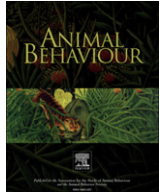


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journal homepage: www.elsevier.com/locate/anbehavAre cleaner fish, *Labroides dimidiatus*, inequity averse?N. J. Raihani^{a,*}, K. McAuliffe^b, S. F. Brosnan^c, R. Bshary^d^a Department of Genetics, Evolution and Environment, University College London, London, U.K.^b Human Evolutionary Biology, Harvard University, Cambridge, MA, U.S.A.^c Department of Psychology, Georgia State University, Atlanta, GA, U.S.A.^d Department of Biology, University of Neuchâtel, Neuchâtel, Switzerland

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Inequity aversion (IA), a willingness to incur temporary costs to prevent unequal outcomes, is common in humans and thought to be beneficial in the context of cooperative relationships with nonkin, since it might allow individuals to regulate contributions to cooperative activities. Attempts to address whether nonhuman animals also show IA have produced mixed results: some studies found that cooperative species are more likely to show IA while others did not. This ambiguity may arise because animals are typically tested for an aversion to working for differential food rewards, even though most tested species do not regularly cooperate to access food. We used the interspecific mutualism between cleaner fish and their reef-fish 'clients' to investigate whether IA exists in a species that regularly cooperates with unrelated individuals in the food domain. Cleaners were tested in pairs of actors and recipients. Actors had to perform a task to provide a food reward to both actor and recipient. Cleaners show consistent food preferences in the wild and under laboratory conditions, allowing us to vary the value of the food reward offered to actor and recipient to test whether actors were less likely to work when recipients received higher value rewards. We performed two experiments: actors worked either for their opposite-sex partner or for a same-sex competitor. We found no evidence that cleaners were sensitive to inequity: actors were equally likely to perform the task in all experimental conditions. We discuss these results in light of theories of the evolution of IA.

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Strong evidence exists that sensitivity to one's own payoffs, relative to those of a partner, often motivates the behaviour of humans in social interactions (Guth et al. 1982; Camerer 2003; Dawes et al. 2007; Tricomi et al. 2010; Zaki & Mitchell 2011) and these results have been upheld (to varying degrees) in tests across different cultures (Henrich et al. 2001). So-called 'inequity aversion' (IA), defined as a willingness to incur immediate payoff reductions in order to achieve more equitable outcomes (Fehr & Schmidt 1999), is thought to be a key proximate mechanism underpinning the evolution of cooperation among unrelated individuals. IA can occur in one of two broad contexts. First, individuals can be averse to outcomes in which they receive less than a social partner ('disadvantageous IA'). Second, individuals may be averse to outcomes in which they receive more than a social partner ('advantageous IA', see Camerer 2003; Dawes et al. 2007; Blake & McAuliffe 2011), although, to our knowledge, there is no evidence for advantageous IA in nonhuman species. The capacity to detect and respond to inequality in social interactions is thought to be

particularly beneficial when individuals can choose interaction partners. Under these circumstances, individuals that play fair should be preferred over individuals that try to monopolize an unequal share of resources. An aversion to inequity therefore allows individuals to avoid being exploited by uncooperative partners (Fehr & Schmidt 1999) and to reduce the possibility that they will be abandoned by disgruntled partners for unfair behaviour (André & Baumard 2011). Moreover, negative responses to inequity can act as a signal to prospective partners that individuals will avoid behaving unfairly with future partners (Brosnan 2011) and that unfair contributions from social partners will not be tolerated (Yamagishi et al. 2009).

Since cooperation is not the exclusive hallmark of human societies, it is pertinent to question whether responses to unequal outcomes might also exist in other social species. According to a recent theory (Brosnan 2006, 2011; but see Chen & Santos 2006), IA may be most likely to have evolved in species that regularly cooperate with nonkin. Specifically, the social hypothesis for the evolution of IA (Brosnan 2006, 2011) posits the following steps for the evolution of responses to inequity aversion. First, organisms evolve the ability to recognize the rewards and payoffs of others and to compare this to their own payoff. Next, organisms evolve the potential to respond to these payoff differences. Finally, organisms

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evolve more specific responses to inequity such as willingness to reduce current payoffs in order to lower the payoffs of individuals experiencing greater rewards. As in humans, it has been argued that the evolution of mechanisms to detect and respond to IA in nonhuman species would be beneficial in a social context because individuals that can recognize and avoid unfair distributions of rewards can recognize and avoid unfair partners.

In support of the hypothesis that IA evolved in a social context, comparative work of responses to unequal payoffs among several primate species provides some evidence for convergent evolution of IA (Brosnan 2011). For example, IA has been demonstrated in capuchins, *Cebus apella* (Brosnan & de Waal 2003; Brosnan et al. 2006; van Wolkenten et al. 2007; Fletcher 2008; but see Roma et al. 2006; Silberberg et al. 2009), chimpanzees, *Pan troglodytes* (Brosnan et al. 2005, 2010; but see Jensen et al. 2007; Bräuer et al. 2006, 2009), cottontop tamarins, *Saguinus oedipus* (Neiworth et al. 2009; but see Brosnan 2011) and longtailed macaques, *Macaca fascicularis* (Massen et al. 2011); all of which are species that are known to cooperate (to varying degrees) with unrelated others in their social group (Hauser et al. 2003; Fragazsy et al. 2004; Langergraber et al. 2007; Gumert & Moon-Ho 2008). In addition, recent evidence from domestic dogs, *Canis lupus familiaris* (whose canid ancestors were socially living species) has shown that individuals are less willing to perform an unrewarded task if a partner receives a reward for the same behaviour (Range et al. 2009). In contrast, there is no evidence for fairness preferences in squirrel monkeys, *Saimiri* spp. (Talbot et al. 2011), which are phylogenetically closely related to capuchins but do not typically cooperate with nonrelatives (Boinski 1987; Boinski et al. 2002), or in orangutans, *Pongo* spp. (Bräuer et al. 2006; Brosnan 2011), which have similar cognitive and reasoning abilities to chimpanzees (Shumaker et al. 2001) but whose relatively solitary social structure means that individuals rarely cooperate with one another in the wild (Wich et al. 2009; Brosnan 2011).

