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Original Article

Cleaner fish coloration decreases predation risk in aggressive fangblenny mimics

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Mimicry systems can be classified by the nature of fitness benefits obtained by the mimic, namely increased mating opportunities (reproductive), increased foraging potential (aggressive), or reduced predation risk (protective). However, there is increasing evidence that mimicry categories are not mutually exclusive and mimics can obtain benefits from more than 1 category. Here, I provide evidence that an aggressive mimic, the bluestriped fangblenny *Plagiotremus rhinorhynchos*, also benefits from reduced predation risk by resembling the juvenile cleaner wrasse *Labroides dimidiatus*, which are thought to be relatively immune from predation due to the mutualistic nature of cleaner–client interactions. Instead of removing ectoparasites from larger reef fish, bluestriped fangblennies approach and attack reef fish removing scales and dermal tissue. Fangblennies can switch between their mimic and nonmimic coloration within 5–10 min, depending on whether their model (the cleaner wrasse) is present or absent. I found that mimic fangblennies increased their risk-taking behavior toward potential predators compared with nonmimic fangblennies. Mimics were also more likely to attack other reef fish in the presence of predators compared with nonmimics. Animals should only increase risk-taking behavior when they perceive the threat of predation to be low. Therefore, this study provides important evidence that cleaner coloration provides protection from predation to both cleaner fish and their mimics, and the benefits of aggressive mimicry of cleaner wrasse have to be reevaluated in the light of these data.

Key words: **aggressive mimicry, coral reef fish, *Plagiotremus* sp., predation risk, protective mimicry, sabre-toothed fangblennies.**

INTRODUCTION

Mimicry is defined as the resemblance of one species to another in order to gain fitness benefits in terms of reduced predation (protective), or increased foraging (aggressive) or reproductive opportunities (reproductive) (Wickler 1968). However, mimics may gain more than 1 type of benefit from resembling their model and therefore rather than classify mimicry systems into mutually exclusive categories, it may be more precise to describe them in terms of overlapping categories (e.g., protective-aggressive mimicry: Nelson and Jackson 2009; Cheney 2010). Indeed, aggressive mimicry systems—defined as species that resemble other unrelated species to increase foraging opportunities (Cott 1940; Wickler 1968)—can involve a protective element, particularly if the mimic resembles a model that is toxic or even beneficial to the signal receiver. For example, Asilid flies closely resemble hymenoptera (bees and wasps) and this similarity is thought to allow them to approach and attack smaller flying insects more easily; however, a close resemblance to bees and wasps should also offer protection from predation (Rettenmeyer 1970). The coral reef fish *Plagiotremus laudandus* gains some protection from predation due to its resemblance to the poison fangblenny *Meiacanthus atrodorsalis*, but also benefits from increased access to potential reef fish victims, which they approach and attack to feed on scales and fins (Smith-Vaniz 1976), when associated with their model (Cheney 2010).

One of the most intriguing examples of aggressive mimicry exists on coral reefs between the bluestriped fangblenny *Plagiotremus rhinorhynchos* and the juvenile cleaner wrasse *Labroides dimidiatus*. Cleaning interactions are frequently cited as a classic example of mutualism: cleaners benefit from consuming ectoparasites from the surface of larger reef fish clients, whereas clients benefit from a reduction in ectoparasites (Grutter 1999) and a reduction in stress hormones (Soares et al. 2011). A reduction in ectoparasite load can allow clients to grow larger (Clague et al. 2011; Waldie et al. 2011) and develop a better body condition (Ros et al. 2011). Cleaners may also benefit from a reduction in predation risk due to the mutualistic relationship with potential predators (Feder 1966; Potts 1973; Losey 1979; Côté 2000). Evidence to support this hypothesis is limited; it is largely based on observations that cleaner fish frequently enter the mouths of predatory reef fish and that only few predation events have been observed at cleaning stations (Côté 2000). With respect to potential causes that may yield such protection from predation, cleaner fish are known to reduce the risk of being eaten by using tactile stimulation (Bshary and Wurth 2001; Grutter 2001, 2004; Soares et al. 2011), which involves

