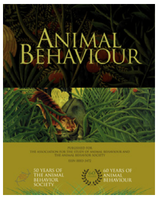
Animal Behaviour 88 (2014) 85–90

Contents lists available at ScienceDirect

Animal Behaviour

journal homepage: www.elsevier.com/locate/anbehav



Geographical variation in the benefits obtained by a coral reef fish mimic

Karen L. Cheney[a,*], Alexandra S. Grutter[a], Redouan Bshary[b]

[a] *School of Biological Sciences, The University of Queensland, Brisbane, Australia*
[b] *Institut de Biologie, Eco-Ethologie, The University of Neuchâtel, Neuchâtel, Switzerland*

ARTICLE INFO

Article history:
Received 22 July 2013
Initial acceptance 20 August 2013
Final acceptance 9 October 2013
Available online 18 December 2013
MS. number: 13-00608R

Keywords:
aggressive mimicry
Aspidontus taeniatus
cleaner wrasse
cleaning symbioses
coral reef fish
Labroides dimidiatus
protective mimicry
sabre-toothed blenny

Mimicry systems are frequently categorized by the type of benefit gained by the mimic's resemblance to its model: protection from threat, including predation (protective mimicry), and increased access to resources, including prey items (aggressive mimicry). These category types may not be mutually exclusive, and some mimics may gain more than one type of benefit. Here we examined a contentious classic textbook example of mimicry between the cleaner wrasse *Labroides dimidiatus* and its mimic, the sabre-toothed blenny *Aspidontus taeniatus*. We found that the benefit obtained by the sabre-toothed blenny varied between four geographical locations. At the Great Barrier Reef, in Indonesia and in the Red Sea, it rarely attacked reef fish victims, but instead relied on other food sources such as substrate items, damselfish eggs and tubeworms. Here, the main function of the mimicry system could be to protect the sabre-toothed blenny from predation (protective mimicry) and was consistent with a previous study in Japan. However, in French Polynesia, the sabre-toothed blenny aggressively attacked reef fish frequently, and potential victims were more likely to pose to solicit a cleaning interaction. Diet analysis from individuals in French Polynesia indicated material was gleaned from the surface of fish, including large pieces of fin, implying an increase in the benefits obtained from attacking reef fish (aggressive mimicry). This study provides a potential second example of a mimicry system in which multiple types of benefits are gained by a mimic, and importantly, that the benefits obtained by the mimic vary between different environmental conditions and/or geographical locations. This may have important implications for the maintenance and evolution of mimicry systems and may reflect different stages of an arms race with potential victims.

Mimicry frequently involves a tripartite communication system in which a mimic benefits from its resemblance to a model during interactions with a selective agent (Wickler, 2013), which may include predators, prey and competitors, and provides one of the best illustrations for the power of evolution through natural selection. The benefits obtained by the mimic fall into two broad categories: (1) protective mimicry and (2) aggressive mimicry. Protective mimicry is defined as a palatable mimic that resembles an unpalatable model, hence the mimic benefits from reduced threat, which includes predation; both Müllerian (Müller, 1879) and Batesian mimicry (Bates, 1862) fall into this category. In aggressive mimicry, the benefits of resemblance to a beneficial or harmless model are increased access to resources, including food items or parental care, by increasing access to prey or beneficial species that would normally avoid the mimic but not the model (Wickler, 1966). Recent studies on coral reef fish have shown that these category types are not mutually exclusive and that some mimics may gain more than one type of benefit. For example, the fangblenny mimic *Plagiotremus laudandus* gains both foraging benefits (aggressive mimicry) and reduced predation risk (protective mimicry) from its resemblance to the poison fangblenny *Meiacanthus atrodorsalis* (Cheney, 2010). Although previous studies have investigated variation in the strength of benefits obtained by the mimic caused by the shifting nature of the relationship between model and signal receiver (Cheney & Côté, 2007; Goodale & Sneddon, 1977; Lindström, Alatalo, & Mappes, 1997), or the abundance of alternative prey (Dill, 1975; Kokko, Mappes, & Lindström, 2003), little work has been done to investigate whether the benefit gained by the mimic shifts depending on geographical location and/or environmental conditions.

