Distance-dependent costs and benefits of aggressive mimicry in a cleaning symbiosis

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In aggressive mimicry, a 'predatory' species resembles a model that is harmless or beneficial to a third species, the 'dupe'. We tested critical predictions of Batesian mimicry models, i.e. that benefits of mimicry to mimics and costs of mimicry to models should be experienced only when model and mimic co-occur, in an aggressive mimicry system involving juvenile bluestreaked cleaner wrasse (*Labroides dimidiatus*) as models and bluestriped fangblennies (*Plagiotremus rhinorhynchus*) as mimics. Cleanerfish mimics encountered nearly twice as many potential victims and had higher striking rates when in proximity to than when away from the model. Conversely, in the presence of mimics, juvenile cleaner wrasses were visited by fewer clients and spent significantly less time foraging. The benefits to mimic and costs to model thus depend on a close spatial association between model and mimic. Batesian mimicry theory may therefore provide a useful initial framework to understand aggressive mimicry.

Keywords: aggressive mimicry; Batesian mimicry; coral reef fish; *Labroides dimidiatus*; *Plagiotremus rhinorhynchus*; *Plagiotremus tapeinosoma*

1. INTRODUCTION

Mimicry is often viewed as a key example of adaptive evolution by natural selection. Although a large body of theory has developed to explain various forms of protective mimicry (e.g. Huheey 1988; Edmunds 2000), other types of mimicry have remained relatively unstudied. This is the case for aggressive mimicry, in which a 'predatory' species resembles a model that is harmless or beneficial to a third species, the 'dupe'. There is currently no specific framework for understanding the maintenance of aggressive mimics in populations. However, models of Batesian mimicry may provide insights because there are strong parallels between the two types of mimicry. In both instances, the duped partner pays a cost when deceived and acts as a selective force, affecting the fitness of both models and mimics. The relationships between model and mimic are also similar, because in both cases the mimic benefits from its resemblance to the model, while the model incurs costs (Huheey 1988; Endler 1991). Importantly, the costs and benefits should be experienced only when model and mimic co-occur (e.g. Pfennig *et al.* 2001).

Here, we test this critical prediction of Batesian mimicry in an aggressive mimicry system involving juvenile bluestreaked cleaner wrasse (*Labroides dimidiatus*; family Labridae) as models and bluestriped fangblennies (*Plagiotremus rhinorhynchus*; family Blenniidae) as mimics. *Labroides dimidiatus* is an active cleanerfish that removes ectoparasites from larger reef fish clients (Grutter 2000). Juveniles are conspicuously coloured, with electric blue lateral stripes on a black body. In its black and blue mimetic colour form, the bluestriped fangblenny shares the juvenile cleaner coloration, but it attacks larger fish to remove tissue and scales (Russell *et al.* 1976; Kuwamura 1981). Other forms (i.e.

brown, olive or orange, with blue stripes) of *P. rhinorhynchus* are also known (Allen *et al.* 2003).

We predicted that mimic foraging success would be higher when in close proximity to the model than when further away. Similarly, we expected that fewer clients would visit juvenile cleaner wrasses in the presence of mimics than in their absence, resulting in reduced cleaner wrasse total foraging time. We also predicted that fish at cleaning stations near mimics would be attacked more frequently than non-client fish, resulting in shorter inspection bout durations than in the absence of mimics. We tested these predictions by means of field observations of foraging activity of cleaner mimics and cleaner wrasses in the presence and absence of models and mimics, respectively.

2. MATERIAL AND METHODS

(a) Study sites and species

Fieldwork was performed on four fringing reefs around the Pacific island of Guam (12°28' N, 144°47' E) from 1 May to 6 June 2003. The study sites were at Gun Beach, Umatac Bay, Tumon Bay and Pago Bay. All sites had abundant juvenile bluestreak cleaner wrasses and smaller numbers of bluestriped fangblennies, at depths ranging from 2 to 18 m. All bluestriped fangblennies located were of the mimetic colour form. We also studied a sympatric, non-mimetic fangblenny, for comparison with bluestriped fangblennies. *Plagiotremus tapeinosoma*, the scale-eating fangblenny, is of a similar size to, and shares habitat and feeding mode with, *P. rhinorhynchus*, but it has a tan-coloured body with dark lateral stripes, which does not resemble the coloration of juvenile cleaner wrasses.

(b) Field observations

During random swims we located 26 'associated' juvenile cleaner wrasses that had a cleaner mimic near their cleaning stations. For each cleaner wrasse with a mimic, we then located, within 10 m, at the same depth and matched for size, a 'lone' juvenile without a mimic in its vicinity. We performed one 30 min

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observation on each cleaner wrasse, during which we recorded the number and species of all clients visiting cleaning stations, whether each client posed (i.e. adopted the stationary pose which signals the need to be cleaned to cleanerfish (Côté *et al.* 1998)), the length of inspection of the client's body by the cleaner wrasse, and in the case of associated cleaners, any interactions between mimics, cleaners and clients. We also noted the outcome of attacks by mimics on clients at cleaning stations (client stayed, chased mimic, or left the station).

