

Cleaner fish cause predators to reduce aggression toward bystanders at cleaning stations

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Mutualisms, in which both participants gain a net benefit, are ubiquitous in all ecosystems, and the importance of understanding their broader ecological context has been demonstrated many times. Indirect effects of mutualisms may have important implications for surrounding ecosystems through changes in density, species composition, or behavior; however, the latter has been difficult to quantify. In fish cleaning mutualisms, cleaners benefit by removing and consuming ectoparasites from clients, whereas clients benefit from a reduction in parasite load. Cleaner fish are also thought to benefit from immunity to predation and use tactile stimulation as a preconflict management strategy to manipulate partners' decisions and to avoid being eaten by piscivorous client fish. Here we show, using a laboratory experiment, that the presence of cleaner fish resulted in nearby fish not involved in the cleaner–client mutualism experiencing less aggression (chases) from predatory clients. In addition, the rate that piscivorous clients chased prey was negatively correlated with the amount of tactile stimulation given to the predator by the cleaner. These data suggest that, in the laboratory, the risk of aggression from predators toward nearby prey fish was greatly reduced as a by-product of cleaner fish presence and tactile stimulation of predators by cleaner fish. These results raise the question of whether cleaning stations act as safe havens from predator aggression.

Mutualisms are defined as interspecific interactions in which participants trade goods or services so that both participants gain a net benefit (Boucher 1985). Mutualistic interactions are ubiquitous in all ecosystems (Boucher 1985) and have historically been studied from a pairwise perspective. However, the importance of understanding their broader ecological context is paramount in understanding community processes, and studies now consider mutualisms to be embedded in community interaction networks of food webs, non-trophic, and indirect effects (e.g., Wootton 1994; Polis and Winemiller 1995; Morin 1999; Vasas and Jordán 2006).

Indirect interactions in mutualisms can occur when a third party species modifies the abundance or behavior of species involved in the mutualism resulting in a positive or negative effect to participating species (Werner 1992; Abrams 1995). For example, the presence of *Pandanus* plants have a strong positive indirect effect on the pollination mutualism between nectar feeding geckos *Phelsuma cepediana* and the Mauritian plant *Trochetia blackburniana*. *Pandanus* plants are a preferred microhabitat for geckos; therefore, visitation rates by geckos to plants are increased and results in an increase of fruit set (Hansen et al. 2007). Conversely, mutualisms can indirectly affect third party species through modifications in species density, composition, and behavior (Wootton 2002). For example, in the mutualism between ants and honeydew-producing insects (hemipterans), ants provide protection to the hemipterans against predators; however, plants that are inhabited by the hemipterans are also indirectly protected from other non-honeydew-producing herbivores (Styrsky and Eubanks 2007). Therefore, when studying mutualisms, it is important to

understand when indirect interactions occur, the mechanisms involved, and how their effects can be predicted. Indirect effects that alter the behavior of a species are well documented in terrestrial and aquatic freshwater communities (e.g., Werner and Peacor 2003), however, have been reported less frequently in marine systems (but see Dill et al. 2003; Grutter and Irving 2007).

In marine fish cleaning mutualisms, cleaners benefit by removing and consuming ectoparasites from clients, whereas clients benefit from a reduction in parasite load (Grutter 1999). Cleaner fish are also thought to benefit from an immunity to predation (Potts 1973; Losey 1979; Côté 2000) and use tactile stimulation as a preconflict management strategy to reduce and possibly eliminate predation risk (Bshary and Würth 2001; Grutter 2004). Tactile stimulation involves the cleaner fish hovering near the client fish and touching the client with the cleaner's pectoral and pelvic fins. Cleaner fish have been shown to provide more tactile stimulation to piscivorous compared with nonpiscivorous client fish (Bshary and Würth 2001) and more so when exposed to hungry than satiated piscivorous clients (Grutter 2004). Nearby potential clients are aware of the interactions between cleaner fish and client fish and can respond accordingly (Bshary 2002; Bshary and D'Souza 2005).

