Animal Behaviour 86 (2013) 611–615

Contents lists available at SciVerse ScienceDirect

Animal Behaviour

journal homepage: www.elsevier.com/locate/anbehav

Indo-Pacific parrotfish exert partner choice in interactions with cleanerfish but Caribbean parrotfish do not

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ARTICLE INFO

Article history:
Received 25 February 2013
Initial acceptance 20 March 2013
Final acceptance 13 June 2013
Available online 6 August 2013
MS. number: 13-00189R

Keywords:
behavioural strategy
conflict
cooperation
Elacatinus spp.
Labroides dimidiatus
mutualism
parrotfish
partner choice

Cooperation theory puts a strong emphasis on partner control mechanisms that have evolved to stabilize cooperation against the temptation of cheating. The marine cleaning mutualism between the Indo-Pacific bluestreack cleaner wrasse, *Labroides dimidiatus*, and its reef fish ‘clients’ has been a model system to study partner control mechanisms and counterstrategies. These cleaners cooperate by eating ectoparasites; however, they can cheat by taking client mucus, which they prefer. Such a conflict may be the exception. For example, Caribbean cleaning gobies, *Elacatinus* spp., prefer to eat ectoparasites instead of mucus. While partner control mechanisms and counterstrategies seem to be absent in cleaning gobies, no study has directly compared cleaner wrasses and cleaning gobies by using the same methods. We examined systematic differences in cleaning interaction patterns and strategic behaviour exhibited by 12 closely related parrotfish species in the two systems. Parrotfish seeking cleaner wrasses visited them more often and spent more time with their cleaner than parrotfish seeking cleaning gobies. Moreover, the clients of cleaner wrasses returned more often to the same cleaner following a positive interaction, whereas the clients of cleaning gobies were less influenced by the outcome of previous interactions. We hypothesize that the higher frequency and repeated nature of interactions observed in the cleaner wrasse system, combined with the need to resolve conflicts, might have been prerequisites for the development of complex behavioural strategies.

Cooperation theory places a strong emphasis on how cheating can undermine the stability of cooperation (Axelrod & Hamilton 1981). To maintain the continuing net benefit of cooperative partnerships, the risk of cheating can be reduced through the use of various strategies (Noë 2006), such as careful partner choice (Noë et al. 1991; Bshary & Grutter 2002a, b; Ferrière et al. 2002; Bshary & Noë 2003; Noë 2006) or trying to exclude cheaters by passive partner choice (sanctioning; Kiers et al. 2003), actively switching partners if a partner cheats (Bshary & Schäffer 2002; Ferrière et al. 2002; Bshary & Grutter 2005; Johnstone & Bshary 2008) and/or punishing cheaters (Clutton-Brock & Parker 1995).

In cleaning mutualisms, conflicts between Indo-Pacific bluestreak cleaner wrasse, *Labroides dimidiatus*, the classic model for cleaning interactions, and their clients over service quality are common. Cleaning interactions entail individual fish clients repeatedly visiting the territories (i.e. cleaning stations) held by cleaners, to have their ectoparasites and dead or infected tissues removed (reviewed by Côté 2000). However, while cleaners search the body and gills of their clients (i.e. while they ‘inspect’), they often feed instead on healthy tissue, scales and mucus, which constitutes cheating (Grutter & Bshary 2003, 2004). To enforce good cleaning service quality, clients use partner control mechanisms, while the specific nature of these mechanisms depends on a client's strategic options (Bshary & Bronstein 2011). For example, predators exert the ‘threat of reciprocity’ in which they could retaliate on cheating cleaners by eating them. On the other hand, nonpredatory clients punish cheaters by aggressive chasing unless they have access to several cleaning stations, in which case they simply switch cleaners (Bshary & Grutter 2002a, 2005). Furthermore, potential clients may observe the cleaner’s services on other fish and thus avoid cheating cleaners (Pinto et al. 2011). Cleaner wrasses, in return, can manipulate client decisions by rubbing their pelvic and pectoral fins on their client’s dorsal area (Bshary & Würth 2001; Grutter 2004). Such tactile stimulation has several effects: it makes clients that are initially unwilling to interact stop for inspection, it allows cleaners to prolong interactions with clients that are about to leave, it serves as preconflict management in

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http://dx.doi.org/10.1016/j.anbehav.2013.06.017

interactions with predators and it allows cheating cleaners that have been punished to reconcile with their clients (Bshary & Würth 2001; Grutter 2004). Clients appear to accept tactile stimulation as payment since it lowers baseline and acute stress levels (e.g. cortisol levels; Soares et al. 2011), an effect that at least in humans is used as an indicator of improved health (Field 1996; Field et al. 2005).

These control mechanisms do not exist in all cleaning mutualisms. A comparison between various cleaner wrasse species in the Red Sea suggests that cleaning evolved as a by-product mutualism (Brown 1983), in which cleaners initially grazed and ingested small benthic invertebrates and later picked these food items from fish, while more complex behavioural interactions and signalling might have evolved only in more specialized species (Barbu et al. 2011). For example, in Caribbean cleaning gobies, *Elacatinus* spp., the level of conflict between cleaners and clients appears to be lower than in the cleaner wrasse system (Soares et al. 2008c, 2010). Indeed, Soares et al. (2008c) found no evidence for punishment, partner switching and manipulation through tactile stimulation. The absence of control strategies and counterstrategies may be explained by the foraging preferences of cleaning gobies: in contrast to cleaner wrasses, cleaning gobies prefer ectoparasites over mucus (Soares et al. 2010). Nevertheless, gobies still eat some mucus from their clients, which is confirmed by clients' jolting behaviour. Jolts are whole-body shudders that occur in response to cleanerfish mouth contact, and their frequency appears to be a good correlate of cheating by cleaners, since they are largely absent when the client is parasitized and frequent when the client is parasite-free (Bshary & Grutter 2002b; Soares et al. 2008b). Moreover, in both systems client jolt frequency is reduced when cleaners inspect in pairs rather than on their own (Bshary et al. 2008; Soares et al. 2009). Thus, there are both similarities and dissimilarities between the cleaner species with respect to cheating behaviour.