To date, all studies looking for evidence of IA in social species have tested subjects for inequity to unequal outcomes in a food domain. Although there is some evidence for collaboration in food acquisition in chimpanzees, capuchins and some canid species (Boesch 1994; Creel & Creel 1995; Rose 1997) and for food sharing in some nonhuman primate species (de Waal 1989, 2000), in most of these species, cooperation more frequently occurs outside the food domain. For example, nonhuman primates frequently cooperate with others by exchanging bouts of allogrooming or by providing support in agonistic encounters (Schino & Aureli 2010). In cooperatively breeding species, such as some callitrichid primates and canid species, individuals might also cooperate by helping to raise the offspring of others (Solomon & French 1997). Because cooperation in most species that have been tested on IA paradigms typically occurs outside of the food domain, it is difficult to infer the ecological validity of IA results. To provide an ecologically relevant test of whether individuals are less likely to work for unequal food rewards therefore requires a model system in which individuals regularly cooperate in the food domain. A model species in this regard is the bluestreak cleaner wrasse, *Labroides dimidiatus*. These are coral reef-dwelling fishes, which are widely distributed throughout the Indo-Pacific region. Cleaner fish hold small territories called cleaning stations, where they have thousands of interactions per day with so-called 'client' fish: allospecific individuals that also live on the reef (Grutter 1996). Cleaners cooperate with clients by removing surface ectoparasites and dead skin (Côté 2000). Although cleaners and clients both benefit from this interaction, there is a conflict of interest since cleaners prefer to feed on mucus rather than ectoparasites (Grutter & Bshary 2003). Since mucus feeding is detrimental to the client (Ebran et al. 1999), this constitutes cheating by the cleaner fish (Bshary & Grutter 2002).

Clients often terminate a cleaning interaction in response to being bitten (Bshary & Grutter 2002). Thus, in order to continue interactions with clients, cleaners are required to forgo immediate benefits by feeding against their preference. Crucially, cleaners sometimes work with unrelated conspecific partners to obtain food rewards (Bshary et al. 2008). Such collaboration occurs in the context of joint client inspections, in which a male and female cleaner fish work together to clean a joint client. Intuitively, one might expect that clients receive a worse cleaning service (less ectoparasite removal and more biting) when they are serviced by a pair of cleaners. This is because clients may often leave in response to being bitten and so both cleaners are tempted to try to cheat the client before the partner does so. In fact, the opposite pattern emerges. Pairs of cleaner fish provide a better service than singletons (Bshary et al. 2008) and the increase in service quality is provided almost entirely by the female cleaner fish, which risks punishment from the male partner if she cheats a joint client and thereby causes it to leave (Bshary et al. 2008; Raihani et al. 2010, 2012a, in press). The fact that males punish females for cheating during joint inspections of model clients raises the exciting possibility that cleaner fish may be aware of the payoffs accrued by an interaction partner and, correspondingly, may show responses to distributional inequity. We tested this possibility in the present study.

Responses to inequity are predicted to be most pronounced in situations in which individuals have to work to earn rewards (Fontenot et al. 2007; Neiworth et al. 2009; Takimoto et al. 2010; Brosnan et al. 2010; Talbot et al. 2011). Accordingly, in this study, we made use of the fact that, in addition to providing cleaning services, cleaner fish sometimes also provide tactile stimulation to clients by using their pectoral and pelvic fins to massage them (Bshary & Würth 2001). Since clients are known to seek out tactile stimulation and because it lowers clients' stress responses (Soares et al. 2011), tactile stimulation can be thought of as an interspecific sociopositive behaviour (Bshary & Würth 2001). Under laboratory conditions, cleaner fish will also provide tactile stimulation to model Plexiglas 'clients' (R. Bshary, personal observation). Thus, we investigated the latency to perform tactile stimulation in return for different food rewards to test cleaners for responses to inequity. The rationale behind our experimental design is that inequity-averse actors would either be less likely to perform tactile stimulation or would take longer to perform tactile stimulation in conditions that yielded unequal payoffs. We conducted two separate studies to test for inequity, in 2010 and 2011, respectively. In 2010, fish were paired with their opposite-sex breeding partner, while in 2011 fish were paired with same-sex competitors. The distinction between the experiments allowed us to test the possibility that fish interacting with a social partner may be less likely to show IA because of interdependencies in fitness (Roberts 2005).

EXPERIMENT 1

Methods

Subjects

All data were collected in 2010 at Lizard Island Research Station, Australia (14°40'S, 145°28'E). Twelve established male–female pairs were caught from the reefs surrounding Lizard Island Research Station. Pairs were housed in aquaria (45 × 30 cm and 25 cm deep) and males were separated from females by use of a transparent Plexiglas partition (Fig. 1a). Six males and six females from different pairs were randomly allocated the role of 'actor' with their opposite-sex partner being allocated the role 'receiver'. These roles remained consistent throughout the experiment. Actors were tested for responses to inequity over 6 days. Experimental trials

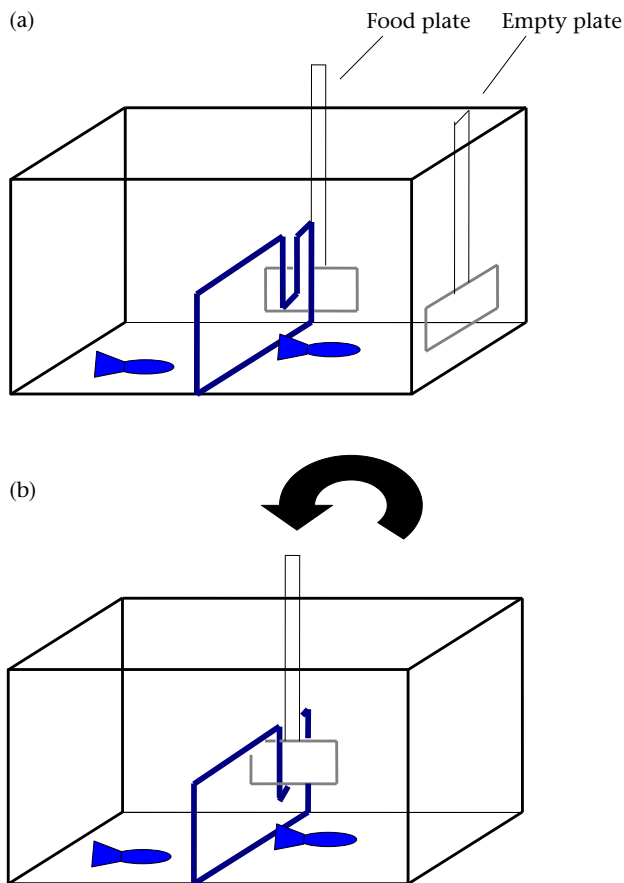


Figure 1. Experimental set-up. Each aquarium housed a pair of fish that were separated by a transparent partition at the centre of the tank (shown in blue). The slot in the partition will accommodate the food plate and ensure that each fish can only feed from one half of the food plate. In (a) the empty plate has been placed in the tank and the food plate rests against the back wall outside the tank. In (b) the food plate has been moved into the tank and each cleaner fish can feed from one half of the plate.