Earlier studies have emphasized potential risks associated with visiting cleaning stations, for example, receiving aggression by territory owners, aggression by other clients, or being susceptible to predation during interactions (Côté et al. 1998; Côté 2000; Cheney and Côté 2001). These hypotheses contrast with 1) the observation that little aggression occurs at cleaning stations (Bshary and Würth 2001), 2) an apparent lack of literature on observed predation events at cleaning stations (Côté 2000), and 3) the hypothesis that tactile stimulation by cleaning organisms have appeasing effects on clients

(Bshary and Würth 2001). If this latter hypothesis was true, it seems possible that the effects of tactile stimulation are not limited to the clients' behavior toward the cleaners but may positively indirectly affect third party species. Therefore, we tested whether the cleaners' preconflict management strategies may also benefit other fish near or queuing at cleaning stations through reduced aggressive behavior and in particular through reduced risk of being hunted by a predatory client.

In our experiment, we explicitly included 2 fangblenny species as prey species that are not clients of cleaner fish to exclude the possibility that a common goal of both predator and prey—the interaction with the cleaner—affects their interaction. Recent observations showed that the blue-striped fangblenny *Plagiotremus rhinorhynchus*, which closely associate with and facultatively resemble juvenile cleaner wrasse *Labroides dimidiatus* (Côté and Cheney 2005), suffer fewer chases from nearby fish when associated with a cleaner wrasse (Côté and Cheney 2007); however, it is unclear whether association or resemblance to the cleaner induced this response. We therefore decided to test experimentally in the laboratory how the presence of cleaning organisms and tactile stimulation affects interspecific predator–prey relationships external to the cleaning mutualism. First, we tested whether piscivorous fish make fewer aggressive chases toward potential prey species when in the presence of cleaners. Second, we investigated whether tactile stimulation by cleaner wrasse was a mechanism that controls aggression by predators toward prey at cleaning stations. If so, we predicted a negative correlation between the amount of tactile stimulation a cleaner gives to a predator and the frequency of a predator chasing prey.

MATERIALS AND METHODS

Study species

As a potential fish predator (the piscivore), we used slingjaw wrasse *Epibulus insidiator* (Labridae, total length [TL] ca., 35 cm), which have a protrusible mouth that unfolds into a long tube that provides strong suction to catch prey of small fish or crustaceans (Randall et al. 1997). *Epibulus insidiator* also served as a client for cleaners.

We used 3 potential “prey” species: blue-striped fangblenny *P. rhinorhynchus* (Blenniidae, TL ca., 8 cm), piano fangblenny *Plagiotremus tapeinosoma* (Blenniidae, TL ca., 8 cm), and initial phase 2-tone wrasse *Thalassoma amblycephalum* (Labridae, TL ca., 8 cm) (Randall et al. 1997). *Plagiotremus rhinorhynchus* varies in coloration from black with one lateral electric blue stripe extending from snout to tail, which is known to mimic the juvenile cleaner wrasse, *L. dimidiatus* (Labridae, TL ca., 8 cm), to olive, brown, or orange with 2 light-blue–white stripes running laterally (Randall et al. 1997; Côté and Cheney 2005). In this study, only olive with light-blue forms were caught and they remained in this color form throughout the duration of the study. We also used the congeneric *P. tapeinosoma*, which are a sympatric, nonmimetic relative of the fangblenny *P. rhinorhynchus* (Randall et al. 1997), and 2-tone wrasse *T. amblycephalum*, which occur in aggregations over shallow reefs and feed on zooplankton.

Three nonpiscivorous client species that were too large to be potential prey of the slingjaw wrasses were also added to provide the cleaners with sufficient clients: bridled monacle bream *Scolopsis bilineatus* (Nemipteridae, TL ca., 20 cm), stag-horn damselfish *Amblyglyphidodon curacao* (Pomacentridae, TL ca., 12 cm), and lunar wrasse *Thalassoma lunare* (Labridae, TL ca., 20 cm), each of similar sizes. In our control trials, pin-stripe wrasse *Halichoeres melanurus* (Labridae TL ca., 8 cm) were used as a replacement for the cleaner wrasse to keep the number of fish in the tanks constant. The pin-stripe wrasse is not a cleaner but is of a similar size and shape to cleaner

wrasse but has alternating green and orange thin stripes running laterally with a black tail tip (Randall et al. 1997).