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the touching of the clients' body surface with the pectoral and pelvic fins. Cleaner provide more tactile stimulation to potential predators compared with nonpredatory client fish (Bshary and Wurth 2001) and more to clients that are hungry compared with satiated piscivorous clients (Grutter 2004). Whether visual cues also play a role in protecting cleaner organisms from predators is less clear. Overall, client reef fish are thought to recognize obligate cleaner fish based on coloration and body pattern (Côté 2000; Stummer et al. 2004). Obligate cleaners have a "uniform" comprising of a lateral body stripe with a combination of black, blue, and yellow color patches (Cheney, Grutter, et al. 2009; Lettieri et al. 2009). This color combination, which transmits well in water and is highly contrasting to the visual systems of a variety of signal receivers (Marshall 2000; Cheney, Grutter, et al. 2009), may ensure cleaners are easily located by client fish and not attacked by predators. Indeed, Lettieri and Streelman (2010) found that cleaner gobies exhibiting green and blue lateral stripes were less likely to be attacked by predators (*Hypoplectrus* hamlets) than noncleaner gobies and hypothesized that these gobies may have evolved chemical defense.

Fangblennies approach and attack a wide range of passing reef fish, including predatory fish (Kuwamura 1981; Côté and Cheney 2007). *Plagiotremus rhinorhynchos* accurately mimics the color and pattern of juvenile cleaner wrasse (Cheney, Skogh, et al. 2009). When not acting as a mimic of a cleaner wrasse, it can display nonmimic color patterns (Côté and Cheney 2005; Cheney et al. 2008; Cheney, Skogh, et al. 2009; Figure 1iii) and, in this case, is frequently found blending in with a variety of other fish species (Cheney, Skogh, et al. 2009). Fangblenny mimics benefit from their association with cleaner wrasse in terms of increased access to potential victims, reduced chasing, and reduced punishment from potential victims (Côté and Cheney 2007; Cheney et al. 2008). However, it is unclear whether the coloration and body pattern of cleaners also reduces predation risk by piscivores. If the mimic coloration yields anti-predation benefits, I predicted that mimics would be more likely to attack potential predators and more likely to attack other fish in the presence of predators, compared with nonmimic bluestriped fangblennies.

MATERIAL AND METHODS

Behavioral observations of focal bluestriped fangblennies were conducted on reefs around Pulau Hoga, Southeast Sulawesi, Indonesia (05°28′S, 123°45′E), in July and August 2006. Fifteen minute observations were conducted on haphazardly located mimic fangblennies (n = 35) and nonmimic fangblennies (n = 25) using SCUBA or snorkel at depths between 2 and 18 m. Individuals were located at least 10 m apart, and the location where they were found was marked with flagging tape to ensure repeat observations were not conducted on the same individual. During each observation, the following was recorded: the total number of attacks, defined as a fangblenny darting toward another reef fish; the species of each fish attacked, and whether the fish was a potential predator or not (based on information from fishbase.org); whether a predator was present within 1 m of the focal fangblenny and for more than 15 s before the attack; other fish (>4 cm total length) that passed or were present within 1 m of the focal fangblenny during the observation, including the presence of juvenile *L. dimidiatus* model; and chases toward the fangblenny from other reef fish, including in retaliation to an attack or spontaneous chases. The percentage of potential fish victims that were attacked was calculated using the number of attacks and the number of fish within 1 m of the fangblenny throughout the observation. When an individual fish could be identified as being attacked multiple times by a fangblenny during an observation, it was counted as one attack to prevent pseudoreplication. Fangblenny size was estimated to the nearest 0.5 cm by the observer placing a ruler on the reef in the vicinity of the focal fish after each observation.

Statistical analysis

Observations during which no predators passed within 1 m of the fangblenny were omitted from the analyses (mimic fangblennies = 5; nonmimic fangblennies = 3) as the study aimed to compare whether predators were attacked by mimics and nonmimics, or ignored. Body size (total length) of fangblennies did not differ between color morph (mean ± SE: mimic = 5.15 ± 0.11, nonmimic = 5.23 ± 0.22; $t_{45.6}$ = −0.45, P = 0.66). Furthermore, there was no relationship between number of attacks or chases due to body size (number of attacks: t_{50} = −0.54, P = 0.60; number of chases: t_{50}= −0.84, P = 0.40); therefore, body size was not considered in the analysis. The total number of attacks was log transformed to meet the assumptions of normality and heteroscedasticity; however, the total number of predator attacks did not meet the assumptions of normality and were modeled with nonparametric tests.