An iconic early example of mimicry involves the sabre-toothed blenny, *Aspidontus taeniatus*, and its model, the cleaner wrasse *Labroides dimidiatus*. This is among the best examples of a vertebrate mimicking the shape, coloration and behaviour of another species (Wickler, 1968). The model's colour pattern varies between life history stages and geographically but is invariably closely matched

---

[*] Correspondence: K. L. Cheney, School of Biological Sciences, The University of Queensland, St Lucia, Brisbane, QLD 4072, Australia.
E-mail address: k.cheney@uq.edu.au (K. L. Cheney).

0003-3472/$38.00 © 2013 The Association for the Study of Animal Behaviour. Published by Elsevier Ltd. All rights reserved.
http://dx.doi.org/10.1016/j.anbehav.2013.11.006

by the mimic (Cheney & Marshall, 2009; Robertson, 2013; Sims et al., 2013; Wickler, 1968). The sabre-toothed blenny also imitates the swimming mode of the wrasse, using mainly the pectoral fins to create undulating movement patterns (Wickler, 1968). The cleaner wrasse removes ectoparasites from other reef fishes, and increasing evidence suggests that its 'clients' obtain net benefits from the interaction (Clague et al., 2011; Ros et al., 2011; Soares, Oliveira, Ros, Grutter, & Bshary, 2011; Waldie, Blomberg, Cheney, Goldizen, & Grutter, 2011). Clients certainly actively approach cleaners and invite inspection with special postures (called 'posing'; Côté, Arnal, & Reynolds, 1998). There is some evidence for the hypothesis first proposed by Trivers (1971) that in return for its services the wrasse is exempt from predation by piscivorous clients (Barbu, Guinand, Bergmuller, Alvarez, & Bshary, 2011; Bshary & Würth, 2001; Cheney, Bshary, & Grutter, 2008a; Côté, 2000; Grutter, 2004). The cleaner wrasse system has become a textbook example for the study of interspecific mutualism from both a game theoretic and a cognitive perspective (Davies, Krebs, & West, 2012; Shettleworth, 2009). The study of potential exploitation of mutualisms by third-party species has a long-standing interest in ecology and evolution (Bronstein, 2001, 2003), and the sabre-toothed blenny seemed to offer a wonderful example (Wickler, 1968).

Despite these features, the system is currently not used in textbooks on general behaviour, ecology or evolution, possibly owing to conflicting evidence concerning the function of the mimicry, which has not been followed up by more detailed studies. Early laboratory experiments and qualitative field observations suggested a clear case of aggressive mimicry, probably further enhanced by protective benefits (Wickler, 1968). It was reported that victims approached the mimic or tolerated its approach, enabling it to bite pieces of flesh (mainly fin) from the victim (Randall & Randall, 1960; Wickler, 1968). Victims learned to avoid mimics in the laboratory (Wickler, 1968), and the same apparently happened in nature as Randall and Randall (1960) stated that victims were typically juveniles. The protective benefits of the mimicry were never explicitly tested, but if the protection of cleaner wrasse from predators were based on visual cues then the sabre-toothed blenny should experience reduced predation risk as well, which has been shown in another cleaner mimic, the bluestriped fangblenny, *Plagiotremus rhinorhynchos* (Cheney, 2013). In fact, Kuwamura (1983) concluded that the mimicry evolved and is maintained because of the protective function, after failing to provide good evidence for aggressive mimicry in the first quantitative field study in southern Japan, supplemented by stomach analyses of a few individuals. His results suggested that sabre-toothed blennies mainly feed on tubeworms, sometimes raid the nests of damselfish, and rarely bite other fishes (Kuwamura, 1983). We are not aware of further data published since then. Instead, research has focused on the bluestriped fangblenny, which mimics only the juvenile coloration of the cleaner wrasse. This species regularly attacks other fish, and benefits from the resemblance in terms of increased foraging (Côté & Cheney, 2004), reduced chasing by potential victims (Côté & Cheney, 2007) and reduced predation risk (Cheney, 2013) and reduces the foraging success of its model (Côté & Cheney, 2004).