Experimental procedures

We set up “mini reef fish ecosystems” in 3 large circular aquaria (1.5 m diameter × 0.7 m deep), containing a piscivorous fish, *E. insidiator*, and nonpiscivorous client species: 3 *A. curacao*, 3 *S. bilineatus*, and 1 *T. lunare*. Large pieces of coral rock were added for shelter. Each aquarium had a different treatment: an adult cleaner wrasse *L. dimidiatus*, a control fish *H. melanurus*, or no treatment fish (Table 1). Control fish were used to test whether nonclient potential prey benefited from the presence of another fish rather than from the presence of a cleaner fish. Single individuals of 3 nonclient potential prey species were introduced to each of the 3 treatment aquaria (Table 1) in turn: *P. rhinorhynchus* ($n = 14$), *P. tapeinosoma* ($n = 9$), and *T. amblycephalum* ($n = 8$), which are all known to be prey items of *E. insidiator* (Cheney KL, personal observation). Individual prey fish were placed in one of the experimental tanks and left to acclimatize for 30 min. The aquarium was observed for 30 min, during which we recorded the number of chases between the piscivore and prey fish, and between other fish in the system. A chase was considered as a fish swimming directly at another individual. Fangblennies of the genus *Plagiotremus* make rapid attacks on other fishes to remove mucus, skin tissue, and scales (Kuwamura 1981). However, in this study, fangblennies were never observed to attack *E. insidiator*. Therefore, chases by *E. insidiator* toward fangblennies were considered predatory, rather than in retaliation to being attacked.

At the end of the first observation period, the nonclient potential prey fish were introduced into the other 2 experimental tanks, which were followed by a 30-min acclimatization period and a 30-min observation period. The order in which individual prey fish experienced the 3 treatments was randomized. After one individual from each prey species was tested, new cleaner fish, control fish, piscivores, and nonpiscivores were used and the experimental treatment for each aquarium was changed.

To test our second hypothesis that tactile stimulation may reduce aggression between predators and their prey, we recorded the amount of time that cleaner wrasse spent providing tactile stimulation to each fish within the tank. Tactile

Table 1
Experimental setup for each treatment with closed circles indicating that a species was present

	Treatment		
	Cleaner	Control fish	No treatment
Piscivore client			
<i>Epibulus insidiator</i> ($n = 1$)	●	●	●
Nonpiscivore clients			
<i>Scolopsis bilineatus</i> ($n = 3$)			
<i>Amblyglyphidodon curacao</i> ($n = 3$)	●	●	●
<i>Thalassoma lunare</i> ($n = 1$)			
Cleaner fish			
<i>Labroides dimidiatus</i>	●	—	—
Control fish			
<i>Halichoeres melanurus</i>	—	●	—

Each individual of our prey species (*Plagiotremus rhinorhynchus*, *Plagiotremus tapeinosoma*, *Thalassoma amblycephalum*) was introduced to each treatment in a randomized fashion.

stimulation is defined as the cleaner hovering near to the client and touching its dorsal fin or belly with its pectoral and pelvic fins (Bshary and Würth 2001). Time was determined as the time from when the cleaner made contact with the client fish until it departed. We also recorded the total amount of time cleaners spent inspecting clients, defined as any event that involved visual examination or contact with the body surface and gills of the client (which included time spent providing tactile stimulation). Again, the length of an inspection event was determined from the time a cleaner fish approached a client fish until it departed. The total number of inspection events was calculated per 30-min observation.

Statistical analyses

In order to examine the relationship between tactile stimulation and number of chases across the 3 nonclient potential prey species (*P. rhinorhynchus*, *P. tapeinosoma*, and *T. amblycephalum*), we used a generalized linear mixed model (GLMM) using SPSS version 15.0 (SPSS Inc., Chicago, IL), with nonclient potential prey species as a fixed factor, tactile stimulation and total inspection time as covariates, and identity of cleaner wrasse/piscivore as a random factor. The number of chases were “count” data; therefore, we used a Poisson distribution with a log-link function to model these data.