were conducted over six rounds per day and each round consisted of two separate plate presentations, separated by a 1 min interval. Cleaners were not fed between rounds. All fish had already been tested in other experiments, all of which involved learning to feed against preference (to forgo prawn items and eat flake items instead). Fish were trained to feed against their preference by the experimenter removing the food plate if the fish ate a prawn item (e.g. see Bshary et al. 2008; Raihani et al. 2010). Nevertheless, all fish readily ate prawn items once the negative consequences of prawn eating were discontinued.

Apparatus and training

All fish were initially trained to feed off Plexiglas plates (15 × 10 cm) containing items of mashed prawn or fish flakes mixed with prawn (hereafter 'flake'), placed on them. Each fish was then assessed for a food preference (propensity to eat one type of food over the other when items were presented in equal quantities on Plexiglas plates). Consistent with previous studies (Bshary & Grutter 2005; Bshary et al. 2008; Raihani et al. 2010), all cleaners showed a consistent preference for prawn over flake over three trials (see Bshary & Grutter 2005 for methods).

Actors were then trained individually to give tactile stimulation to a Plexiglas plate containing no food items (hereafter 'empty plate'). In response to successful tactile stimulation from actors, a second, food-bearing plate (hereafter 'food plate') that was previously visible but inaccessible was made available to both members of the pair to feed from (Fig. 1b). Using the transparent partition separating the fish, we were able to ensure that each member of the pair was only able to feed from one half of the food plate (Fig. 1b). To be included in experimental testing, actors had to perform the tactile stimulation task successfully for two different food plates at the start of each day. All actors met these eligibility criteria on each experimental day.

The exact appearance of food plates varied depending on the experimental treatment (see 'Procedure' for details of experimental treatments). All food plates were divided in half using coloured electrical tape. Each half contained the food items that would be made available to each member of the pair (Fig. 2). The food plate was positioned at the halfway point, on the outside of the tank, so

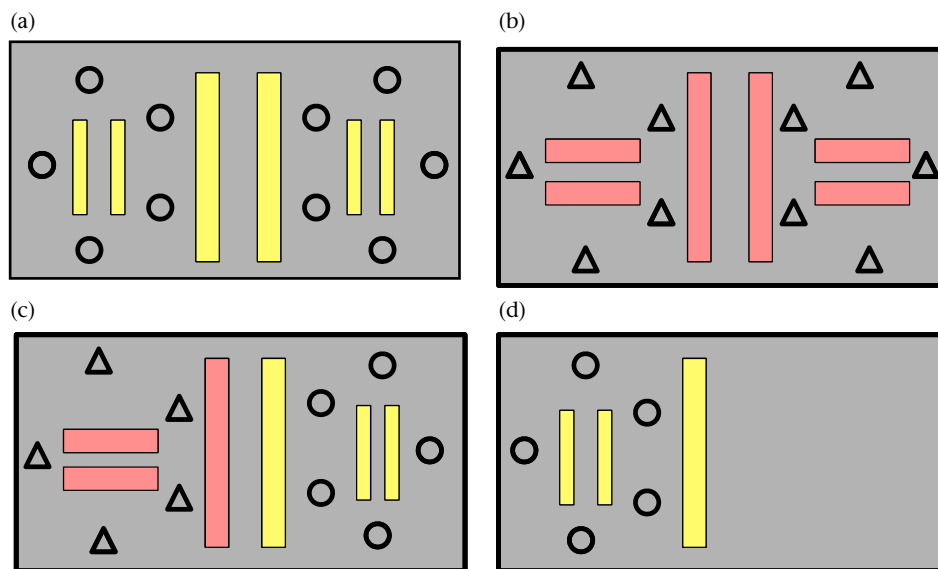


Figure 2. Plate types. (a) Low-equity (LEQ) plate, where both fish received five flake items; (b) high-equity (HEQ) plate, where both fish received five prawn items; (c) inequity (INEQ) plate, where the actor received five flake items while the recipient received five prawn items. This plate was also used for the nonsocial control (NSC) and distraction control (DIST) treatments. (d) Reward inequality (R-INEQ) plate, where the actor received no food while the recipient received five flake items.

that each cleaner could see the food it would receive and also the food that would be available to the partner (Fig. 1a). Each fish received either five flake items, five prawn items or nothing, depending on the treatment. To increase the chances that fish would recognize whether they would be receiving flake items or prawn items, flake items were placed within 1.5 cm diameter black circles while prawn items were placed in similar-sized black triangles (Fig. 2). The positions of flake and prawn items, respectively, were held constant and yellow electrical tape was used in association with flake items while pink electrical tape was used in association with prawn items (Fig. 2). Previous work has shown that cleaners are able to distinguish between flake and prawn items presented on Plexiglas plates in this way (e.g. Bshary et al. 2008; Raihani et al. 2010).

Cleaners interacted with each of the four experimental plates several times per day (two trials per round, one round of each experimental treatment per day). Thus, over the course of the 6-day experiment, each actor interacted with each plate 12–36 times, depending on experimental plate type. Based on past work (Bshary & Grutter 2005), this level of interaction should have provided ample opportunity for actors to learn the association between performing tactile stimulation and the relevant food reward according to plate type.

Procedure

At the beginning of each trial, the food plate was placed against the outside back wall of the aquarium (Fig. 1a). Food plates were oriented towards the fish so that each member of the pair could see the food that was on the plate. Next, the empty plate was introduced into the aquarium and actors were allowed up to 60 s to perform tactile stimulation to the empty plate. Actors were considered to have performed the task if they touched the empty plate with either their pectoral or pelvic fins. At this point, the food plate was introduced into the aquarium and both fish could feed from their respective halves of the plate (Fig. 1b).

