A protective function for aggressive mimicry?

Isabelle M. Côté^{1,*} and Karen L. Cheney²

¹Department of Biological Sciences, Simon Fraser University, Burnaby, British Columbia, Canada V5A 1S6

²School of Integrative Biology, The University of Queensland, Brisbane, Queensland 4072, Australia

Mimicry often involves a protective element, whereby the risk of predation on mimics is reduced owing to their resemblance to unpalatable models. However, protection from predation has so far seemed unimportant in aggressive mimicry, where mimics are usually predators rather than prey. Here, we demonstrate that bluestriped fangblennies (*Plagiotremus rhinorhynchus*), which are aggressive mimics of juvenile bluestreak cleaner wrasse (*Labroides dimidiatus*), derive significant protection benefits from their resemblance to cleaner fish. Field observations revealed that mimetic fangblennies were chased by potential victims less often than individuals of a closely related, ecologically and behaviourally similar but non-mimetic species (*Plagiotremus tapeinosoma*). After attacks, proximity to models protected mimics from retaliation by victims, but the effect of colour similarity was less clear. Both colour resemblance and physical proximity to models thus appear to protect cleaner-fish mimics from aggression by potential and actual victims of their attacks. Our results suggest that the mimicry types observed in nature, which are usually distinguished on the basis of the benefits accrued to mimics, may in fact overlap greatly in the benefits provided.

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

1. INTRODUCTION

Mimicry often involves a protective element. For example, in Batesian mimicry, palatable mimics resemble unpalatable models, thereby lowering the rate of predation on the former (Bates 1862; Lea & Turner 1972; Ohsaki 1995; Caley & Schluter 2003). Similarly, Müllerian mimics converge on colour patterns to enhance the aposematic signal of unpalatability and reduce predation on both species (Müller 1879; Benson 1972). By contrast, aggressive mimics resemble a harmless model, which allows them to approach and prey on the model itself and/or on unsuspecting third parties (Wickler 1966). Protection from predation for mimics has so far seemed unimportant in aggressive mimicry compared with other types of mimicry, largely because aggressive mimics are usually predators rather than prey.

Here, we test whether protection benefits can be accrued to aggressive mimics in a system involving bluestriped fangblennies (*Plagiotremus rhinorhynchus*) as aggressive mimics of juvenile bluestreak cleaner wrasse (*Labroides dimidiatus*; Kuwamura 1981; Côté & Cheney 2005). Although colour resemblance between species has long been used as the main criterion for assuming the presence of mimicry, there is growing awareness that colour similarity alone is insufficient to claim mimicry and that additional conditions, such as spatial association between mimic and model, relative rarity of the mimic compared with the model and evidence of benefits of association for mimics and costs for models, must be met to confirm the existence of mimicry (Pfennig *et al.* 2001; Caley & Schluter 2003; Eagle & Jones 2004). By all of these criteria, the aggressive mimicry of juvenile bluestreak

cleaner wrasse by bluestriped fangblenny is now firmly established (Côté & Cheney 2004; Moland & Jones 2004). In its mimetic form, the bluestriped fangblenny shares the juvenile cleaner's blue and black coloration, but instead of removing ectoparasites as the cleaner wrasse does (Grutter 2000), it attacks passing fish with rapid strikes to remove tissue and scales (Côté & Cheney 2004, 2005; Moland & Jones 2004). Mimetic fangblennies usually display a close spatial association with cleaner wrasses and are typically rarer than them (Côté & Cheney 2004; Moland & Jones 2004). Juvenile cleaner wrasses are visited by fewer clients and have shorter foraging times in the presence of mimics (Côté & Cheney 2004). Conversely, the rate of encounters with potential victims and attack rate of mimics are significantly higher when juvenile cleaner wrasses are nearby (Côté & Cheney 2004; Moland & Jones 2004).

These benefits may not be the only ones accrued by mimics. Moland & Jones (2004) found that bluestriped fangblennies experienced increased aggression from potential victims after juvenile cleaner wrasses were removed from their vicinity, suggesting that cleaner mimics may also benefit in terms of reduced predation or injury—a benefit typically associated with Batesian and Müllerian mimicry. However, the bluestriped fangblennies under study were in non-mimetic colours, i.e. shades of orange, green or brown, which mimetic *P. rhinorhynchus* can adopt depending on social context (Moland & Jones 2004; Côté & Cheney 2005). It is therefore unclear whether it was similarity in colour or simply physical association with models that lowered aggression by potential victims towards fangblennies in the presence of cleaner wrasses.