RESULTS

There was no significant difference in the total number of fish that passed or were present within 1 m of the focal fangblenny for each color morph per 15 min observation (mean ± SD: mimic = 20.5 ± 3.2, nonmimic = 24.1 ± 4.5; $t_{43.1}$ = −0.67, P = 0.51) or when predators and nonpredators were considered separately (predators: $t_{49.6}$ = 0.25, P = 0.80; nonpredators: $t_{39.4}$ = −0.67, P = 0.50). In total, 52 species of coral reef fish were attacked by fangblennies and each fangblenny color morph attacked a similar total number of species (mimic = 41, nonmimic = 42). Nonpredatory fish that were attacked by fangblennies included

Figure 1
Photographs of the study species. (i) Juvenile cleaner wrasse *Labroides dimidiatus*; (ii) mimic bluestriped fangblenny *Plagiotremus rhinorhynchos*; and (iii) nonmimic bluestriped fangblenny *P. rhinorhynchos*.

damselfish (e.g., *Amblyglyphidodon curacao*, *Pomacentrus lepidolepsis*, *Chrysiptera talboti*), surgeonfish (e.g., *Acanthurus nigrofuscus*, *Ctenochaetus striatus*), anthias (e.g., *Pseudanthias tuka*, *Pseudanthias hutchi*), parrotfish (e.g., *Chlorurus sordidius*), and soldierfish (e.g., *Myripristis murdjan*). Predatory fish species that were attacked included groupers (e.g., *Cephalophpolis urodeta* and *Epinephelus fasciatus*) and trumpetfish (*Aulostomus chinensis*).

Mimic fangblennies were more likely to attack predators than nonmimic fangblennies (total number of attacks on predators: Wilcoxon rank sum test $W = 410$, $n_1 = 30$, $n_2 = 22$, $P = 0.02$; percentage of predators passing 1 m from the focal fangblenny that were attacked: Wilcoxon rank sum test $W = 407$, $n_1 = 30$, $n_2 = 22$, $P = 0.02$; Figure 2i,ii). For mimic fangblennies, there was no correlation between number of attacks on predators and time that a cleaner was present in the immediate vicinity (Spearman $\rho = 0.12$, $n = 30$, $P = 0.54$). Mimic fangblennies were also more likely to attack fish in the presence of a nearby predator compared with nonmimic fangblennies ($t_{51} = -2.34$, $P = 0.04$; Figure 3). In contrast, there was no difference between the number of attacks on nonpredatory fish by mimics and nonmimics fangblennies (total number of attacks on nonpredators: $t_{47.4} = 0.09$, $P = 0.93$; percentage of nonpredators that were attacked: $t_{37.8} = -0.15$, $P = 0.88$; Figure 2i,ii).

Chases by predators toward fangblennies were relatively rare but were greater toward nonmimic fangblennies compared with mimic fangblennies (Wilcoxon rank sum test, $n_1 = 30$, $n_2 = 22$, $P = 0.01$; Figure 2iii); 75% (3/4) of these chases by predators were spontaneous rather than in retaliation to an attack. There were no differences in the number of chases by nonpredators toward mimic and nonmimic fangblennies ($t_{34.0} = 0.20$, $P = 0.84$; Figure 2iii); 61% (30/49) of chases by nonpredators were spontaneous rather than in retaliation to an attack.

DISCUSSION

Mimic bluestriped fangblennies, which closely resemble and display the same coloration as juvenile cleaner wrasse, were more likely to exhibit risk-taking behavior—defined here as attacking predatory fish and attacking nonpredatory fish in the presence of nearby predators—compared with nonmimic bluestriped