RESULTS

Three prey fishes (2 *P. rhinorhynchus* and 1 *P. tapeinosoma*) were eaten by *E. insidiator* during the study either in the control fish treatment (1 *P. rhinorhynchus*) or in the no treatment fish (1 *P. rhinorhynchus* and 1 *P. tapeinosoma*). These fish were not included in further data analyses.

We found that the numbers of chases by *E. insidiator* toward potential prey fish (*P. rhinorhynchus* and *P. tapeinosoma*) were significantly reduced when a cleaner fish was present compared with when a control noncleaning fish (*H. melanurus*) or no treatment fish was present (repeated measures analysis of variance [ANOVA]: *P. rhinorhynchus* $F_{2,22} = 11.75$, $P < 0.01$, partial eta square = 0.52; *P. tapeinosoma* $F_{2,14} = 12.13$, $P = 0.01$, partial eta square = 0.63; Figure 1). Chases toward the third potential prey species, *T. amblycephalum*, were also reduced when a cleaner fish was present; however, this result was not significant (*T. amblycephalum*: $F_{2,14} = 2.70$, $P = 0.10$; partial eta square = 0.28; Figure 1). Overall, predatory chases by *E. insidiator* were most common toward *P. rhinorhynchus* (mean \pm standard deviation [SD]) = 6.6 ± 4.9 chases 30 min^{-1}) and *P. tapeinosoma* (4.1 ± 4.0) and were less frequent toward *T. amblycephalum* (2.1 ± 1.6).

The reduction of predator chasing in the presence of cleaner fish persisted after the frequency was corrected for the time each predator spent in cleaning interactions ([number of chases/[30 min - time spent being cleaned] \times 30 min; repeated measures ANOVA: *P. rhinorhynchus* $F_{2,22} = 9.93$, $P = 0.001$; *P. tapeinosoma* $F_{2,14} = 10.57$, $P = 0.002$). Therefore, the reduced chasing was not due to a trade-off between time spent hunting and time spent in cleaning interactions.

There was no difference in the number of chases by nonpiscivorous fish toward each prey species (*P. rhinorhynchus*: mean \pm SD 9.8 ± 4.8 ; *P. tapeinosoma*: 10.0 ± 5.4 ; *T. amblycephalum*: 10.5 ± 4.7), and it did not vary according to cleaner wrasse presence/absence (all observations: $F_{2,48} = 1.26$, $P = 0.29$; *P. rhinorhynchus*: $F_{2,22} = 0.51$, $P = 0.61$; *P. tapeinosoma*: $F_{2,14} = 2.67$, $P = 0.10$; *T. amblycephalum*: $F_{2,14} = 0.87$, $P = 0.91$). There was also no significant difference in number of chases between client species (all treatments: $F < 2.49$, $P > 0.14$). Therefore, other nonpredatory aggression (e.g., territorial aggression) was not affected by the presence of cleaner wrasse.

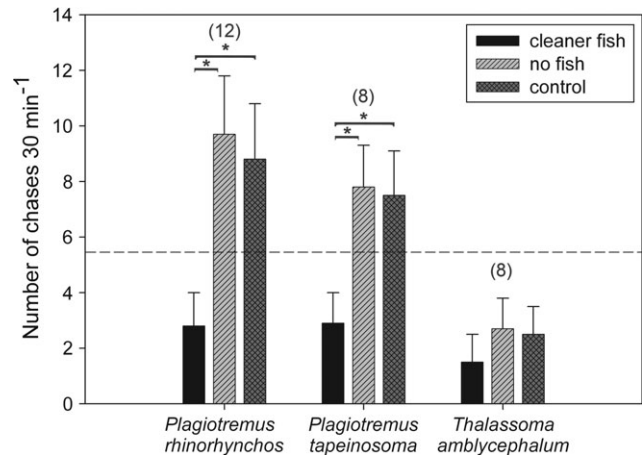


Figure 1

Mean (\pm 1 standard error) number of chases of a potential prey fish by a piscivore fish (*Epibubus insidiator*) per 30-min observations. Black bars represent experiment with cleaner fish (*Labroides dimidiatus*); light gray with diagonal stripes, no fish; dark bars with cross-hatching, control fish. Sample sizes are shown in parentheses. * indicates significant difference between treatments (paired *t*-test, $P < 0.05$). Dashed line indicates an extrapolated value of number of chases when mean tactile stimulation levels is equal to zero for *Plagiotremus rhinorhynchus* and *Plagiotremus tapeinosoma* combined.