To determine whether aggressive cleaner mimics derive significant protective benefits from their resemblance to cleaner wrasses, we compared the rates of chasing by

* Author for correspondence (imcote@sfu.ca).

potential and actual victims of mimetic bluestriped fangblennies and non-mimetic scale-eating fangblennies, *Plagiotremus tapeinosoma*, a close relative that has a similar feeding mode to *P. rhinorhynchos*; however, scale-eating fangblennies never associate with juvenile cleaner wrasse. Comparing the rates of chasing of bluestriped fangblennies when they were and were not closely associated with cleaner-wrasse models then allowed us to measure the effect of spatial proximity, independently of colour similarity.

2. MATERIAL AND METHODS

(a) Study sites and species

Fieldwork was carried out 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.

Because all bluestriped fangblennies located were of the black-and-blue mimetic colour form, it was not possible to use non-mimetic *P. rhinorhynchos* to examine the effect of colour similarity to the cleaner model on rates of chasing by fish victims. Instead, we used scale-eating fangblennies *P. tapeinosoma*, which have a white or tan underside and dorsal stripe, with a wide, broken black lateral stripe running from snout to tail. This species is not a known mimic of any other fish. Despite the obvious differences in colour patterns, the two fangblenny species share remarkable ecological and behavioural similarities. At our study sites, the two species were found at similar depths (mean $\pm$ 1 s.d.; bluestriped, 4.4 ± 2.1 m; scale-eating, 3.6 ± 1.8 m; $t_{49} = 1.14$, $p = 0.14$), and their home ranges were fully interspersed across the study reefs, suggesting that reef fishes commonly encounter both species. There was no difference in body size between the species (mean $\pm$ 1 s.d.; bluestriped, 6.8 ± 0.9 cm; scale-eating, 7.1 ± 0.6 cm; $t_{49} = 1.14$, $p = 0.26$). Like bluestriped fangblennies, scale-eating fangblennies attack fish swimming nearby with rapid lunges (Randall *et al.* 1997; Côté & Cheney 2004), and attacks by both species elicit similar, apparently painful, reactions from fish victims upon contact (I. M. Côté & K. L. Cheney 2007, unpublished work). An analysis of community similarity, using the software PRIMER (Plymouth Routines in Multivariate Ecological Research v. 5.2.4; PRIMER-E Ltd, Plymouth Marine Laboratory, Plymouth, UK), revealed no difference in the composition of the victim-species assemblages between the two fangblennies (ANOSIM, $R = 0.05$, $p = 0.11$), suggesting that they target a similar array of reef fish. The sparse information available on the diet of each species suggests that for both, mucus, scales and dermal tissue of fish predominate in gut contents (www.fishbase.org, accessed 13 June 2007). It remains possible that the two species differ in some unmeasured way that would influence how victims react to their presence or attacks, but given the similarities between the species, this seems unlikely.

(b) Field observations

We carried out one 30 min observation on each of 33 cleaner mimics (bluestriped fangblennies) and 18 non-mimetic scale-eating fangblennies located during random swims. We recorded the number of species of all reef fish of more than 5 cm total length passing within 50 cm of the focal fangblenny, and any attacks by fangblennies on passing fish. We also recorded the time spent by the fangblenny within

50 cm of any neighbouring juvenile cleaner and the number of chases experienced by fangblennies from potential and actual victims. To ensure that a single 30 min observation period yielded representative data, we carried out a second 30 min observation on 10 of the 33 mimics.

