scenario) cleaners, however, faced the problem that eating prawn on one plate led to the removal of both plates (Fig. 3c). Thus, the second bystander plate could form an image and respond negatively to the cleaner, by leaving and avoiding an interaction, if the cleaner cheated the first plate. Given these rules of plate behaviour, cleaner fish had to use varying rules to optimize their foraging success: the optimal solutions shown in Fig. 3.

The cleaner was kept to one half of the aquarium with a clear partition, while the plate(s) was placed against an aquarium side (always the same side) in the other half. Once the plate(s) was in place, we removed the partition so that the cleaner could begin foraging. For each cleaner, we calculated the percentage of flake items eaten per plate per scenario.

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Supplementary Information is linked to the online version of the paper at www.nature.com/nature.

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