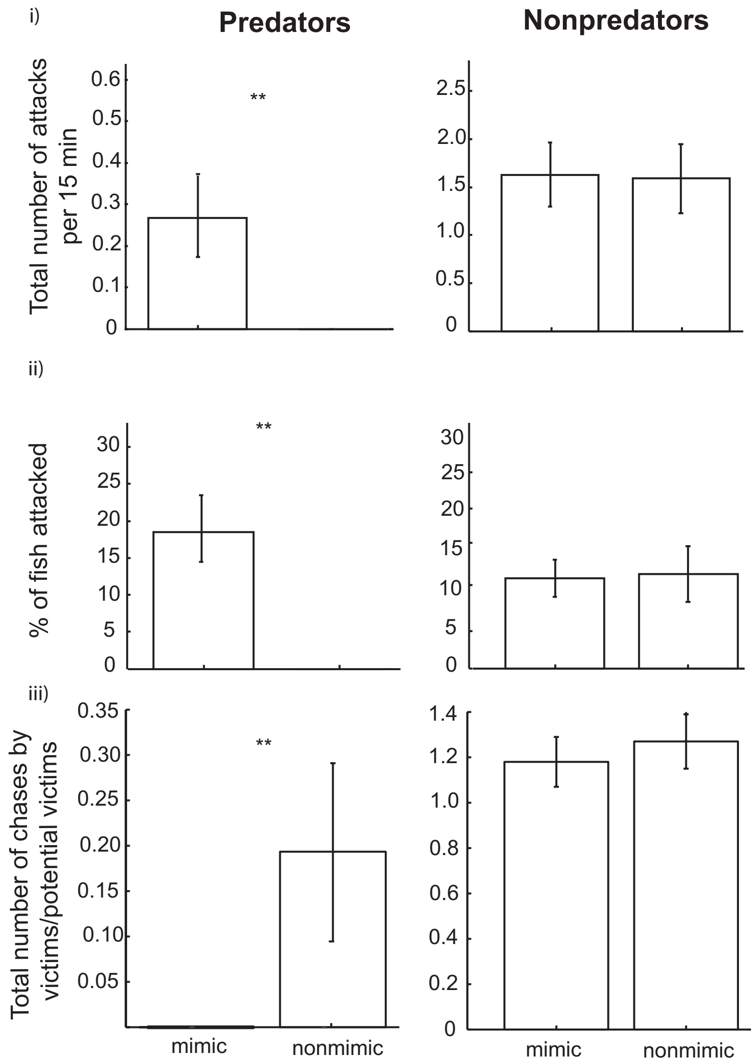

Figure 2
(i) Number of attacks by fangblenny toward reef fish, (ii) percentage of fish attacked by fangblenny, and (iii) chases from reef fish toward fangblenny. Bars represent mean and error bars represent 1 SE. ** represents significant difference between bars.

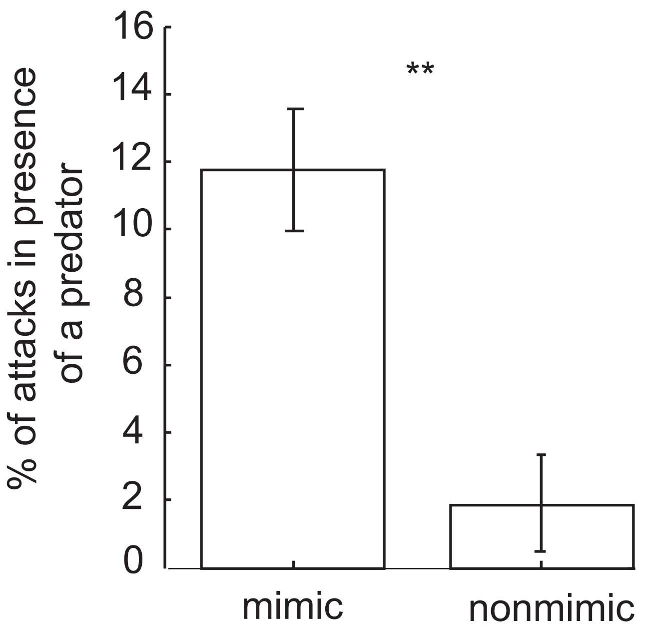

Figure 3
Number of attacks toward reef fish by each color morph in the presence of a predator. Bars represent mean and error bars represent 1 SE. ** represents significant difference between bars.

fangblennies. An increase in risk-taking behavior in mimic fangblennies, irrespective of the time that a cleaner wrasse was present in the immediate vicinity, suggests that cleaner coloration may help protect cleaner fish and their mimics from predation attempts.