All observations were carried out 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 chases performed by potential and actual victims when the mimic was near (less than 50 cm) and away (more than 50 cm) from a juvenile cleaner wrasse. Rates were expressed per 100 potential victims (excluding those that were attacked) or per 100 attacks while near or away and were compared (near versus away) with Wilcoxon matched sign test. Only observations in which mimics spent more than 60 s near a cleaner wrasse were considered in these analyses, reducing the sample to 24 individuals. Of these, nine attacked no passing fish, thus $n = 15$ in analyses of chasing rates by actual victims. Similarly, for each observation of scale-eating fangblennies, we calculated rates of chases per 100 potential victims and per 100 attacks. One scale-eating fangblenny did not attack any passing fish while observed and was thus excluded from the latter analysis (thus $n = 17$). Since scale-eating blennies were never extensively associated with juvenile cleaner wrasses (maximum time spent within 50 cm of cleaner wrasse = 23 s per 30 min), their rates of chases were compared with Mann-Whitney tests to only those of mimics when away from models. Whenever possible, we noted when the same fish repeatedly swam near fangblennies. Because fish were not marked, a few individuals may have contributed more than once to the total number of potential victims; however, this is unlikely to have occurred often given the high density of fish at the study sites.

There was a significant correlation between the numbers of strikes by mimics in the first and second observations ($r_{10} = 0.88$, $p = 0.001$). Similarly, there was a significant correlation between the times spent by mimics within 50 cm of juvenile cleaner wrasses in both observation periods ($r_{10} = 0.69$, $p = 0.03$). 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

The similarity in colour between bluestriped fangblennies and their cleaner-fish model affected the pre-emptive chases by potential victims towards cleaner mimics. There was no difference between the rates at which potential victims chased mimics when mimics were near and away from juvenile cleaner wrasses (figure 1; Wilcoxon signed-rank test, $Z = 1.36$, $n = 24$, $p = 0.17$). However, mimics that were away from a cleaner fish model were chased significantly less often by potential victims than were scale-eating fangblennies, which are non-mimetic and never associated with cleaner wrasses (figure 1; Mann-Whitney test, $U = 87.5$, $n_1 = 24$, $n_2 = 18$, $p = 0.001$).

By contrast, spatial association between mimic and their model appeared to be important in determining retaliatory actions by victims of fangblenny attacks. The rate of chases by victims was significantly lower towards

Figure 1. The rate of chases by potential victims (number of chases per 100 fish swimming nearby) towards mimetic and non-mimetic fangblennies when near and far from a juvenile cleaner wrasse model and of non-mimetic scale-eating fangblennies, which are always found far from juvenile cleaner wrasses. Medians (thick lines) and interquartile ranges are shown. Sample sizes are given in parentheses. ** $p \leq 0.001$ in Mann–Whitney test.

Figure 2. The rate of chases by actual victims (number of chases per 100 fish attacked) towards mimetic and non-mimetic fangblennies when near and far from a juvenile cleaner-wrasse model and of non-mimetic scale-eating fangblennies, which are always found far from juvenile cleaner wrasses. Means (thick lines) and interquartile ranges are shown. Sample sizes are given in parentheses. * $p \leq 0.05$ in Wilcoxon matched sign test.

mimics that were near a cleaner wrasse than towards those that were not (figure 2; Wilcoxon matched sign test, $Z = 2.05$, $n = 15$, $p = 0.04$). However, in the absence of cleaner wrasses in the vicinity, victims retaliated upon being attacked as frequently against mimics as they did against scale-eating fangblennies (figure 2; Mann–Whitney test, $U = 210.5$, $n_1 = 15$, $n_2 = 17$, $p = 0.76$).

4. DISCUSSION

Bluestriped fangblennies appear to be protected from aggression by potential reef fish victims owing to their colour similarity to juvenile cleaner wrasses, even in the absence of the latter. Most of the potential and actual victims were herbivores and invertivores (93% of all fish) rather than piscivores (7%), thus their attacks were not predatory. However, at least on two occasions, attacks by herbivores appeared to cause injuries to fangblennies (I.M. Côté & K. L. Cheney 2007, personal observations), hence a reduction in rate of chasing is likely to represent a benefit to cleaner mimics.