Cleaner wrasse spent a large proportion of their time inspecting clients (all species: mean \pm SD = 432.0 ± 232.4 s 30 min^{-1}) and providing tactile stimulation to clients (all species: mean \pm SD = 229.2 ± 127.4 s 30 min^{-1}). The amount of tactile stimulation given was positively correlated with the total time spent inspecting clients ($r_s = 0.83$, $n = 28$, $P < 0.001$) and the total number of cleaning interactions ($r_s = 0.68$, $n = 28$, $P < 0.001$). There was no difference in the amount of time spent inspecting clients, providing tactile stimulation or the number of cleaning interactions between trials when the different prey species were tested ($F_{2,27} < 2.03$, $P > 0.15$).

The largest amount of tactile stimulation was given to the piscivorous *E. insidiator* (*E. insidiator*: 145.9 ± 84.2 ; *A. curacao*: 43.3 ± 39.7 ; *S. bilineatus*: 28.3 ± 26.6 ; *T. lunare*: 11.7 ± 11.2). Overall, the number of chases by *E. insidiator* toward prey fish decreased as the amount of tactile stimulation given to *E. insidiator* increased (GLMM: $z = -3.24$, $P = 0.001$). This was significant for *P. rhinorhynchus* ($r^2 = 0.35$, $n = 12$, $P = 0.04$) and *P. tapeinosoma* ($r^2 = 0.61$, $n = 8$, $P = 0.02$), but not for *T. amblycephalum* ($r^2 < 0.01$, $n = 8$, $P = 0.96$; Figure 2).

DISCUSSION

We have shown experimentally that the presence of cleaner wrasse reduces the frequency of aggressive chases by a piscivore toward potential prey species. Cleaner fish presence accounted for 52% and 63% of the variation in the number of chases toward prey species *P. rhinorhynchus* and *P. tapeinosoma*, respectively; however, the effect of cleaner fish presence was not significant for the prey *T. amblycephalum*, which was rarely chased. Possibly, *T. amblycephalum* is a nonpreferred prey item for *E. insidiator*, which would explain why it was chased less than the others. The reduction in chases toward *P. rhinorhynchus* and *P. tapeinosoma* was not due to a trade-off between time spent hunting and time spent being inspected by cleaners, as the reduction of predator chasing in the presence of cleaner fish persisted even after the frequency was corrected for the time each predator spent cleaning.

The reduction in chases toward potential prey species was negatively correlated with the amount of tactile stimulation

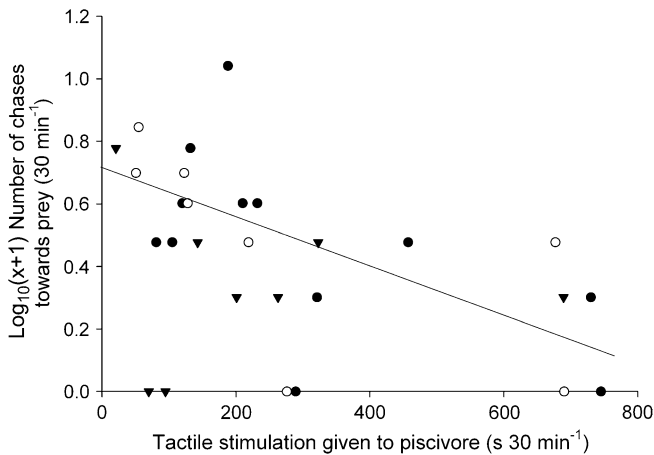


Figure 2

The amount of tactile stimulation given to the piscivorous fish (*Epibulus insidiator*) by cleaner fish (*Labroides dimidiatus*) in relation to the number of chases by the piscivorous fish toward the potential prey fish. Black circles *Plagiotremus rhinorhynchus*, white circles *Plagiotremus tapeinosoma*, and black triangles *Thalassoma amblycephalum*. Solid trend line was calculated for *P. rhinorhynchus* and *P. tapeinosoma* combined ($y = -0.0008x + 0.7152$, $r^2 = 0.44$). *T. amblycephalum* was omitted from trend analyses as the correlation was nonsignificant ($P > 0.05$).

