



Articles

Competition encourages cooperation: client fish receive higher-quality service when cleaner fish compete

Thomas C. Adam*

Department of Ecology, Evolution, and Marine Biology, University of California, Santa Barbara

ARTICLE INFO

Article history:

Received 26 September 2009
Initial acceptance 24 November 2009
Final acceptance 4 February 2010
Available online 27 March 2010
MS. number: A09-00635R

Keywords:

biological market
bluestreak cleaner wrasse
Chaetodon ornatissimus
cleaning mutualism
conflict
cooperation
Labroides dimidiatus
ornate butterflyfish
partner choice

Partner choice is likely to be an important mechanism for the maintenance of cooperation in many mutualisms, and cleaner mutualisms among fish have been a model system for testing predictions of partner choice theories. Fish seeking to be cleaned (clients) face two potential problems: cleaners may cheat them by feeding on tissue or mucous, and they may have to wait for service from a cleaner. Previous work on interactions between the bluestreak cleaner wrasse, *Labroides dimidiatus*, and its clients indicates that cleaners provide higher-quality service to species that have the option of switching partners. These results have been interpreted as evidence that partner choice leads cleaners to behave cooperatively; however, alternative explanations exist for these between-species patterns. Here I focus on interactions between the bluestreak cleaner wrasse and a single client species that varies in its ability to switch partners to test the prediction that clients receive higher-quality service when cleaners have to compete for access to them. The results indicate that cleaners give ornate butterflyfish, *Chaetodon ornatissimus*, priority of access to their services when these clients can switch partners; however, ornate butterflyfish are not cheated less often when they have access to multiple cleaner stations, and they frequently respond to cheating by aggressively chasing cleaners. In combination with previous work, these results indicate that partner choice influences cooperative interactions between bluestreak cleaner wrasse and their clients, but that some clients with the ability to switch partners may use other strategies (i.e. punishment) to limit cheating by cleaners.

© 2010 The Association for the Study of Animal Behaviour. Published by Elsevier Ltd. All rights reserved.

Understanding the evolution of cooperation between unrelated individuals is a major challenge of evolutionary biology and has been the focus of much theoretical and empirical work (Trivers 1971; Dugatkin 1997; Nowak & Sigmund 2005). While game theoretical models based on repeated interactions between a pair of individuals (i.e. the Iterated Prisoner's Dilemma, IPD; Axelrod & Hamilton 1981) long have been a framework for understanding cooperative interactions, these models rarely describe important features of mutualisms in nature (Bergstrom et al. 2003; Sachs et al. 2004; West et al. 2007). In contrast, the idea that partner choice can lead to cooperation is emerging as a general framework for understanding many cooperative interactions including mutualisms (Eshel & Cavalli-Sforza 1982; Bull & Rice 1991; Noë et al. 1991; Noë & Hammerstein 1994). In particular, the salient features of some mutualisms can be described as biological markets where different classes of traders exchange goods or services. In a biological market, individuals from one class preferentially interact with the members of the other class that provide the highest-quality

goods or services, and as a consequence competition for access to partners can lead to increasingly cooperative behaviour (Noë et al. 1991; Noë & Hammerstein 1994). A market framework is useful for describing many mutualisms because partners almost always exchange different goods or services and at least one class of trader often has the ability to choose among multiple partners (Hoeksema & Bruna 2000; Bshary & Bronstein 2004). Indeed, some obligate pollination mutualisms (e.g. yucca–moth: Pellmyr & Huth 1994), nutrient exchange mutualisms (e.g. mycorrhizal fungi–plant: Hoeksema & Schwartz 2001; rhizobia bacteria–plant: Simms et al. 2006), protection mutualisms (e.g. ant–butterfly: Pierce et al. 2002; shrimp–fish: Thompson et al. 2006) and cleaner mutualisms (Bshary 2001) all have characteristics of biological markets.

Cleaner mutualisms among fish have been an important model system for testing predictions of market theory (Bshary 2001; Bshary & Schaffer 2002; Bshary & Grutter 2002a; Soares et al. 2008a). In many cleaner mutualisms, cleaner fish occupy spatially discrete territories (cleaner stations) where they remove parasites from cooperating client fish (Côté 2000). While parasite removal clearly benefits clients, cleaners can (and often do) cheat clients by eating mucous or tissue in addition to parasites (reviewed in Côté 2000; see also Bshary & Grutter 2002a). However, most clients do not have the option of cheating cleaners, precluding the

* Correspondence: T. C. Adam, Department of Ecology, Evolution, and Marine Biology, University of California, Santa Barbara, CA 93106, U.S.A.
E-mail address: adam@lifesci.ucsb.edu

maintenance of cooperation by IPD strategies (e.g. cooperate or cheat based on the behaviour of your partner in the previous interaction). Alternatively, it has been proposed that cooperation between cleaners and clients could be maintained by partner choice if clients preferentially interact with cleaners that either have behaved cooperatively in previous interactions (Bshary 2001; Bshary & Noë 2003), or have been observed behaving cooperatively with other clients (a form of indirect reciprocity termed image scoring) (Bshary & D'Souza 2005; Bshary & Grutter 2006). Indeed, there is evidence that some clients are capable of these behaviours (Bshary 2001; Bshary & Schaffer 2002; Bshary & D'Souza 2005; Bshary & Grutter 2006), and that cleaners provide higher-quality service to client species that have the option of switching partners (Bshary 2001). Furthermore, client species that lack the option of partner choice (because they have small home ranges and are restricted to a single cleaner station) often respond to cheating by aggressively chasing cleaners, suggesting that clients resort to punishment (*sensu* Clutton-Brock & Parker 1995) as a strategy to control cheating when they cannot use partner choice (Bshary & Grutter 2002a, 2005). Finally, experiments where client behaviours have been simulated have shown that cleaners quickly learn to distinguish 'clients' that are able to choose among cleaners from 'clients' that lack the option of switching partners, suggesting that cleaners are capable of categorizing clients based on past experiences and that the behaviour of cleaners in nature may result in part from learning (Bshary & Grutter 2002b).