Predation is a strong selective force that can cause prey to adjust their behavior in order to survive (Lima and Dill 1990; Ferrari et al. 2009). In particular, predation risk can influence how and when animals forage, social activities such as courtship and herding, and escape responses such as fleeing or the use of shelters (Lima and Dill 1990; Magurran 1999). Animals often avoid predators (Lima and Dill 1990) and reduce their activities and/or seek shelter when they assess their risk of predation to be high (Lima and Dill 1990; Milinski 1993). Risk-taking behavior that could cause significant harm and even death, such as how and when to attack prey, should be conducted when the fitness costs of such a behavior is limited (Jackson et al. 2002). Predatory fish (Slingjaw wrasse, *Epibulus insidiator*) have been observed to attack and consume fangblennies in the laboratory (Cheney et al. 2008), and other species have been observed consuming fangblennies in the field (Lizardfish *Synodus* sp. and Rock hind *Epinephelus* sp.; Cheney KL, personal observations, 2004–2010). Therefore, fangblennies may increase their chance of being preyed on when they attack a predator or by attacking fish in the presence of a predator. When attacking their victims, fangblennies often dart out into the water column from the protection of the reef making them presumably more susceptible to predation, especially from sit-and-wait predators, which may be camouflaged and difficult to detect. Furthermore, after repeated attacks by a fangblenny, predators may learn to recognize the difference between mimics and models, and the benefit of resembling a cleaner will be lost (Cheney 2008). When the risk of predation is significantly reduced by the mimics' visual appearance, the benefits of attacking a predator over a less risky nonpredator could include increased nutritional value per attack (removal of larger scales, more mucus) or a greater chance that the attack is successful (larger client surface area).

Predators chased nonmimic fangblennies less frequently than mimic fangblennies. Chasing by reef fish has shown to act as punishment toward fangblennies, as it decreases the risk of future attacks by fangblennies (Bshary and Bshary 2010b); after an attack, chasing increases the probability that the fangblenny will switch species it attacks. Chases toward fangblennies may be costly in terms of energetic expenditure and the risk of being physically harmed (Côté and Cheney 2007; Bshary and Bshary 2010a, 2010b). There is considerable variation between fangblenny individuals when considering which species to attack (Bshary and Bshary 2010a). Variation can be potentially explained by differences in personality traits, local victim species composition, specialization on location or species type, and individual learning. However, here we show that decisions can also be influenced on current coloration and perceived predation risk.

Cleaner fish have evolved some of the most conspicuous color patterns in the marine environment (Cheney, Grutter, et al. 2009); the blue stripes of cleaner fish are one of the most chromatically contrasting color patterns compared with sponge and coral background habitats (Lettieri et al. 2009). Furthermore, the blue coloration is visible to a wide range of client reef fish, including predators, which frequently possess dichromatic vision (Cheney, Grutter, et al. 2009; Lettieri et al. 2009). When given equally palatable food items, fish also appear to have a response bias against blue and yellow colored objects and instead prefer red and green objects (Smith et al. 2004; Cheney et al. 2013). Conspicuous blue and yellow color patterns are also used in the marine environment to warn predators of toxicity (e.g., in blue-ringed octopus and nudibranch molluscs such as *Chromodoris elisabethina*). Therefore, whether this observation is a learnt or unlearnt response bias is unclear. Unlearnt biases can potentially evolve readily when learnt avoidance to these species is too costly (Stevens and Ruxton 2012); for example, encounters with a venomous blue-ringed octopus could result in death. Interestingly, Lettieri and Streelman (2010) suggested that cleaning gobies (*Elacatinus* sp.) that display blue coloration may have evolved a chemical defense as they were rejected by hamlet predators more frequently than other gobies.

Previously, bluestriped fangblenny mimics have been shown to benefit from their association with cleaner wrasse in terms of increased access to potential victims and higher strike rates (Côté and Cheney 2004) and reduced chasing and punishment from potential victims (Côté and Cheney 2007). However, it is unclear whether proximity to cleaner wrasse or coloration was responsible for these incurred benefits. Mimic bluestriped fangblennies that were located away from cleaner wrasse were chased less frequently than a congener, *Plagiotremus tapeinosoma*, which does not act as a mimic and does not associate with cleaner wrasse, indicating that coloration may play a protective benefit. However, here we could not control for interspecific differences as nonmimic bluestriped fangblennies were not present at this particular study site (Côté and Cheney 2007).

Coral reef fish display an amazing diversity of color patterns, and studies such as these are beginning to elucidate some of their functions. This is the first study to demonstrate that body coloration reduces predation risk in cleaner fish and their mimics. This study also provides further evidence to demonstrate that mimicry systems can offer dual benefits to the mimic in terms of protection from predation and increased access to victims (protective-aggressive mimicry: Nelson and Jackson 2009; Cheney 2010).

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