received by predators from cleaner wrasse. Tactile stimulation accounted for 35% and 61% of the variation in chases toward *P. rhinorhynchus* and *P. tapeinosoma*, respectively; however, again this was not significant for *T. amblycephalum*. Therefore, tactile stimulation accounted for a large percentage of the variation in aggressive chases and appears to act as a mechanism for reducing aggression by predators. Previous studies (Bshary and Würth 2001; Grutter 2004) have provided evidence that cleaners use tactile stimulation as a preconflict management strategy. Indeed, cleaners provide more tactile stimulation to hungry predators compared with satiated ones (Grutter 2004). Tactile stimulation also extends the time a client stays at a cleaning station and may prevent aggressive chasing of cleaner after a cleaner fish bite (Bshary and Würth 2001).

The mere visual presence of a cleaner wrasse could also reduce the number of aggressive chases. However, in this study, cleaner wrasse gave tactile stimulation to the predator in each of our trials. Therefore, to confirm whether the presence of a cleaner wrasse alone (i.e., without tactile stimulation) reduces the number of chases by predatory clients, a physical barrier would need to be placed between cleaner and predator to prevent contact between the 2. If we extrapolate our data to examine the number of chases when tactile stimulation is equal to zero, the number of chases appears to be much lower than when there is no cleaner wrasse present (Figure 1), providing some support for the hypothesis that cleaner fish presence, without tactile stimulation, plays a role in reducing aggression.

A reduction in aggression by predators at cleaning stations may not only act as an indirect benefit to potential prey at cleaning stations but also modify the community in positive ways that could loop back to benefit the cleaners. For example, cleaners may directly benefit from a calmer environment resulting in longer cleaning interactions and increased number of clients to cleaning stations. Indeed, we found longer cleaning interactions and increased number of clients when tactile stimulation increased and aggression decreased, but the 2 variables were confounded. However, in a previous study, cleaning stations that had aggressive fangblenny mimics present, which instead of cleaning clients nip at their scales, mucus,

and body tissue, were visited by fewer clients and suffered from a reduction in time spent cleaning (Côté and Cheney 2004), which supports this hypothesis. Other potential benefits could include a reduction in the risk to the cleaner of being injured or accidentally consumed while engaged in cleaning interactions. Clients may also benefit from a reduced risk of being consumed while adopting a cleaning posture and may be more willing to remain near a cleaning station when a predator is being cleaned. However, these benefits remain to be tested.

In humans, mediators are impartial individuals used to facilitate cooperation between conflicting parties (Bercovitch and Lamare 1993; Johnson DW and Johnson RT 1996; Wall et al. 2001). Mediation, however, has rarely been addressed in other animals with the exception of a few studies involving the presence of conflict mediators. In several cases, male harem holders mediate conflicts between their harem females (Bshary and Lamprecht 1994; Schradin and Lamprecht 2000). Idiosyncratic observations on mediating in conflicts in chimpanzees have also been described (de Waal and van Roosmalen 1979). We suggest that marine cleaner fish may act as mediators of conflict by reducing aggression between predators and prey and consequently accrue a fitness benefit in terms of increased cleaning time and number of clients. However, to corroborate whether cleaners act as mediators or whether this is simply an indirect consequence of cleaning interactions, further studies should investigate whether cleaner fish increase the amount of tactile stimulation to predators when a potential prey species is present.

Regardless, the effects of mutualistic interactions between cleaners and their clients on the local fish community appear to be more extensive and complex than originally thought—cleaning interactions appear to benefit species external to the cleaner–client mutualism, which in turn could loop back to benefit the cleaners. Although our study involves data from an artificial system, our results corroborate observations in the field that aggressive interactions are rare at cleaning stations (Bshary 2001). Thus, cleaning stations may act as “safe havens” in which predatory interactions are diminished.

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