While these observations strongly support the role of partner choice mechanisms in maintaining cooperation in cleaner mutualisms, alternative explanations exist for many of the patterns. For example, client species with the option of switching partners may harbour more parasites because they generally tend to be larger in body size or because they spend less time interacting with cleaners than resident clients (Bshary 2001; Bshary & Noë 2003). Consequently, cleaners could be responding to parasite load or client size rather than the ability of clients to switch partners (but see Soares *et al.* 2008b). Therefore, unequivocal support for partner choice as a mechanism influencing cleaner behaviour cannot be obtained solely from these between-species comparisons. Furthermore, while experiments lend support to the idea that partner choice influences cleaner behaviour, the fact that cleaners are capable of distinguishing between simulated behaviour of a pair of 'clients' with and without the option of switching partners does not necessarily mean they are cueing in on this feature in nature (Bshary & Grutter 2002b).

An approach that would complement the current state of knowledge on the role of partner choice in structuring cleaner–client interactions would be to investigate a single client species that exhibits variation in the ability to choose among multiple cleaners independent of other potentially confounding factors (e.g. body size, the amount of time spent being cleaned). Some territorial butterflyfish (Chaetodontidae) may fulfil this requirement because pairs often occupy exclusive territories that they defend from conspecifics, and it is likely that these territories will exhibit variation in the number of cleaner stations in them. If cleaners have to compete for access to clients, and they are capable of cueing in on the ability of their clients to choose among multiple partners, then market theory predicts that cleaners should provide higher-quality service to clients with multiple cleaner stations in their territory. To investigate this hypothesis I mapped territories of pairs of ornate butterflyfish, *Chaetodon ornatissimus*, and recorded the behaviour of focal individuals with different numbers of cleaner stations in their territories. Specifically, I tested the following three predictions: (1) access to focal fish by individual cleaners decreases as the number of cleaner stations in a focal fish's territory increases; (2) focal fish are less likely to return to a cleaner for their next interaction when that cleaner

behaved uncooperatively in their previous interaction; and (3) focal fish with multiple cleaner stations in their territory receive higher-quality service from cleaners. Furthermore, I also tested whether ornate butterflyfish that lacked the option of switching partners (because they had a single cleaner station in their territory) were more likely to use punishment in response to cheating by cleaners as would also be predicted by market theory.

METHODS

Study Site and Organisms

I collected all data between July and September 2008, in the Maharepa lagoon on the north shore of Moorea, French Polynesia (17°30'S, 149°50'W). The lagoon habitat consisted of small, semi-isolated patch reefs separated by low-relief substrate (coral pavement and rubble). I used GPS to map all patch reefs in a ~50 000 m² area of the lagoon and marked all cleaner stations (reefs occupied by one or more juvenile and/or adult bluestreak cleaner wrasse, *Labroides dimidiatus*). Ornate butterflyfish, *C. ornatissimus*, were the most abundant species of butterflyfish at the study site and are preferred clients of bluestreak cleaner wrasse on Moorea (Adam 2010). Within the study area, ornate butterflyfish are predominantly found in pairs that occupy exclusive territories (size range ~100–1400 m²) that they defend from conspecifics (T.C.A., unpublished data). Territories of ornate butterflyfish could contain zero, or one or more cleaner stations. However, several other species of cleaners are common at the study site in addition to bluestreak cleaner wrasse. These include the facultative cleaners, six-line wrasse, *Pseudocheilinus hexataenia*, and juvenile six-bar wrasse, *Thalassoma hardwicke*, and the obligate bicolor cleaner wrasse, *Labroides bicolor*. Six-line wrasse and juvenile six-bar wrasse were present in all ornate butterflyfish territories, and consequently ornate butterflyfish probably had access to these facultative cleaners even if they did not have access to a bluestreak cleaner wrasse.

Behavioural Observations

Snorkelers conducted 60 min observations of ornate butterflyfish during daylight hours to determine territory boundaries and assess behavioural interactions between ornate butterflyfish and its cleaners (several observations included in analyses were less than 60 min because observers occasionally abandoned an observation after losing visual contact with a focal fish). The sizes of focal ornate butterflyfish were estimated visually to the nearest 0.5 cm with the aid of a ruler drawn on an underwater slate; estimated sizes ranged from 13 to 18 cm total length, TL (mean $\pm$ SD = 16.2 $\pm$ 1.4 cm), and pair members were nearly always indistinguishable based on size. The territories of ornate butterflyfish were stable over the length of the study, and consequently, pairs could be identified based on their territories; individuals in some territories were observed on two separate occasions. While observers kept track of individuals during single observations by identifying small body markings that distinguished pair members, these markings were not conspicuous enough to distinguish between pair members during repeated observations. In total, individual fish in 32 territories were observed for 43 h. All analyses were conducted on pooled data for each territory (pair of fish).

While following a focal fish, observers recorded all cleaning events, including cleaning by species other than the bluestreak cleaner wrasse, as well as the details of each event. Cleaning events were defined as occurring when cleaners inspected focal fish for parasites, establishing or nearly establishing physical contact in the process. If contact with a focal fish was broken (as a result of the

behaviour of the cleaner or the focal fish) for more than 2 s and later resumed, it was scored as a new event. If events were in close succession and focal fish continued soliciting cleaning (i.e. they did not leave the immediate vicinity or resume feeding), these events were considered a single prolonged interaction (consisting of multiple events). I will consistently use this terminology throughout the remainder of the paper. Details recorded included: (1) the location of the cleaning event, (2) the duration of the event, (3) whether or not focal fish showed aggression towards the cleaner following an event (aggressive behaviour consisted of fish chasing cleaners often in fast, tight circles), (4) whether the cleaner or the focal fish terminated the interaction (focal fish terminated interactions by swimming away, while cleaners terminated interactions by swimming away or by beginning to inspect a new client), and (5) whether focal fish terminated an interaction by jolting and quickly swimming away (jolts by clients often indicate cheating by bluestreak cleaner wrasse; Bshary & Grutter 2002a). Observers also recorded instances when focal fish solicited inspection by a cleaner (by stopping and spreading its pectoral and dorsal fins) but was ignored (i.e. the cleaner was in close proximity to the client but did not approach and inspect it).