In each presentation, we recorded (1) whether actors performed tactile stimulation within the allotted time slot; (2) if so, the latency of the actor to perform tactile stimulation to the empty plate; and (3) the number of food items eaten by each fish during each successful trial. If the actor did not perform tactile stimulation within the allotted time period then both plates were removed and that was the end of the trial. We predicted that if cleaners were inequity averse, then actors would either be less likely to perform tactile stimulation, or would take longer to perform tactile stimulation, in conditions that yielded unequal payoffs. However, to control for the possibility that lowered response rates or slower reaction times could be caused by other variables, several additional treatments were also necessary (see Table 1 for descriptions).

Table 1
Treatment names and their descriptions

Treatment	Description
High equity (HEQ)	Both fish received five prawn items
Low equity (LEQ)	Both fish received five flake items
Inequity (INEQ)	Actor received five flake items while recipient received five prawn items
Nonsocial control (NSC)	Actor worked to get access to the INEQ plate but the recipient was prevented from feeding and hidden by use of an opaque partition
Distraction control (DIST)	Actor worked for the INEQ plate; the recipient was prevented from feeding by use of a transparent partition but was still visible to the actor
Reward inequity (R-INEQ)	Recipient received five flake items while actor received no food

Cleaners experienced a different treatment during each round (but the same treatment in both presentations of each round). The order in which treatments were presented was fully randomized and counterbalanced across pairs using a Latin square.

By comparing actors' responses to high-equity (HEQ) and low-equity (LEQ) plates, we could compare whether actors were generally more motivated to work for preferred food rewards. Further comparison of responses to inequity (INEQ) compared to LEQ allowed us to determine whether any variation in actor response was due to a reduced motivation to work for less-preferred food or, more specifically, to the unequal distribution of preferred and less-preferred food on the plate. The nonsocial (NSC) treatment was essential to determine whether any decreased propensity to work for the INEQ plate was due to a frustration effect (at seeing the preferred food but being unable to get access to it) rather than a response to inequity per se (e.g. Brosnan & de Waal 2003; Roma et al. 2006; Silberberg et al. 2009). The distraction (DIST) treatment allowed us to control for the possibility that slower reaction times could be caused by a combination of frustration (at seeing inaccessible preferred food) and distraction (seeing the conspecific near the preferred food) rather than an aversion to inequity per se. Finally, the reward inequity (R-INEQ) treatment allowed us to measure whether actors may only show responses to inequity in response to a qualitative difference in outcomes (recipient rewarded, actor unrewarded) rather than a quantitative difference in outcomes (recipient receives preferred food, actor receives less-preferred food), as has previously been shown in a study using domestic dogs (Range et al. 2009). All trials were performed by two experimenters. N.R. placed food items on plates, presented the plates to the fish and recorded the latency to perform tactile stimulation. K.M. videotaped each trial.

Analysis

We first investigated whether the proportion of presentations in which actors performed tactile stimulation varied according to treatment. We calculated the mean proportion of occasions on which actors performed tactile stimulation in the first and second presentations, respectively. Cleaners performed tactile stimulation in more than 99% of presentations (see Results) meaning that further analysis to investigate variation in propensity to work for differential food rewards was not possible.

Next, we investigated whether latency to perform tactile stimulation (s) varied according to treatment. We calculated the mean latency to perform tactile stimulation in each treatment per presentation. This value was log transformed and set as the response term in a linear mixed model (LMM) with normal error distribution. Treatment (plate type), presentation (first or second) and cleaner sex, plus all two-way interactions, were included as explanatory terms. Actor ID was included as a random term to control for the effect of repeated measures on the distribution of the data. A maximal model including all explanatory terms and two-way interactions was built. Terms were then individually dropped from this model; we retained only those whose removal resulted in a significant decrease in the model's explanatory power. The significance of dropped terms was assessed by re-adding them to the minimal model (the model containing only significant terms).

Finally, we wanted to investigate the factors affecting the proportion of available food items that were eaten by the cleaners. However, cleaners ate more than 99% of all food items they were offered (see Results), meaning that further analysis to investigate the factors affecting feeding behaviour was not possible.

Data were analysed using R version 2.8.1 (www.r-project.org) and were checked to ensure they conformed to the assumptions of the tests used. All two-way interactions were checked but are presented only when significant at $P < 0.05$.

Ethical note

This work was approved by the University of Queensland Animal Ethics Approval Committee under licence number SBS/086/11/SSF. All fish were caught from reefs surrounding Lizard Island Research Station. Fish were caught using barrier nets and placed in large individual bags full of sea water. They were then transported from the site of capture to Lizard Island Research Station. Depending on the site of capture, transport took between 5 min and 20 min. Captures were approved by the general organizational Queensland Fisheries Permit and GBRMPA permit granted to Lizard Island Research Station. In the laboratory, fish were housed with their established opposite-sex partner in large glass aquaria and allowed to acclimatize for 2 weeks. All aquaria were situated in closed saltwater laboratories. During the acclimatization period, fish were fed ad libitum using Plexiglas plates smeared with mashed prawn. In the laboratory, daylight hours were maintained between 0700 and 1700 hours. All fish remained healthy during the study. After the experiments, fish were released at their site of capture.

Results

Actors performed tactile stimulation on $99.5 \pm 0.02\%$ of all presentations so further analysis to investigate variation in propensity to perform the task according to treatment was not possible. The mean latency to perform tactile stimulation was 6.74 ± 0.5 s in the first presentation and 6.19 ± 0.5 s in the second presentation. According to our model, there was no significant difference in latency to perform tactile stimulation across presentations ($\chi^2_1 = 0.43$, $P = 0.51$). We did not detect a significant effect of treatment on latency to perform tactile stimulation ($\chi^2_5 = 2.01$, $P = 0.85$; Fig. 3), although on average females were slower than males to perform tactile stimulation across all treatments ($\chi^2_1 = 6.14$, $P = 0.01$; Fig. 4). Cleaners ate $99.7 \pm 0.0\%$ of all food items they were offered, meaning that additional analysis to determine the factors affecting variation in proportion of food items eaten was not possible.