In this study, we carried out a first direct comparison between Indo-Pacific cleaner wrasses and Caribbean cleaning gobies. To exclude potential effects of differences in client composition, we focused on the family Scaridae (parrotfish). Parrotfish are ideal for a comparison because members of this family are found in both oceans. Moreover, representatives of some genera (e.g. the genus *Scarus*) are present in both regions; thus *Scarus* species exposed to cleaners in different oceans are more closely related to each other than they are to other sympatric parrotfish species. Using identical methods, we quantified the degree to which parrotfish clients depend on cleaning, the use of tactile stimulation, the extent of cheating and the use of partner switching to control cheating in each system. The notion that client species with access to several cleaner wrasses exert partner choice is based on observations of a single parrotfish species, namely *Hipposcarus harid* (Bshary & Schäffer 2002). Thus, our study allowed us to compare the two cleaning mutualisms and also to evaluate how general partner switching is as a strategy against cheating by cleanerfish.

METHODS

Study Sites and Species

Our study focused on Caribbean cleaning gobies and Indo-Pacific bluestreak cleaner wrasses. In the Caribbean, observations were conducted on four fringing reefs off the west coast of Barbados, West Indies, between March and November 2005. All reefs showed a typical spur-and-groove development at their seaward edge, and all were degraded, with relatively low live coral cover and high algal cover. In the Red Sea, behavioural observations were carried out in Mersa Bareika (Egypt), a protected bay with many reef patches within Ras Mohammed National Park. Three sets of observations were obtained: between May and July in 1998 and 1999 and between August and October in 2009. Approval for the study was obtained from the Portuguese National Authority for Animal Health (oficio circular no. 9–0420/000/000, 20 January 2011) and the Egyptian Environmental Affairs Agency.

At both locations, we focused on the commonest species of parrotfish on the study reefs. In Barbados the species included members of the genera *Scarus* and *Sparisoma*: *Scarus vetula*, *Scarus taeniopterus*, *Scarus iserti*, *Sparisoma aurofrenatum*, *Sparisoma rubripinne*, *Sparisoma chrysopterum* and *Sparisoma viride*, while in Egypt the species also included the genus *Scarus* but also representatives of the genera *Chlorurus* and *Hipposcarus*: *Chlorurus sordidus*, *H. harid*, *Scarus gibbus*, *Scarus niger* and *Scarus ferrugineus*. In total, our focal species belong to two clades: one comprising the genus *Sparisoma* and the other comprising all other genera. All these species exhibit sex change, switching from a relatively drab-coloured initial phase characteristic of females (and primary males in some species) to a brilliantly coloured, usually larger male terminal phase (Deloach 1999).

Behavioural Observations

Data on parrotfish behaviour were collected throughout the day (0600–1700 hours) through focal follow observations of an average of 30 individuals per species at each location. Focal clients were selected haphazardly by snorkellers or roving scuba divers and observations began immediately upon sighting. Each individual was observed for a maximum of 90 min, with a snorkeller diver or a scuba diver following the focal parrotfish from a minimum distance of 3–5 m. During focal follows, we noted all visits to cleaning stations by focal fish and any interactions with cleaners. Specifically, we recorded (1) the duration of inspection by the cleaner, (2) all client jolts and parrotfish behaviour after jolting (e.g. interruption of the cleaning interaction with prompt departure) and (3) any instances of tactile stimulation by cleaners and parrotfish behaviour before, during and after such events. Each client interaction with cleaners was classified as either 'negative' when the interaction ended with a client swimming away after a jolt, or 'positive' when clients were attended by cleaners and the interaction did not end with a client jolt. We defined tactile stimulation as occurring when cleaners hovered above the client while touching it using pectoral and pelvic fins (Potts 1973; Bshary & Würth 2001). Because clients were not tagged during the study, it is possible that individuals were observed more than once. However, we selected parrotfish from different parts of the reefs during the focal follows to reduce the possibility of repeated observations.

Statistical Analysis

To measure the degree to which parrotfish clients depend on cleaning, the use of tactile stimulation and the extent of cheating, we calculated mean values for each parrotfish species for (1) the frequency of parrotfish visits to cleaning stations (number of visits per 10 min observation), (2) the mean duration of inspection by cleaners (mean length of inspection bouts for each parrotfish, and then an overall mean per species), (3) the proportion of interactions in which the cleaners used tactile stimulation on clients (calculated for each individual, and then averaged within species), and (4) the frequency of jolts (number of jolts per 100 s of inspection). We first investigated the influence of time of day (morning versus afternoon observations), using just the data collected in 2009, on inspection duration, client jolt rates and the proportion of tactile stimulation provided and found no differences (independent-samples *t* tests: inspection duration: $t_{304} = -1.53$, $P = 0.12$; frequency of jolts: $t_{304} = -0.65$, $P = 0.52$; proportion of interactions with tactile