Questions and Data Analyses

Is cleaning time for ornate butterflyfish limited by the availability of cleaner stations?

I used two approaches to explore the extent to which ornate butterflyfish rely on bluestreak cleaner wrasse to be cleaned. First, I compared the total proportion of time spent being cleaned (by all cleaners) for focal fish with and without bluestreak cleaner stations in their territory. Second, I tested for an association between the number of bluestreak cleaner stations in a focal fish's territory and the proportion of time that it spent being cleaned by other species.

Do cleaners have to compete for access to ornate butterflyfish?

To investigate whether there is potential for competition among bluestreak cleaner wrasse for access to ornate butterflyfish, I calculated the mean per-capita cleaning rate of bluestreak cleaner wrasse on focal fish (seconds cleaned per hour per number of bluestreak cleaner wrasse in territory) for each territory, and tested for an association between these rates and the number of bluestreak cleaner stations in a territory. In addition, I tested whether focal fish were less likely to return to a particular cleaner station for their next inspection when they had access to multiple cleaner stations. Finally, I used a matched-pairs design to test whether individuals were less likely to return to a cleaner station if they had been cheated in a previous interaction with that cleaner. While it is not possible to know for certain when a client has been cheated by a cleaner, body jolts of clients appear to be highly correlated with cheating by bluestreak cleaner wrasse (Bshary & Grutter 2002a), and clients frequently chase cleaners or quickly swim away following jolts, presumably in response to cheating (Bshary 2001; Bshary & Grutter 2002a; Bshary & Schäffer 2002). Therefore, I inferred that clients were cheated when they responded to a bite by the cleaner either by jolting and quickly swimming away or by chasing the cleaner. Because of the matched-pair design, only individuals that sought cleaning following interactions where they had and had not been cheated were included in the analysis. I predicted that individual cleaners would have less access to focal fish when focal fish had access to multiple cleaner stations. I also predicted that focal fish would be more likely to return to a cleaner station for their next inspection when they had not been cheated at that cleaner station in their previous interaction.

Do ornate butterflyfish with and without access to multiple cleaner stations differ in value?

While I sought to minimize differences in client value by following a small size range of a single client species, systematic differences could exist if ornate butterflyfish with access to multiple cleaner stations are consistently different in size (since there is a positive correlation between client size and ectoparasite load; Grutter & Poulin 1998), or spend more or less time being cleaned by cleaners (since cleaners reduce the ectoparasite load of client fish; Grutter 1999) than ornate butterflyfish without access to multiple cleaner stations. To address these possibilities, I tested whether clients with and without access to multiple cleaner stations differed in size and/or the amount of time they spent being cleaned.

Do ornate butterflyfish with access to multiple bluestreak cleaner wrasse receive higher-quality service from cleaners?

To investigate whether ornate butterflyfish receive higher-quality service from bluestreak cleaner wrasse when they have multiple cleaner stations in their territories, I compared the frequency that cleaners ignored and cheated focal fish (number of events per 60 min of observation, and number of events per minute cleaned, respectively) with and without access to multiple cleaner stations. I also compared the proportion of interactions that were terminated by the cleaner when cleaning focal fish that did and did not have access to multiple cleaner stations, as well as the duration of individual cleaning events. The duration of cleaning events tended to be skewed with a few very long events, so I determined the median event duration for each focal fish and used these values in statistical analyses (rather than using the mean). If ornate butterflyfish receive higher-quality service from cleaners when cleaners have to compete, then I predicted that focal fish with access to multiple cleaner stations would be ignored less frequently, would experience less cheating from cleaners, would have longer cleaning event durations, and would have fewer interactions terminated by the cleaner compared to clients that only had access to a single cleaner station.

Finally, I compared the frequency of aggressive responses (number of aggressive acts/min cleaned) of ornate butterflyfish with a single cleaner station in their territories with those having multiple cleaner stations available to them. I predicted that fish that only had access to a single cleaner station would be more likely to respond aggressively to perceived cheating events because they did not have the option of switching partners.

Statistics

With one exception, responses were continuous or ordinal, and significant differences or associations were identified with two-tailed rank-based tests (Kendall's tau for ordinal or continuous predictors, Wilcoxon signed-ranks test for matched pairs, Wilcoxon two-sample test for categorical predictors, and rank-based ANCOVA (Quade 1967) for categorical predictors with a covariate). Since focal fish with access to multiple cleaner stations (median size = 17 cm) were significantly larger than those without access (median size = 16 cm) (see Results), I used a stratified sample of fish between 16 cm and 17 cm TL for all analyses of cleaner behaviour. This allowed me to simultaneously test for an influence of client size and access to multiple cleaners on cleaner behaviour. For ANCOVA, I checked homogeneity of slopes and removed nonsignificant interactions (all $P > 0.35$); residuals were also inspected to ensure normality and homogeneity of variances. Because focal fish were rarely ignored, these events were treated as a binary response (i.e. clients were either ignored or not ignored by a cleaner during an observation). There is no general equivalent of

ANCOVA for binary responses with small sample size; consequently, I used Fisher's exact test (on the stratified sample) to identify significant differences between focal fish with and without access to multiple cleaner stations. I also used Fisher's exact test, separately for fish with and without access to multiple cleaner stations, to independently test for an association between size and whether or not a client was ignored (for this test, focal fish were separated into two categories: fish less than 16 cm TL, and fish greater than or equal to 16 cm TL). All tests were two tailed.