Discussion

In this experiment, in which cleaners worked with their opposite-sex breeding partner, they almost always performed the tactile stimulation task (even in the R-INEQ treatment, in which the actor received no food) and we found no effect of treatment on the latency to perform the task. Thus cleaners were apparently equally motivated to work for all plate types. These results raise three possible interpretations. First, it is possible that cleaner fish are not sensitive to inequity (see *General discussion*). Second, it may be the case that our experimental set-up was not appropriate for uncovering responses to inequity (see *General discussion*). A third possibility, however, is that male and female cleaner fish have overlapping fitness interests (Roberts 2005) and that this explains why we failed to find any pattern in responses to inequity. Interdependence can be defined as the extent to which one individual's fitness is dependent on that of its partner (Roberts 2005). Interdependent individuals that cooperate may benefit indirectly via increases in the partner's fitness, in much the same way that individuals may accrue kin-selected benefits when they invest to help relatives (Hamilton 1964a, b). Interdependencies in fitness may often arise when individuals have to work together to raise young and may contribute to maintaining cooperative behaviour under these circumstances (e.g. see Raihani & Bshary 2011). Interdependent individuals are therefore expected to be more tolerant of inequity than individuals whose fitness interests do not overlap, since harming a partner to obtain equal outcomes also harms

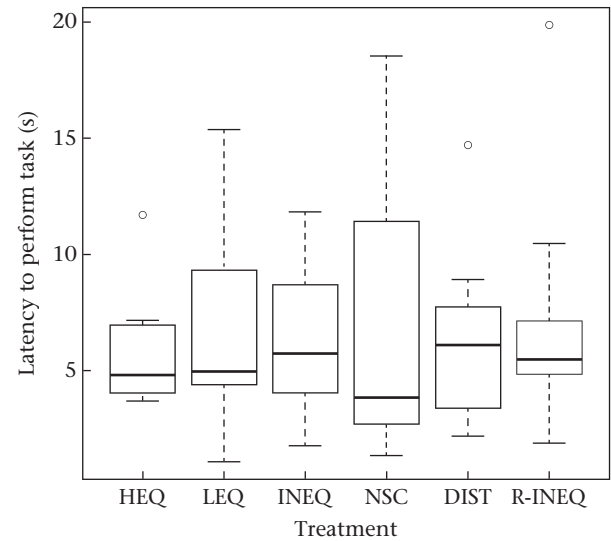


Figure 3. Box plot of latency (s) to perform tactile stimulation according to treatment in experiment 1 generated from raw data (high equity (HEQ), both fish received five prawn items; low equity (LEQ), both fish received five flake items; inequity (INEQ), the actor received five flake items while the recipient received five prawn items; nonsocial control (NSC), INEQ treatment where the recipient was hidden by an opaque barrier; distraction control (DIST), INEQ treatment where the recipient was behind a transparent barrier; reward inequity (R-INEQ), the actor received no food while the recipient received five flake items). The thick black line in each box depicts the median latency for each treatment while the upper and lower ends of the box correspond to the upper and lower quartiles of the distribution. The dashed lines show the upper and lower latencies for each treatment. Open circles represent outliers.

oneself to some extent (Brosnan 2011). Interdependence between partners has been invoked to explain why there is so little evidence of IA among cooperatively breeding species (Brosnan 2011), and why chimpanzees in stable social groups are more tolerant of inequity than those living in more transient social environments (Brosnan et al. 2005). Male and female cleaner fish in this experiment were caught from reefs as established social pairs. Thus, it is

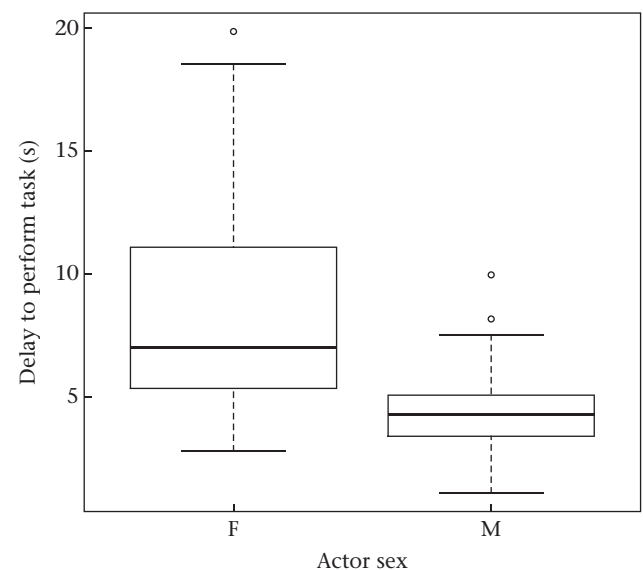


Figure 4. Box plot of latency (s) to perform tactile stimulation according to actor sex (M = male, F = female) in experiment 1. The thick black line in each box depicts the median latency for each treatment while the upper and lower ends of the box correspond to the upper and lower quartiles of the distribution. The dashed lines show the upper and lower latencies for each treatment. Open circles represent outliers.

possible that they have interdependent fitness meaning that we cannot rule out this latter explanation for failure to find IA in this experiment.

Females were generally slower than males to perform tactile stimulation for food rewards in this experiment. Ours is the first study of *L. dimidiatus* to find sex differences in tactile stimulation behaviour. It is possible that females were slower to perform tactile stimulation because they are generally slower than males in all activities. Alternatively, females may be generally more reticent to perform tactile stimulation to obtain food rewards. It is not yet known whether females are less likely than males to perform tactile stimulation to real clients under natural conditions. Further work investigating the causes of sex differences in this aspect of prosocial behaviour in cleaner fish is needed.

In this experiment, cleaners also ate almost all of the available food items and did not reveal a consistent preference for prawn items over flake items, as we had expected. However, we did not supplement the cleaners' food either between rounds or at the end of the day and so cleaners might have been generally motivated to eat (and to work for food rewards), regardless of whether the food was preferred prawn or less-preferred flake. Related to this, it is possible that tactile stimulation was not costly enough to prevent food-motivated cleaners from performing tactile stimulation in virtually all presentations.

To test the possibility that motivational factors influenced cleaner fish performance in experiment 1, we ran a second experiment in which we fed the actors prior to each round. Additionally, in experiment 2 we paired males with males as opposed to their breeding partner. The logic for this pairing is that individuals may be less likely to show responses to distributional inequity when they work with a breeding partner owing to interdependencies in fitness between breeding pairs (Roberts 2005). We paired males as opposed to females because it is arguable that two females from the same group may also be interdependent (albeit to a lesser extent than the male and female breeding pair) since females may change sex to become males and then breed with the remaining females in the group. We used two males because we reasoned that if cleaners were ever going to show aversion to a partner receiving a higher quality food reward than themselves, it would be in a situation in which they were paired with an individual with which they had no overlapping fitness interests.

