



Are cleaner fish, *Labroides dimidiatus*, inequity averse?

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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

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