RESULTS

Ornate Butterflyfish with Access to Bluestreak Cleaners Are Cleaned More Often

Ornate butterflyfish pairs had between zero and four cleaner stations present in their territory (eight pairs had no cleaner stations, 11 pairs had one, and the remaining 13 pairs had two or more; Fig. 1). All pairs with at least one cleaner station in their territory visited that cleaner station to be cleaned at least once during the one or two short (60 min or less) observation period(s), and all pairs with more than one cleaner station in their territory visited at least two of them (Fig. 1). Focal butterflyfish that had at least one cleaner station in their territory spent significantly more time being cleaned than those that lacked a bluestreak cleaner station in their territory (Wilcoxon two-sample test: $W_2 = 39.5$, $N_1 = 24$, $N_2 = 8$, $P < 0.0001$; Fig. 2). In addition, individuals spent less time being cleaned by species other than bluestreak cleaner wrasse as the number of cleaner stations in their territory increased (Kendall's rank coefficient: $\tau = -0.34$, $P = 0.027$; Fig. 3).

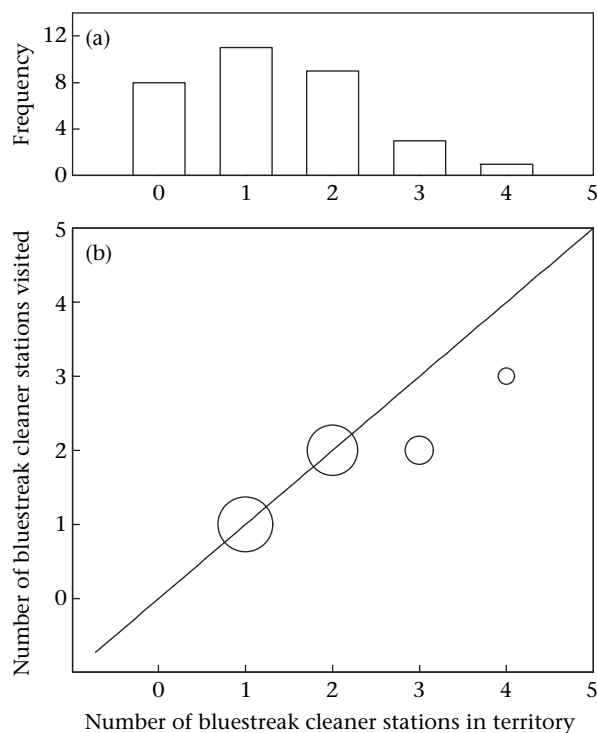


Figure 1. (a) Frequency distribution of the number of bluestreak cleaner stations in ornate butterflyfish territories. (b) Number of bluestreak cleaner stations visited relative to the number of bluestreak cleaner stations in a territory for individuals with at least one cleaner station in their territory (stations were only considered visited if a focal fish was cleaned or solicited cleaning at those locations). The area of each circle is proportional to the number of data points, which can be seen in the frequency distribution in (a). Circles falling to the right of the one-to-one line indicate that not all cleaner stations in a territory were visited during an observation(s).

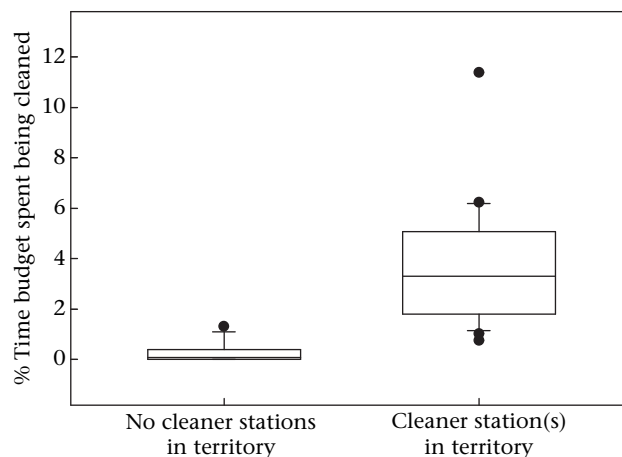


Figure 2. Box and whisker plot of the time spent being cleaned (% of total time observed) for ornate butterflyfish with ($N = 24$) and without ($N = 8$) bluestreak cleaner stations in their territory. Boxes are medians with 25th and 75th quartiles. Whiskers are 10th and 90th percentiles and dots are data points that fall outside the 10th and 90th percentiles (determined using the Cleveland method in Sigma Plot 10.0).

Bluestreak Cleaner Wrasse May Compete for Access to Ornate Butterflyfish

Per-capita cleaning rates of focal ornate butterflyfish by bluestreak cleaner wrasse were negatively associated with the number of cleaner stations in an ornate butterflyfish territory (Kendall's rank coefficient: $\tau = 0.40$, $P = 0.015$; Fig. 4). In addition, individuals with access to multiple cleaner stations were less likely to return to a cleaner station for their next inspection (median $P_{\text{return}} = 0.57$) than were individuals with access to a single cleaner station (median $P_{\text{return}} = 1$) (Wilcoxon two-sample test: $W_2 = 197$, $N_1 = 13$, $N_2 = 11$, $P = 0.0003$). Individuals were not significantly less likely to return to a cleaner station for their next interaction when they had been cheated at that cleaner station in their previous interaction (Wilcoxon signed-ranks test: $W_+ = 17.5$, $N = 6$, $P = 0.157$).