EXPERIMENT 2

Methods

Subjects

All data were collected at Lizard Island Research Station in 2011. In experiment 2, actors were paired with same-sex competitors rather than breeding partners. Ten male cleaner fish were caught and split into five male–male pairs. As in experiment 1, fish were housed in pairs in aquaria and were separated by a transparent Plexiglas partition. Of these 10 males, eight were tested in both the actor and the receiver role (on alternating days); the other two males did not learn to perform tactile stimulation to the empty plate and were tested only as receivers (also only tested on alternating days). In experiment 2, actors were fed prior to each round to ensure that variation in responses to different treatments was not obscured by the fact that cleaners were simply hungry and therefore motivated to work for any reward. Experimental trials were conducted over 4 days with 12 rounds (consisting of two rounds per treatment, and two presentation trials per round) per day, as in experiment 1. The fish had not been used in a previous experiment, so they had not been trained to feed against their preference prior to beginning the study.

Apparatus and training

The same apparatus and training as in experiment 1 were used. As in experiment 1, cleaners interacted with each of the four experimental plates multiple times per day (two trials per round, two rounds of each experimental treatment per day, 2 experimental days per actor). Thus, over the course of the 4-day experiment, each actor interacted with each plate 8–24 times, depending on experimental plate type.

Procedure

The same procedure as for experiment 1 was followed, except that actors were only allowed 45 s (rather than 60 s) to perform tactile stimulation to the empty plate. This was because N.R. was the sole experimenter for experiment 2 and so reducing the time to 45 s ensured that 10 rounds per day could be conducted. In experiment 1, of the 866 trials in which actors did perform tactile stimulation to the plate, they did so within 45 s on 99.4% of all occasions. Owing to the time constraints imposed by having just one experimenter for experiment 2, these trials were not videotaped.

Analysis

As in experiment 1, we first investigated whether the proportion of presentations in which actors performed tactile stimulation varied according to treatment. The proportion of presentations in which actors performed tactile stimulation was arcsine square-root transformed and set as the response term in an LMM with normal error distribution. Treatment (plate type) and presentation (first or second) were included as explanatory terms and actor ID as a random term to control for the effect of repeated measures on the distribution of the data.

Next, we investigated whether latency to perform tactile stimulation (s) varied according to treatment. The mean latency to perform tactile stimulation for each treatment was calculated for first and second presentations, respectively. This value was log transformed and set as the response term in an LMM with normal error distribution. Treatment (plate type) and presentation (first or second) were included as explanatory terms. Actor ID was included as a random term to control for the effect of repeated measures on the distribution of the data.

Finally, we investigated the factors affecting the proportion of available food items that were eaten by the cleaner fish in this experiment. The proportion of food items eaten in each presentation of each treatment was arcsine square-root transformed and set as the response term in an LMM with item type (flake or prawn), treatment (plate type), presentation (first or second) and role (actor or recipient) set as explanatory terms. Male ID was included as a random term to control for the effect of repeated measures on the distribution of the data.

Results

Cleaners performed tactile stimulation on $75.8 \pm 3.7\%$ of first presentations and on $71.9 \pm 3.9\%$ of second presentations. We found no significant difference in the proportion of trials in which males performed tactile stimulation across first and second presentations ($\chi^2_1 = 0.45, P = 0.50$). We found that the proportion of trials in which males performed tactile stimulation was significantly affected by treatment ($\chi^2_5 = 15.8, P = 0.008$; Fig. 5). Collapsing factor levels revealed that this effect was due to males being less likely to perform tactile stimulation in the NSC treatment, compared to all other treatments ($\chi^2_1 = 11.6, P = 0.0007$; Fig. 5).

The mean latency to perform tactile stimulation was 17.0 ± 1.5 s in the first presentation and 19.3 ± 1.5 s in the second presentation. We found a nonsignificant trend for a longer latency to perform tactile stimulation in the second presentation relative to the first

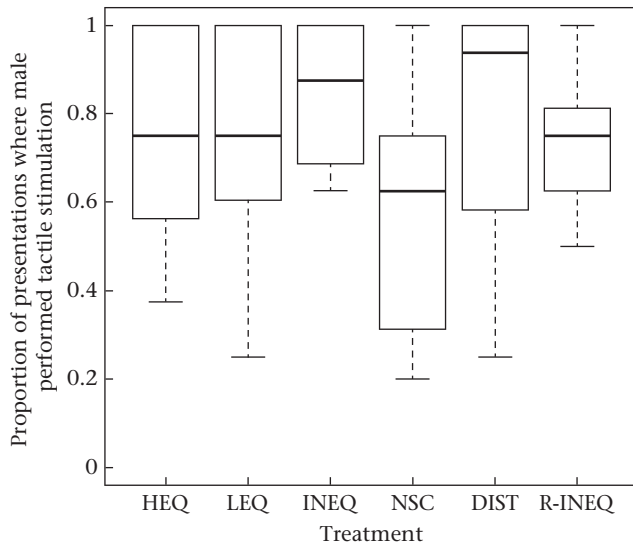


Figure 5. The proportion of presentations where males performed tactile stimulation according to treatment in experiment 2 generated from raw data (high equity (HEQ), both fish received five prawn items; low equity (LEQ), both fish received five flake items; inequity (INEQ), the actor received five flake items while the recipient received five prawn items; nonsocial control (NSC), INEQ treatment where the recipient was hidden by an opaque barrier; distraction control (DIST), INEQ treatment where the recipient was behind a transparent barrier; reward inequity (R-INEQ), the actor received no food while the recipient received five flake items). The thick black line in each box depicts the median proportion for each treatment while the upper and lower ends of the box correspond to the upper and lower quartiles of the distribution. The dashed lines show the upper and lower proportions for each treatment.

($\chi^2_1 = 3.83$, $P = 0.05$). There was no further significant effect of treatment on latency to perform tactile stimulation ($\chi^2_5 = 8.04$, $P = 0.15$; Fig. 6).