Cleaner fish are identified as such by their clients by signals such as small body size and the presence of lateral stripes (Stummer *et al.* 2004). Unambiguous signalling of cleaning activity may explain why cleaners are rarely preyed upon by clients (Côté 2000). Our results suggest that the mimicry of these signals by bluestriped fangblennies is effective, at least at a distance, because potential victims swimming nearby chase mimics significantly less frequently than they do non-mimetic fangblennies. However, reef fish very rarely adopted for cleaner mimics the incitation pose which is readily displayed to elicit cleaning from cleaner wrasses (Côté & Cheney 2004; Johnson & Hull 2006). Moreover, fish posing for cleaner mimics were rarely attacked by them (Côté & Cheney 2004; Johnson & Hull 2006). Neither of these two observations is consistent with the conventional notion that cleaner mimics use their resemblance to cleaner fish to dupe potential victims into approaching them closely to facilitate attack. Instead, our results suggest that the colour similarity to cleaners allows bluestriped fangblennies to swim safely at some distance from potential victims, which is sufficient given the long range of their attack lunges (approx. 1–2 m, personal observations).

Upon attack, however, cleaner mimics appear to be protected from aggression by victims mainly by their physical proximity to cleaner fish models. The presence of both a juvenile cleaner wrasse and a bluestriped fangblenny at the site of an attack may confuse victims as to the identity of the aggressor. Indeed, victims sometimes chased the nearest juvenile cleaner wrasse after a mimic attack (personal observations). It is possible that colour similarity also plays a role in decreasing retaliatory chases by victims. The retaliatory chasing rate towards mimics away from models exceeded that towards non-mimics, who are always away from models, by more than threefold. This difference was, however, not significant, perhaps owing to the small sample sizes.

The retaliatory chases by victims of mimic attacks were reminiscent of the aggressive chases given by clients to cleaner fish after a jolt-inducing bite by the latter. Such bites have been shown to represent 'dishonest' cleaning (i.e. taking mucus and scales instead of ectoparasites; Bshary 2002), and aggressive chasing by bitten clients increases the likelihood that subsequent interactions with the punished cleaner will remain honest (Bshary & Schaeffer 2002). If, in fact, the rate of retaliatory chasing of mimics does exceed that of non-mimics when they are far from models, and hence confusion as to the identity of the aggressor is not an issue, this suggests that mimics may be perceived as cleaners by victims after an attack. The high aggression that mimics experience when away from models could thus be associated with punishment of

cheating by victims in the (misperceived) context of the reciprocal altruism that typically occurs between cleaners and clients (Bshary & Schaeffer 2002; Bshary & Grutter 2005). Nevertheless, whether mimics are the target of retaliatory chases owing to a confusion effect (owing to proximity to model) or to mistaken identity (owing to colour similarity to cleaners), the benefit of punishment that should be accrued by victims in terms of enhanced honesty of mimics in subsequent interactions is very unlikely to materialize.

Both colour similarity and physical proximity to their model therefore appear to protect cleaner-fish mimics from aggression by potential and actual victims of their attacks. The possibility remains that association with juvenile cleaners alone lowers victims' chases against fangblennies. We could not test this because the bluestriped fangblennies at our study site were never observed in non-mimetic colours, even when away from models, and non-mimetic scale-eating blennies never associated with cleaner fish. However, a previous study found that large bluestriped fangblennies, which exceeded the size of juvenile cleaner wrasses, lost their mimetic coloration but remained associated with cleaners (Moland & Jones 2004). Such an observation begs the question of why other non-mimetic fish, such as scale-eating fangblennies, do not seek proximity to cleaner wrasses if spatial association with cleaners alone confers a protective umbrella.

We conclude that the benefits of aggressive mimicry to bluestriped fangblennies include not only increased rate of encounter with potential victims and increased attack (foraging) rate (Côté & Cheney 2004; Moland & Jones 2004), but also protection against aggression by potential victims. It is not clear whether the latter benefit was important for the evolution of the association between cleaner mimics and their models or whether it is simply a consequence of an association that has arisen as a result of alternative benefits. It is interesting in this context to note that the foraging success of cleaner mimics did not vary with the rate at which they were chased by potential victims, whether near or away from cleaner wrasses ($r_s < 0.22$, $p > 0.29$ in both cases). The two benefits are therefore not a simple trade-off. Multiple benefits are also emerging in systems traditionally assigned to Batesian mimicry, particularly in coral reef fish (reviewed by Moland *et al.* 2005). These studies and ours suggest that there may be substantial overlap in the benefits gained by different mimics, which calls into question the conventional categorization on the basis of benefits accrued of different mimicry types observed in nature.

This research adhered to legal and ethical requirements of Guam where the work was carried out, and to all institutional guidelines.

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