Ornate Butterflyfish with and without Access to Multiple Cleaner Stations Are Not Likely to Differ in Value

There was no difference in the total proportion of time that clients with and without access to multiple cleaner stations spent

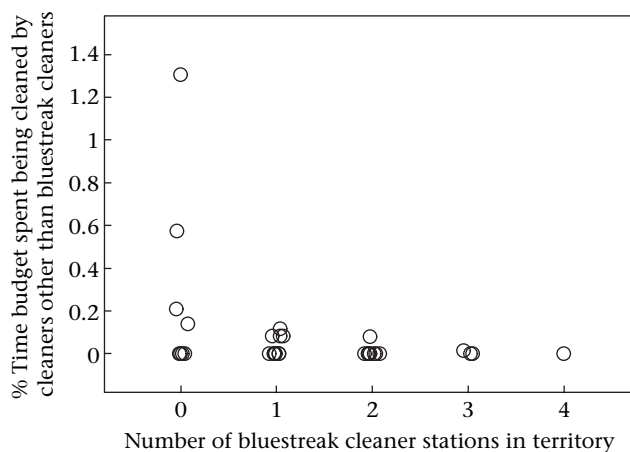


Figure 3. Percentage of a focal fish's time budget that was spent being cleaned by cleaners other than bluestreak cleaner wrasse relative to the number of bluestreak cleaner stations in each focal fish's territory. Note that data points are jittered slightly along the X axis to reveal overlapping points. Sample sizes are also indicated by the frequency distribution in Fig. 1a.

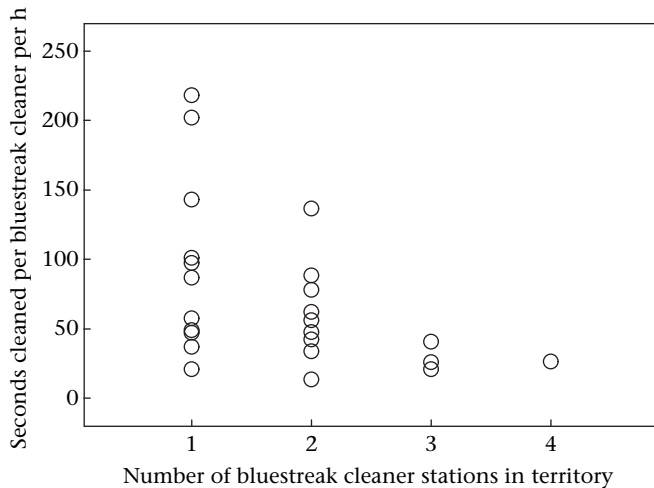


Figure 4. Mean per-capita cleaning rates of bluestreak cleaner wrasse on focal fish relative to the number of cleaner stations in a focal fish's territory.

being cleaned in both the full (Wilcoxon two-sample test: $W_2 = 127$, $N_1 = 13$, $N_2 = 11$, $P = 0.57$) and stratified ($W_2 = 48$, $N_1 = 8$, $N_2 = 7$, $P = 0.40$) samples. Clients with access to multiple cleaner stations were significantly larger than clients without access in the full sample ($W_2 = 82$, $N_1 = 13$, $N_2 = 11$, $P = 0.0006$), but not after stratifying the data ($W_2 = 44$, $N_1 = 8$, $N_2 = 7$, $P = 0.20$).

Ornate Butterflyfish with Access to Multiple Cleaner Stations Receive Higher-quality Service from Cleaners

Focal fish were never ignored when they had more than one cleaner station in their territory. In total, five of 11 fish with a single cleaner station in their territory were observed being ignored; among these, smaller individuals were not ignored significantly more often by cleaners than were larger individuals (Fisher's exact test: $P = 0.24$). From the stratified sample, two of the seven butterflyfish without access to multiple cleaner stations were observed being ignored at least once, but this was not significantly more often than individuals with access to multiple cleaner stations (Fisher's exact test: $P = 0.20$). The frequency of cheating events was relatively low (median = 0.28 cheating events/min cleaned), and there was no evidence that individuals with access to multiple cleaner stations were cheated less frequently than individuals without access (ANCOVA: $F_{1,12} = 1.01$, $P = 0.33$); however, smaller individuals were cheated significantly more often than larger individuals ($F_{1,12} = 5.16$, $P = 0.042$). In contrast, focal fish that did not have access to multiple cleaner stations were more likely to have interactions terminated by bluestreak cleaner wrasse ($F_{1,12} = 9.35$, $P = 0.0099$; Fig. 5a). Furthermore, focal fish were inspected for significantly longer per cleaning event when they had access to multiple cleaner stations ($F_{1,12} = 16.69$, $P = 0.0015$; Fig. 5b). There was no significant correlation between client size and the likelihood that a bluestreak cleaner wrasse would terminate an interaction with a client ($F_{1,12} = 1.20$, $P = 0.29$), nor was there a correlation between client size and inspection duration ($F_{1,12} = 0.27$, $P = 0.86$).

The frequency that focal fish initiated aggression towards bluestreak cleaner wrasse was relatively low (median = 0.13 chases/min cleaned) and did not differ between focal fish with and without access to multiple cleaner stations (Wilcoxon two-sample test: $W_2 = 122$, $N_1 = 13$, $N_2 = 11$, $P = 0.40$). Nevertheless, slightly more than half of the focal fish (13 of 24) were observed initiating aggression towards a bluestreak cleaner wrasse at least once. In