Cleaners ate $82.7 \pm 3\%$ of available food items in the first presentation and $78.0 \pm 3\%$ of available food items in the second presentation. The tendency to eat fewer of the available food items in the second presentation was not significant ($\chi^2_1 = 2.77$, $P = 0.10$). Cleaners showed a consistent preference for prawn items over flake items in this experiment. Individuals ate a higher proportion of prawn items than flake items ($\chi^2_1 = 63.3$, $P < 0.001$; Fig. 7). There was no significant effect of role ($\chi^2_1 = 0.48$, $P = 0.49$) or of treatment ($\chi^2_5 = 5.14$, $P = 0.40$) on the proportion of food items eaten.

Discussion

In this experiment, male cleaners performed the tactile stimulation task for a same-sex breeding competitor. In this context, cleaner pairs cannot be considered to have interdependent fitness. We acknowledge the possibility that males did not realize that the recipient was an unfamiliar male, rather than a familiar female partner, although previous work has shown that cleaners are capable of recognizing and responding to an unfamiliar conspecific (Raihani et al., in press). Despite ruling out interdependencies in fitness as far as we could, we did not find evidence that male cleaners were sensitive to inequity when performing a task to obtain a food reward. Thus, it does not seem to be the case that cleaner fish failed to show IA because of overlapping fitness interests in experiment 1. In experiment 2, males were less likely to perform tactile stimulation in the NSC treatment than in all other treatments. Without a corresponding decrease in propensity to perform tactile stimulation in either the INEQ or the DIST treatments this cannot be taken as evidence of a frustration effect, at seeing preferred food but being unable to get access to it. Rather we suggest that the insertion of the large opaque partition (used to

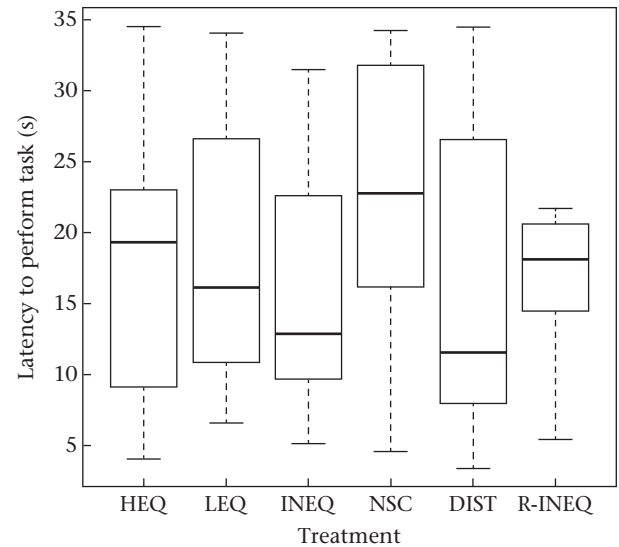


Figure 6. Box plot of the latency (s) to perform tactile stimulation in experiment 2 generated from raw data (high equity (HEQ), both fish received five prawn items; low equity (LEQ), both fish received five flake items; inequity (INEQ), the actor received five flake items while the recipient received five prawn items; nonsocial control (NSC), INEQ treatment where the recipient was hidden by an opaque barrier; distraction control (DIST), INEQ treatment where the recipient was behind a transparent barrier; reward inequity (R-INEQ), the actor received no food while the recipient received five flake items). The thick black line in each box depicts the median latency for each treatment while the upper and lower ends of the box correspond to the upper and lower quartiles of the distribution. The dashed lines show the upper and lower latencies for each treatment.

block the view of the recipient fish) may have somehow scared or intimidated the actor fish to the extent that this caused a reduction in response rates in this treatment. Fish in experiment 2 may have been more sensitive to such environmental disturbances than fish in experiment 1 because the fish used in experiment 2 had spent less time doing experiments in the laboratory than the fish used in experiment 1. The insertion of the transparent partition in the DIST treatment (used to prevent the recipient from getting access to the

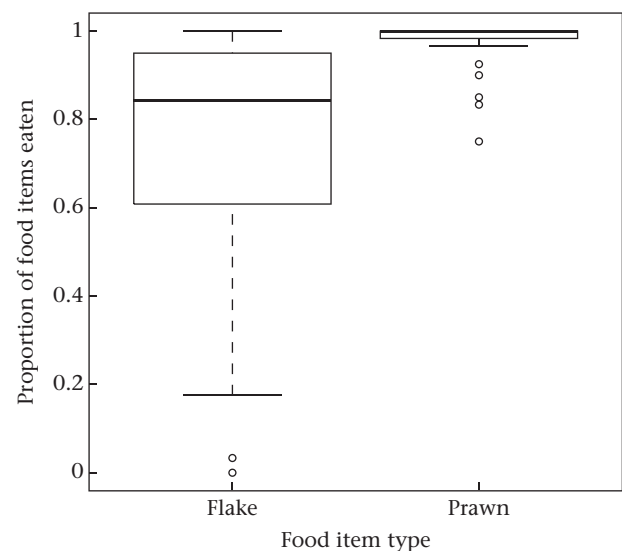


Figure 7. The proportion of food items eaten according to item type in experiment 2. Box plot was generated from raw data. The thick black line in each box depicts the median proportion for each treatment while the upper and lower ends of the box correspond to the upper and lower quartiles of the distribution. The dashed lines show the upper and lower proportions for each treatment. Open circles represent outliers.

plate while keeping the recipient in view) may not have had the same effect since the transparent partition was effectively invisible once it had been placed in the tank.

In experiment 2, actors were apparently more likely to refuse to perform tactile stimulation to the empty plate and also seemed to delay for longer before performing tactile stimulation. However, as in experiment 1, we failed to find any pattern in latency to work across the different treatments. Rather than cleaners being less motivated to work for a male competitor, we suggest that cleaners in experiment 2 were generally less motivated to work for food rewards since in this experiment the male actors were fed between trials, whereas no supplemental feeding took place in experiment 1. The nonsignificant increase in latency to work for food rewards between first and second presentations, as well as the nonsignificant tendency to eat fewer food items in the second presentations, also supports the idea that cleaners were less motivated to work for food rewards as they became increasingly satiated. Unlike experiment 1, in experiment 2 we found that cleaners ate a lower proportion of flake than prawn items. Again, this could be because the fish in experiment 2 were generally more satiated and therefore less inclined to eat flake items.