In addition, we performed one 30 min observation on each of 33 cleaner mimics and 18 scale-eating fangblennies, located during random swims. We recorded the number and species of all reef fish of more than 5 cm (total length) passing within 50 cm of the focal fangblenny, and fangblenny behaviour towards each potential victim: no reaction, avoidance, and strikes. We also recorded whether potential victims posed for mimics, any interactions with cleaner wrasses or their clients, and the time spent by the fangblenny within 50 cm of a juvenile cleaner. To ensure that a single 30 min observation period yielded representative data, we performed a second 30 min observation on 10 of the 33 mimics.

To quantify the spatial association of *P. rhinorhynchus* and the non-mimetic *P. tapeinosoma* with cleaner wrasses, we noted the distance of each fangblenny to the nearest juvenile cleaner upon first sighting. All observations were performed using SCUBA. The locations of all observed cleaner wrasses and fangblennies were marked with numbered tags and mapped to prevent accidental repeat observations.

(c) Statistical analyses

For each observation of cleaner mimics, we calculated the rate of encounter with potential victims and striking rate when the mimic was near (less than 50 cm) and away (more than 50 cm) from a juvenile cleaner wrasse. Rates were expressed per 30 min spent near or away, and were compared, means of a paired *t*-test. Only observations in which mimics spent more than 60 s near a cleaner wrasse were considered in these analyses. Whenever possible, we noted when the same fish repeatedly swam near mimics or was repeatedly inspected by cleaners. However, because fish were not marked, a few individuals may have contributed more than once to the total number of potential victims and clients.

For each observation of cleaner wrasses, the duration of each inspection bout was recorded. An inspection bout was defined as the time during which a cleaner inspected a single client. All bout lengths within an observation period were summed to obtained total inspection time. All rates were expressed per 30 min observation.

There was a significant correlation between the numbers of strikes by mimics in the first and second observations ($r = 0.88$, $n = 10$, $p = 0.001$). Similarly, there was a significant correlation between the times spent by mimics within 50 cm of juvenile cleaner wrasses in both observation periods ($r = 0.69$, $n = 10$, $p = 0.03$). A single 30 min observation period was therefore considered to be representative, and data from only the first observation periods were used in subsequent analyses.

3. RESULTS

(a) Spatial association between mimic and model

Thirty-one of 33 mimics (94%) were found within 1 m of a juvenile cleaner wrasse at the time of first sighting. By comparison, only 47% (8/17) of non-mimetic scale-eating fangblennies were found as close to juvenile cleaner wrasses ($\chi^2_1 = 10.9$, $p < 0.001$). In addition, cleaner mimics spent significantly more time within 50 cm of juvenile cleaner

wrasses than scale-eating fangblennies (means $\pm$ s.d.; mimics: 325.1 ± 75.5 s per 30 min, $n = 33$; scale-eating: 3.8 ± 1.6 s per 30 min, $n = 18$; $t_{32.03} = 4.25$, $p < 0.001$).

(b) Victim behaviour

Few potential victims (0.7%, 10 of 1390 striking opportunities) showed avoidance responses when swimming within 50 cm of cleaner mimics. In addition, potential victims exhibited full incitation pose near mimics on only 6 occasions (0.4% of striking opportunities), compared with nearly half (47%, or 321/681 cleaning opportunities) of clients at cleaning stations ($\chi^2_1 = 745.2$, $p < 0.001$). The mimic attacked only one of the six posing victims, and the attack failed.

(c) Benefit to mimics of association with models

Mimics encountered significantly more potential victims when in close proximity to juvenile cleaner wrasses than when further away (figure 1a; paired $t_{19} = 2.23$, $p = 0.04$). The striking rate of mimics was also significantly higher near juvenile cleaners (figure 1b; paired $t_{19} = 2.38$, $p = 0.03$).

(d) Costs to models of association with mimics

Cleaner mimics rarely attacked clients being cleaned. The rate of attacks on clients at cleaning stations (6.5%, or 3 of 46 potential victims being cleaned during mimic observations) was not significantly different from the rate of attack on fish passing within 50 cm of mimics (10.5%, 148/1390; $\chi^2_1 = 0.80$, $p = 0.36$), suggesting that clients were no more likely to be attacked than non-clients.

Juvenile cleaner wrasses associated with a mimic were visited by significantly fewer clients (figure 2a; paired $t_{25} = 5.97$, $p < 0.001$). Associated cleaner wrasses also spent significantly less time inspecting clients than lone cleaners (figure 2b; paired $t_{25} = 5.18$, $p < 0.001$). There was no difference in inspection bout length between juvenile cleaners with and without a mimic nearby (associated cleaners (mean $\pm$ 1 scale): 9.7 ± 3.2 s per 30 min; lone cleaners: 8.9 ± 4.3 s per 30 min; paired $t_{25} = 0.98$, $p = 0.34$).

Finally, juvenile cleaner wrasses rarely interacted with cleaner mimics. Only 4 of 33 mimics observed (12%) were aggressively chased by juvenile cleaner wrasses. Interestingly, in 7 of 33 observations of mimics (21%), the associated cleaner wrasse inspected the cleaner mimic following a full incitation pose by the latter.