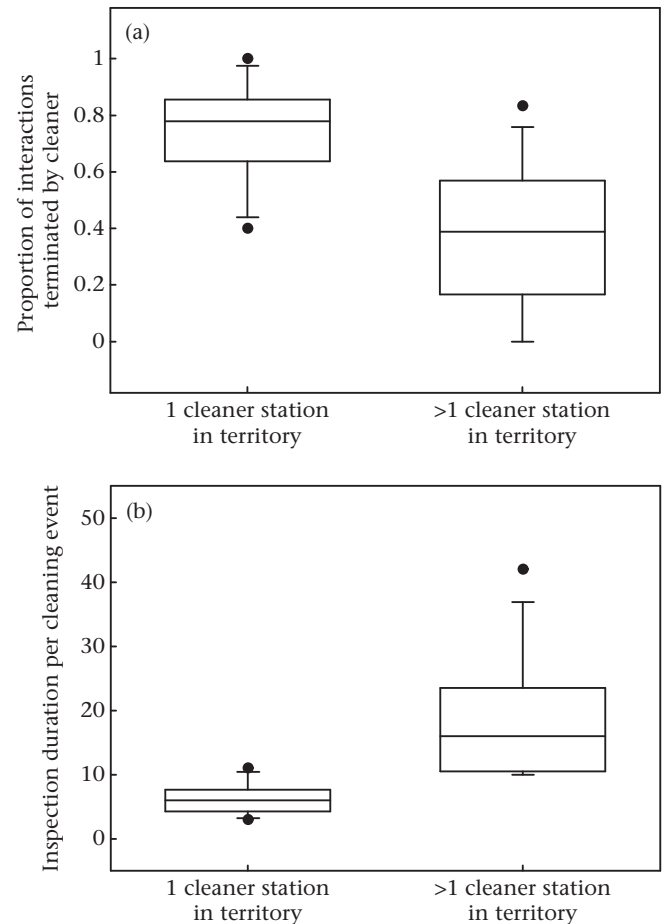


Figure 5. Box and whisker plots of (a) the proportion of interactions that were terminated by bluestreak cleaner wrasse when cleaning clients with ($N = 8$) and without ($N = 7$) access to multiple cleaner stations and (b) the median inspection duration for client fish with ($N = 8$) and without ($N = 7$) access to multiple cleaner stations. Boxes are medians with 25th and 75th quartiles. Whiskers are 10th and 90th percentiles and dots are data points that fall outside the 10th and 90th percentiles (determined using the Cleveland method in Sigma Plot 10.0).

contrast, just four of 24 fish were observed to jolt and quickly swim away from a bluestreak cleaner wrasse without chasing it.

DISCUSSION

Influence of Partner Choice and Competition on Cooperation

It is becoming increasingly clear that partner choice is an important mechanism for the maintenance of cooperation in some mutualisms (Noë 2001; Bshary & Bronstein 2004; Sachs et al. 2004). In a biological market framework, individuals can invest less in an interaction when their services are in high demand (relative to their supply). As a consequence, competition within a species for access to partners can lead to greater cooperative behaviour between mutualistic partners (Noë 2001). Bluestreak cleaner wrasse appear to be in competition for access to ornate butterflyfish since the amount of time cleaners had access to these preferred clients was inversely associated with the number of cleaner stations in an ornate butterflyfish's territory. Furthermore, cleaners invested more per interaction with individuals that had access to multiple cleaner stations, presumably because these clients frequently switch partners. While there was no evidence that cleaners cheated these clients less often, they spent more time

cleaning them per event and they were less likely to terminate interactions with them. These patterns indicate that bluestreak cleaner wrasse give clients with easy access to multiple cleaner stations priority of access to their services, while clients without this access are forced to wait while cleaners service other clients; this matches expectations from market theory.

Bshary (2001) found similar patterns when comparing client species with and without the option of switching partners (i.e. client species with large home ranges received priority of access to cleaners compared to resident clients). While the between-species patterns observed by Bshary (2001) strongly suggest that the ability of clients to choose among multiple cleaners influences cooperative interactions between cleaners and clients, Bshary (2001) and Bshary & Noë (2003) discussed two plausible alternative explanations. Both explanations were related to the potential value of clients as food sources, and how this could covary with the ability of clients to switch partners. First, because there is a positive relationship between fish size and parasite load (Grutter & Poulin 1998), client species with the option of switching partners could have more parasites because they are often larger than clients that are restricted to a single cleaner station. Second, because clients with the option of switching partners spend less time at cleaner stations than resident fish, they could have more parasites if they interact with cleaners less often. These explanations are unlikely to pertain to my results. By following a narrow size range of a single client species, I was able to control for potential differences in client value. Indeed, clients with and without access to multiple cleaner stations did not differ in size or the amount of time they spent being cleaned (in my stratified sample), and thus were unlikely to vary systematically in their value to cleaners. Interestingly, while larger ornate butterflyfish were cheated less often than smaller individuals, there was no evidence that client size affected any other aspects of service quality, at least within the narrow size range I investigated.

Importantly, while this study only considered interactions between bluestreak cleaner wrasse and ornate butterflyfish, cleaners interact with many other clients. Therefore, it is possible that systematic differences in the visiting rates of other clients at cleaner stations influenced the results. For example, if cleaner stations that occurred singly in ornate butterflyfish territories were visited by more clients, the patterns observed could be driven by competition between clients for access to cleaners. While it is difficult to formally evaluate this hypothesis without additional data, I believe it is unlikely for two reasons. First, cleaner stations that occurred singly in ornate butterflyfish territories were evenly distributed throughout the study site and did not appear to be visited by more clients than other cleaner stations. Second, butterflyfish are preferred over most other client species (~95% of clients that visit cleaner stations at this site; Adam 2010), and it therefore seems unlikely that cleaners would dramatically shift their behaviour towards ornate butterflyfish in response to most other clients. Thus, together with the observations of Bshary and colleagues (Bshary 2001; Bshary & Grutter 2002a; Bshary & Schaffer 2002), these results support the hypothesis that the ability of clients to choose among multiple partners influences cooperative interactions between bluestreak cleaner wrasse and their clients.