GENERAL DISCUSSION

We tested cleaner fish for responses to inequity in two experiments, one in which fish were paired with a familiar breeding partner and another in which fish were paired with an unfamiliar same-sex competitor. Our results in the two experiments were broadly the same: cleaners were apparently insensitive to inequity and were equally likely to work to gain access to a food plate, regardless of the distribution of preferred and less-preferred food items on the plate. Below, we highlight some limitations of our study, as well as discussing our results in a more general context.

On paper, cleaner fish are an ideal candidate species to look for evidence of IA. They regularly cooperate with nonkin (both conspecifics and allospecifics) and are apparently sensitive to the actions of their conspecific partners when they work together to clean a joint client (Raihani et al. 2010, 2012a, in press). Furthermore, they routinely cooperate in the food domain, setting them apart from other species that have been tested in IA paradigms. Nevertheless, we did not find any evidence to support the hypothesis that cleaner fish are inequity averse. This may be because our experimental method was not appropriate for uncovering responses to inequity. Specifically, it is possible that cleaners did not understand or did not pay attention to the contingencies between performing tactile stimulation and the food reward they (and the partner) would receive. A failure to understand the contingencies of the experiment could have arisen in one of two ways. First, cleaners may have failed to learn the association between performing tactile stimulation and gaining access to the food plate, although this seems unlikely. Observations in the wild and laboratory experiments have demonstrated that cleaners are able to learn the association between their current behaviour and the behaviour of current and prospective clients. For example, cleaners often perform tactile stimulation to prevent a client from leaving (Bshary & Würth 2001) and it has been demonstrated that cleaner fish improve the service quality they offer to a current client when they are watched by a bystander who may leave if it witnesses cheating by the cleaner (Bshary 2002; Pinto et al. 2011). Furthermore, in the current experiments, cleaners often swam directly to the back of the tank after they performed tactile stimulation to receive their food reward (N. Raihani, personal observation), suggesting that they understood the association between performing the task and receiving the food reward. A second possibility is that cleaners were unable to see the food plate clearly when it was placed at the back of the tank.

Although cleaners almost always swam towards the food plate when it was placed on the outside rear wall of the tank (N. Raihani, personal observation), it is possible that they were either unable to see, or simply did not attend to, the distribution of food items on the plate. To try to control for the possibility that cleaners could not see the distribution of food on the plate prior to its introduction into the tank, we always offered two plate presentations of the same type in each round to help cleaners learn that they always had two consecutive presentations of the same food plate. Despite this feature of our experimental set-up, it remains possible that cleaners simply did not learn the rule that plate type in the first presentation was a reliable predictor of plate type in the second. The fact that cleaners were apparently equally likely to work for less-preferred flake items as they were for high-value prawn items, and that cleaners regularly worked in the R-INEQ condition in which they received no food, also hints that they may not have seen or attended to cues regarding plate type prior to performing tactile stimulation.

Another possibility is that our experimental design to test for IA is not a good analogue of the context in which cleaner fish would display IA in the wild. For example, when a pair of cleaners provides a joint service to a client then it is not the case that one of the pair can eat preferred food (mucus) with impunity while the partner can only eat less-preferred ectoparasites. Instead, both cleaners theoretically have the option to eat the preferred food but, equally, both will share in the costs of client departure if the client terminates the interaction as a consequence of being bitten (Bshary et al. 2008). In addition, since males are highly unlikely to work with another male cleaner fish to clean a joint client, they may not have evolved preferences for equal outcomes when interacting with same-sex male partners, as was the case in experiment 2.

On a more general level, despite regularly cooperating with nonkin, and therefore seeming to be a prime candidate to support the social hypothesis for the evolution of inequity aversion, it is questionable whether additional features of cleaner fish ecology would select for sensitivity to partners' payoffs and associated responses to inequity. If not then it is reasonable to question whether cleaners actually attended to the cues regarding plate type and the distribution of rewards prior to performing tactile stimulation. Cleaner fish more typically work alone than with a partner. Pairwise inspections, when they occur, tend to be with the same individual (the largest female on the territory, Robertson 1972; Bshary et al. 2008). Thus, the scope for partner choice in response to inequity may be limited in this system. Since IA is thought to be a mechanism that allows individuals to judge when to switch partners, cleaner fish may not stand to benefit from monitoring the payoffs of others, relative to their own, in social interactions.

Although cleaner fish do not regularly swap interaction partners, there is evidence that males will punish females if females cheat during inspections of joint model clients, causing the client to leave (Raihani et al. 2010, 2012a, in press). The fact that males respond to female foraging behaviour raises the possibility that males could be sensitive to the payoffs accrued by female partners during joint client inspections and also that male punishment represents a mechanism to reduce unequal outcomes in joint interactions (that is, partner choice may trade off with punishment; Brosnan 2011; Raihani et al. 2012b). However, while our experiments were not conducted in a punishment context, we found no evidence to suggest that males were sensitive to the payoffs accrued by a partner during joint client inspections. Furthermore, it may well be the case that male punishment of cheating females does not require the male to compare his own payoffs to those gained by the female. Instead, males could adjust punishment in response to the external cue of the client's sudden departure and the associated reduction in his own payoffs (in terms of food intake). Indeed, in a recent experiment designed to test whether

the severity of male punishment was adjusted to the seriousness of the female partner's crime (Raihani et al. 2012a), we found that males punished females equally severely in situations in which females did cheat (by eating a prawn item and causing the plate to leave) and in situations in which female cheating was simulated (by the experimenter removing the plate regardless of female foraging behaviour, N. Raihani, unpublished data). Thus, in cleaner fish at least, punishment may more likely be a response to a payoff reduction rather than distributional inequity and therefore may not operate as a mechanism to restore equality in social interactions but rather to increase the male's payoffs regardless of those accrued by the female (Raihani & McAuliffe, 2012).

To sum up, although cleaners regularly cooperate with unrelated others in the food domain, we found no evidence that they were sensitive to inequity in this experimental context. Although we cannot rule out the possibility that the fish did not understand the rules of the experiment, results from this study suggest that cleaner fish are not inequity averse and that they may not need to attend to the payoffs of conspecifics to regulate cooperation. Further studies of nonhuman species that regularly cooperate with nonkin will be enormously useful in supporting or refuting the hypothesis that inequity aversion is most likely to have evolved in social species that routinely cooperate with nonkin.

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