Owing to the contradictory results from previous studies and our own interest in how mimicry systems may vary depending on geographical location, we collected data on sabre-toothed blenny individuals from four different locations: the Red Sea, Indonesia, the Great Barrier Reef and French Polynesia. Our main aim was to test whether the observations by Kuwamura (1983) generally apply to the sabre-toothed blenny or whether there is regional variation with respect to the benefits obtained by the mimicry. This could have important implications for the evolution and diversification of mimicry systems. We hence quantified the frequencies of mimic attacks on reef fish victims, whether reef fish posed towards the mimic to invite inspection (indicating that the fish was deceived by the mimic), unprovoked aggression by damsels and other species, nest raiding, and foraging on other identifiable food sources such as tubeworms. We also examined food items found in the gut of sabre-toothed blennies in one location (French Polynesia).

Aggressive mimicry could come in two forms: (1) deception that allows an increase in foraging by attacking reef fish victims to feed on scales, fins or other body tissue; or (2) deception that allows mimics to enter and raid damselfish nests. Most observed sabre-toothed blenny mimics were adult individuals mimicking the cleaners' adult coloration. However, two individuals from Indonesia were juveniles mimicking the cleaners' juvenile coloration. Based on these two individuals, we also investigated the possibility that the importance of aggressive mimicry varies with life history stage.

METHODS

Behavioural observations of focal sabre-toothed blennies were conducted on reefs around: Pulau Hoga, Southeast Sulawesi, Indonesia (05°28′S, 123°45′E), in July and August 2006 ($N = 8$ adults; $N = 2$ juveniles); Lizard Island, Great Barrier Reef, Australia (03°27′S and 151°55′E) in December 2005 and January 2006 ($N = 6$ adults); Moorea, French Polynesia (17°29′S, 149°49′W) in March and April 2000 ($N = 14$ adults); and Ras Mohammad National Park in Sinai, Red Sea, Egypt (28°10′N, 34°56′E) in 2003, 2006 and 2007 ($N = 21$ adults). Observations on haphazardly located sabre-toothed blennies were conducted by an observer between 0700 and 1630 hours using scuba-diving or snorkelling equipment at depths between 1 and 8 m. We found no evidence that time of day or depth affected our results. Each individual was observed for either 30 or 60 min, depending on location (30 min in French Polynesia; 60 min for other locations). For observations conducted on the Great Barrier Reef and in Indonesia, we found a significant correlation between foraging events between the first 30 min and second 30 min ($r_{14} = 0.91$, $P < 0.001$); therefore results are presented per 30 min for all locations. Individuals ranged from 7.0 to 13.0 cm standard length (SL).

During each observation, the following was recorded: the total number of attacks, defined as a sabre-toothed blenny darting towards another reef fish and making visible contact with the fish; the species of each fish attacked; posing by reef fish towards a sabre-toothed blenny (as per Côté et al., 1998); other foraging observations, including bites by sabre-toothed blennies on the substrate, raids into damselfish nests and attacks on tubeworms; unprovoked chases towards sabre-toothed blennies from other reef fish, including damselfish. On one occasion, an individual fish was identified as being attacked multiple times by a sabre-toothed blenny, but this was counted as one attack to prevent pseudoreplication.

We also conducted diet analysis on nine sabre-toothed blenny individuals from French Polynesia that were collected in April 2000. Fish were captured between 0915 and 1230 hours, killed immediately with a blow to the head and pithed with a sharp knife. Brain death was confirmed by observation of no opercular movements for a few minutes after pithing. Ethics approval was obtained from The University of Queensland Animal Ethics Committee. Fish were fixed underwater by filling the gut cavity with 50% formalin in filtered salt water (57 μm) using a 25 G × 16 mm needle and 1 ml syringe. Fish ranged in length from 5.5 to 8.0 cm SL. The whole fish or mid-section of the fish was fixed 1–2 h later in 10% formalin in sea water. In the laboratory, guts were dissected from the body of the individual and contents were carefully sorted in a counting tray. Items in the following categories were counted: fish eggs, pieces of fish skin and/or fin, and substrate items (e.g. sand, micromolluscs). The amount or 'volume' of different food items was estimated following Grutter (1997) with line transects and expressed as % food cover. This