Proximate Cues and Behavioural Plasticity of Cooperating Partners

Many mechanisms have been proposed for the maintenance of cooperation between partners when there is strong potential for conflict, and it is likely that multiple mechanisms operate in most systems (Sachs et al. 2004; West et al. 2007). In the cleaner mutualism between bluestreak cleaner wrasse and their clients, it

has been hypothesized that a combination of partner choice, indirect reciprocity (image scoring) and punishment are responsible for maintaining cooperative behaviour between cleaners and clients (Bshary 2001; Bshary & Grutter 2002a, 2006; Bshary & Schaffer 2002). Inherent to each of these mechanisms are certain capabilities that cleaners and/or clients should possess. For example, all three mechanisms require that clients are able to detect cheating by cleaners, a task which they are apparently quite capable of (Bshary & Grutter 2002a). In addition, for partner choice to influence the level of cooperation that cleaners show towards clients with and without the option of switching partners, cleaners should have a way of differentiating and categorizing these clients. This could potentially be accomplished by 'rules of thumb' that rely on covariance between certain client characteristics and their ability to choose among multiple partners (for example, provide high-quality service to large clients). Alternatively, if cleaners can learn to distinguish between clients with and without the option of switching partners, then cleaner behaviour could be highly specific and much more plastic. Indeed, experiments have demonstrated that cleaners are capable of learning to distinguish between the simulated behaviour of clients with different strategies for controlling cheating (Bshary & Grutter 2002b), strongly suggesting some level of plasticity in cleaner behaviour. Nevertheless, cleaners probably interact with many hundreds of individuals each day belonging to as many as 100 or more different species (Grutter 1996; Bshary 2001), bringing into question their ability to distinguish so many individuals in nature. The fact that cleaners clearly exhibited different behaviour towards ornate butterflyfish with and without the option of switching partners suggests that the behaviour of bluestreak cleaner wrasse in nature results in part from learning and that cleaners may indeed cue in on the ability of some of their clients to choose among multiple partners.

Like most clients, ornate butterflyfish are capable of determining when cleaners behave uncooperatively and of responding to that behaviour by chasing the cleaner and/or terminating the interaction with them. Interestingly however, in contrast to what Bshary & Grutter (2002a) found for their interspecific comparisons, ornate butterflyfish with and without access to multiple cleaner stations both regularly responded to cheating cleaners by chasing them, suggesting that this could be an unconditional strategy for controlling cheating in this species. In addition, focal ornate butterflyfish used this strategy more often than simply swimming away following a perceived cheating event by the cleaner, even when they had the option of switching partners. Several potential explanations for these patterns exist. First, chasing by ornate butterflyfish did not always result in the termination of an interaction, and consequently rather than being viewed as a form of punishment that will have future payoffs, it could be considered a form of immediate partner control that may benefit ornate butterflyfish more than waiting to be cleaned by another cleaner. Second, while ornate butterflyfish were clearly given priority of access to cleaners when they had the option of switching partners (they were cleaned longer per interaction and had fewer interactions terminated by the cleaner), they did not appear to be cheated any less often by cleaners. Consequently, partner choice alone may not be adequate to prevent cheating by cleaners. Finally, while cleaners are involved in thousands of cleaning events each day, making them excellent candidates for conditioning/learning, individual clients are only involved in a small fraction of these, and consequently they may be more likely to rely on fixed strategies. It is also worth noting that aggressive or bold behaviours are often correlated (Sih et al. 2004), and it is also possible that client species with smaller home ranges are generally more territorial and that this greater tendency to chase other fish is easily expressed in a different context when being cheated by cleaners.

Conclusion

By investigating interactions between cleaner fish and a single species of client exhibiting variation in the ability to choose among multiple cleaners, this study provides empirical support for a role of partner choice in influencing cooperative interactions between cleaner fish and their clients. In addition, the results are consistent with the market theory prediction that competition among cleaners for access to clients should result in cleaners offering higher-quality service. Finally, the results indicate that cleaners may cue in on the ability of some of their clients to choose among multiple partners, as has been suggested by experiments where client behaviour has been simulated (Bshary & Grutter 2002b). In contrast, while ornate butterflyfish seek out multiple partners when they are available, they also appear to use aggression as a fixed strategy of partner control regardless of whether they have the option of switching partners.

Acknowledgments

I thank R. Schmitt, S. Holbrook and R. Warner for valuable critique and discussion, A. Adam for excellent assistance in the field, J. Oates for assistance with GPS, W. Rice for the use of his p_tables and stn_ct statistical programs, and G. Bergsma for discussion and editorial suggestions. I also acknowledge two anonymous referees for comments that greatly improved this manuscript. This research was supported by awards to R. Schmitt and S. Holbrook from the U.S. National Science Foundation (OCE 99-10677; OCE 04-17412), the W.M. Keck Foundation, and the Gordon and Betty Moore Foundation. This is a contribution of the Moorea Coral Reef LTER and is Contribution No. 179 of the University of California Berkeley Gump Research Station. This research adhered to the ASAB/ABS Guidelines for the Use of Animals in Research, the legal requirements of the U.S.A. and French Polynesia, and was approved by the Institutional Animal Care and Use Committee (IACUC) at the University of California, Santa Barbara (IACUC protocol number 2-06-639).