4. DISCUSSION

Cleanerfish mimics benefit from their resemblance to cleaners in terms of enhanced foraging rate. Conversely, they impose a significant foraging cost on their model. Blue-striped fangblennies encountered nearly twice as many potential victims and had higher striking rates when near juvenile bluestreak cleaner wrasse. In the presence of mimics, juvenile cleaner wrasses experienced a 38% reduction in the number of client visits, which resulted in a 29% decrease in total inspection time. Inspection time in *Labroides dimidiatus* correlates with the number of bites taken on clients (Grutter 1996). Association with mimics may therefore have a significant detrimental impact on the energy intake of cleaner wrasses. The benefits to mimic and costs to model thus depend on the co-occurrence of model and mimic, as predicted by models of Batesian mimicry

Figure 1. (a) Number of potential victims encountered per 30 min, and (b) number of strikes per 30 min by cleaner mimics near (less than 50 cm) and further away (more than 50 cm) from juvenile cleaner wrasses. Means are shown $\pm$ 1 s.e.m.; $n = 20$ in both cases.

(Huheey 1988; Endler 1991). Such models may provide a useful initial framework to understand aggressive mimicry.

There are, however, some differences between the two types of mimicry that will need to be incorporated into the Batesian framework. For example, whereas in Batesian mimicry the predator is the duped party, the predatory role in aggressive mimicry is instead fulfilled by the mimic, which depends wholly on the duped individual's approach rather than avoidance of its attacks. The resemblance of mimic to model must therefore be convincing at a distance to attract potential victims but may not be as close as expected for Batesian mimics (Sheppard 1959; Huheey 1984). In this study, most potential victims showed no avoidance when swimming within 50 cm of mimics, despite being within the striking range of *P. rhinorhynchus* (up to 3 m; I.M.C. personal observations). However, fish rarely adopted for mimics the full incitation posture that is readily displayed for cleaners. This suggests that at close range fish can recognise mimics. Stummer *et al.* (2004) have shown that a small body size and the presence of lateral stripes are two long-distance signals used by fish clients to recognise *L. dimidiatus* cleaners. Both signals are displayed by blue-striped tangblennies. After initial attraction based on these cues, however, client interest in cleaners is maintained by other signals, such as colour, displays or physical contact

Figure 2. (a) Number of visiting clients per 30 min and (b) total inspection time (seconds per 30 min) for juvenile cleaner wrasses with and without a cleaner mimic in the vicinity of the cleaning station. Means are shown $\pm$ 1 s.e.m.; $n = 26$ in both cases.

between cleaner and client (Stummer *et al.* 2004), which appear not to be provided by mimics.

The nature of the relationship between model and dupe is also different in Batesian and aggressive mimicry. Batesian models are potential prey for dupes, but are protected by their unpalatability (Bates 1862). By contrast, fish clients and cleaner wrasses enjoy a mutualistic relationship in which clients experience decreases in their ectoparasite loads (e.g. Grutter 1999) and cleaners gain nutrition from client-gleaned ectoparasites (Grutter 1996). The success of mimics depends on the maintenance of this positive relationship, which attracts high densities of fish to cleaning stations. This may explain why mimics rarely attacked clients engaged in cleaning but preyed upon victims swimming near cleaning stations. When mimics did attack fish being cleaned, such attacks ended cleaning interactions, with frequent subsequent chasing of the cleaner by the client (I. M. Côté and K. L. Cheney, personal observations, this study). Attacks by mimics may be perceived by clients as cheating by cleaners, resulting in a reduced propensity of clients to revisit cleaners (Bshary & Schäfer 2002).

Finally, because Batesian mimics disrupt the predator's learned avoidance responses of the model (Lea & Turner 1972; Turner *et al.* 1984), the mortalities of model and

mimic are related both to the relative frequency of models and mimics and to the strength of noxiousness of the model (e.g. Lindström *et al.* 1997). Cheating in mutualistic relationships, either by cleaners or mimics, can also be maintained through frequency-dependent selection (e.g. Freckleton & Côté 2003). As a result, the success of cleaner mimics should be expected to vary with the local abundance of juvenile cleaner wrasses. However, this relationship might be altered by client ectoparasite loads because of the potentially greater importance of cleaning services to heavily infested clients. Areas of high ectoparasite intensities, where clients visit cleaners at higher rates (Bansemer *et al.* 2002), may therefore be able to support relatively more mimics without a breakdown of cleaner–client relationships than ectoparasite-poor areas.

In summary, we found that benefits to mimics of resembling cleaner wrasses and costs to cleaners of association with mimics are accrued in the joint presence of model and mimic. Although the original prediction from Batesian theory was formulated mainly in reference to inter-population differences in the presence or absence of mimic or model, we found that the prediction was verified on a very small spatial scale. We highlighted differences between Batesian and aggressive mimicry, such as in the identity of the predator and the nature of the relationship between model and dupe. The Batesian theoretical framework may therefore require modifications to incorporate these differences, but it provides a suitable initial framework to understand the origin and maintenance of aggressive mimicry.

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