References

- Adam, T. C. 2010. Cooperation in a cleaner fish mutualism and its ecological implications. Ph.D. dissertation, University of California, Santa Barbara.
- Axelrod, R. & Hamilton, W. D. 1981. The evolution of cooperation. *Science*, **211**, 1390–1396.
- Bergstrom, C. T., Bronstein, R. J. L., Bshary, R., Connor, R. C., Daly, M., Frank, S. A., Gintis, H., Keller, L., Leimar, O., Noë, R. & Queller, D. C. 2003. Group report: interspecific mutualism puzzles and predictions. In: *Genetic and Cultural Evolution of Cooperation* (Ed. by P. Hammerstein), pp. 241–256. Cambridge, Massachusetts: MIT Press.
- Bull, J. J. & Rice, W. R. 1991. Distinguishing mechanisms for the evolution of cooperation. *Journal of Theoretical Biology*, **149**, 63–74.
- Bshary, R. 2001. The cleaner fish market. In: *Economics in Nature* (Ed. by R. Noë, J. A. R. A. M. van Hooff & P. Hammerstein), pp. 146–172. Cambridge: Cambridge University Press.
- Bshary, R. & Bronstein, J. L. 2004. Game structures in mutualistic interactions: what can the evidence tell us about the kind of models we need? *Advances in the Study of Behavior*, **34**, 59–101.
- Bshary, R. & D'Souza, A. 2005. Cooperation in communication networks: indirect reciprocity between cleaner fish and client reef fish. In: *Genetic and Cultural Evolution of Cooperation* (Ed. by P. Hammerstein), pp. 521–539. Cambridge, Massachusetts: MIT Press.
- Bshary, R. & Grutter, A. S. 2002a. Asymmetric cheating opportunities and partner control in a cleaner fish mutualism. *Animal Behaviour*, **63**, 547–555.
- Bshary, R. & Grutter, A. S. 2002b. Experimental evidence that partner choice is a driving force in the payoff distribution among cooperators or mutualists: the cleaner fish case. *Ecology Letters*, **5**, 130–136.
- Bshary, R. & Grutter, A. S. 2005. Punishment and partner switching cause cooperative behaviour in a cleaning mutualism. *Biological Letters*, **1**, 396–399.
- Bshary, R. & Grutter, A. S. 2006. Image scoring causes cooperation in a cleaning mutualism. *Nature*, **441**, 975–978.
- Bshary, R. & Noë, R. 2003. The ubiquitous influence of partner choice on the dynamics of cleaner fish–client reef fish interactions. In: *Genetic and Cultural Evolution of Cooperation* (Ed. by P. Hammerstein), pp. 167–184. Cambridge, Massachusetts: MIT Press.
- Bshary, R. & Schäffer, D. 2002. Choosy reef fish select cleaner fish that provide high-quality service. *Animal Behaviour*, **63**, 557–564.
- Clutton-Brock, T. H. & Parker, G. A. 1995. Punishment in animal societies. *Nature*, **373**, 209–215.
- Côté, I. M. 2000. Evolution and ecology of cleaning symbiosis in the sea. *Oceanography and Marine Biology: an Annual Review*, **38**, 311–355.
- Dugatkin, L. A. 1997. *Cooperation among Animals: an Evolutionary Perspective*. New York: Oxford University Press.
- Eshel, I. & Cavalli-Sforza, L. L. 1982. Assortment of encounters and evolution of cooperativeness. *Proceedings of the National Academy of Sciences, U.S.A.*, **79**, 1331–1335.
- Grutter, A. S. 1996. Parasite removal rates by the cleaner wrasse *Labroides dimidiatus*. *Marine Ecology Progress Series*, **130**, 61–70.
- Grutter, A. S. 1999. Cleaner fish really do clean. *Nature*, **398**, 672–673.
- Grutter, A. S. & Poulin, R. 1998. Intraspecific and interspecific relationships between host size and the abundance of parasitic gnathiid isopods on coral reef fishes. *Marine Ecology Progress Series*, **164**, 263–271.
- Hoeksema, J. D. & Bruna, E. M. 2000. Pursuing the big questions about interspecific mutualism: a review of theoretical approaches. *Oecologia*, **125**, 321–330.
- Hoeksema, J. D. & Schwartz, M. W. 2001. Expanding comparative-advantage biological market models: contingency of mutualism on partners' resource requirements and acquisition trade-offs. *Proceedings of the Royal Society B*, **270**, 913–919.
- Noë, R. 2001. Biological markets: partner choice as the driving force behind the evolution of mutualisms. In: *Economics in Nature* (Ed. by R. Noë, J. A. R. A. M. van Hooff & P. Hammerstein), pp. 83–118. Cambridge: Cambridge University Press.
- Noë, R. & Hammerstein, P. 1994. Biological markets: supply and demand determine the effect of partner choice in cooperation, mutualism and mating. *Behavioral Ecology and Sociobiology*, **35**, 1–11.
- Noë, R., van Schaik, C. P. & van Hoof, J. A. R. A. M. 1991. The market effect: an explanation for pay-off asymmetries among collaborating animals. *Ethology*, **87**, 97–118.
- Nowak, M. A. & Sigmund, K. 2005. Evolution of indirect reciprocity. *Nature*, **437**, 1291–1298.
- Pellmyr, O. & Huth, C. J. 1994. Evolutionary stability of mutualism between yuccas and yucca moths. *Nature*, **372**, 257–260.
- Pierce, N. E., Braby, M. F., Heath, A., Lohman, D. J., Mathew, J., Rand, D. B. & Travassos, M. A. 2002. The ecology and evolution of ant association in the Lycaenidae (Lepidoptera). *Annual Review of Entomology*, **47**, 733–771.
- Quade, D. 1967. Rank analysis of covariance. *Journal of the American Statistical Association*, **62**, 1187–1200.
- Sachs, J. L., Mueller, U. G., Wilcox, T. P. & Bull, J. J. 2004. The evolution of cooperation. *Quarterly Review of Biology*, **79**, 135–160.
- Sih, A., Bell, A. & Johnson, J. C. 2004. Behavioural syndromes: an ecological and evolutionary overview. *Trends in Ecology & Evolution*, **19**, 372–378.
- Simms, E. L., Taylor, D. L., Povich, J., Shefferson, R. P., Sachs, J. L., Urbina, M. & Tausczik, Y. 2006. An empirical test of partner choice mechanisms in a wild legume–rhizobium interaction. *Proceedings of the Royal Society B*, **273**, 77–81.
- Soares, M. C., Bshary, R., Cardoso, S. C. & Côté, I. M. 2008a. Does competition for clients increase service quality in cleaning gobies? *Ethology*, **114**, 625–632.
- Soares, M. C., Bshary, R. & Côté, I. M. 2008b. Does cleanerfish service quality depend on client value or choice options? *Animal Behaviour*, **76**, 123–130.
- Thompson, A. R., Nisbet, R. M. & Schmitt, R. J. 2006. Dynamics of mutualist populations that are demographically open. *Journal of Animal Ecology*, **75**, 1239–1251.
- Trivers, R. L. 1971. The evolution of reciprocal altruism. *Quarterly Review of Biology*, **46**, 35–57.
- West, S. A., Griffin, A. S. & Gardner, A. 2007. Evolutionary explanations for cooperation. *Current Biology*, **17**, R661–R672.