Multiple selective pressures apply to a coral reef fish mimic: a case of Batesian–aggressive mimicry

Karen L. Cheney*

School of Biological Sciences, The University of Queensland, St Lucia, Queensland 4072, Australia

Mimics closely resemble unrelated species to avoid predation, capture prey or gain access to hosts or reproductive opportunities. However, the classification of mimicry systems into three established evolutionary mechanisms (protection, reproduction and foraging) can be contentious because multiple benefits may be gained by mimics, causing the evolution of such systems to be driven by more than one selective agent. However, data on such systems are generally speculative or anecdotal. This study provides empirical evidence that dual benefits apply to a coral reef fish mimic in terms of increased access to food (aggressive mimicry) and reduced predation risk (Batesian mimicry). Bicolour fangblennies *Plagiotremus laudandus* gained access to more reef fish victims, which they attack to feed on fins and scales, when they spent more time associated with their model *Meiacanthus atrodorsalis*. Furthermore, exact replicas of *P. laudandus* incurred fewer approaches from potential predators compared with control replicas that varied in resemblance to *P. laudandus*. Predators with trichromatic visual systems (three distinct spectral sensitivities) could potentially distinguish between replicas based on colour based on theoretical vision models. Therefore, this mimicry system could be best described as Batesian–aggressive mimicry in which mimicry evolution is driven by multiple simultaneous selective pressures.

Keywords: Batesian mimicry; aggressive mimicry; coral reef fishes; *Plagiotremus laudandus*; evolution; selective pressures

1. INTRODUCTION

Mimicry is a classical example of Darwinian adaptation by natural selection in which mimics evolve to resemble other species to gain a fitness advantage. Traditionally, the classification of mimicry systems is based on the functional and ecological relationships between participants (Pasteur 1982), and in recent studies have been condensed into three mutually exclusive categories: protective, aggressive (or foraging) and reproductive mimicry (Zabka & Tembrock 1986; Starrett 1993) based on benefits accrued by the mimic. However, systems in which mimics gain multiple benefits spanning functional categories may exist (Malcolm 1990). Such mimicry systems may challenge the assumption that mimicry types are driven by three discrete evolutionary mechanisms (protection, reproduction and foraging), and simultaneous selective pressures may act on these systems.

For example, flies from the family Asilidae and the syrphid fly *Volucella* are considered to be aggressive mimics—defined as a predator or parasite that resembles another non-threatening (or even inviting) species to gain access to prey or hosts (Cott 1940; Wickler 1968)—of hymenoptera (bees and wasps), which they resemble closely. Asilids prey on smaller flying insects and it is thought that their similarity to hymenoptera allows them to approach their victims more closely before carrying out an attack. However, asilids do not approach their prey in a manner that would suggest that they are under

disguise, and classical Batesian mimicry—defined as palatable species resembling toxic ones to avoid predation (Bates 1862)—may also be used to describe this form of mimicry (Poulton 1904; Evans & Eberhard 1970; Rettenmeyer 1970). Interestingly, this is a long-standing debate, as a rather heated discussion occurred between Poulton and Bateson in letters to Nature in 1892 on whether *Volucella* was an aggressive or a Batesian mimic (starting with Bateson 1892). However, a combination of mimicry types, termed Batesian–aggressive mimicry, may explain this type of mimicry system more accurately.

Another example involves snake mimics, such as king snakes from the *Lampropeltis* genus, which resemble venomous coral snakes. They are apparent Batesian mimics as they are protected from predators only in areas where the model is present and not in areas where the model is absent (Pfennig *et al.* 2001). However, it has been suggested that their conspicuous appearance may also assist in foraging, either by accessing bird nestlings as their parents react strongly to their bright coloration, or for other snake species as their presence may inhibit other predators attacking potential prey (Pough 1988; Malcolm 1990). They could therefore benefit both in terms of protection from potential predators and increased foraging access to prey (Malcolm 1990). However, to date, evidence to support mimicry types in which dual benefits may apply has been putative or circumstantial (robber flies, Poulton 1904; Evans & Eberhard 1970; Rettenmeyer 1970; coral snake mimicry, Malcolm 1990; reef fishes, Moland *et al.* 2005).

In this study, the putative example of Batesian–aggressive mimicry was investigated on coral reefs in the

*k.cheney@uq.edu.au

Figure 1. (a) Photographs of (i) *M. atrodorsalis* and (ii) *P. laudandus* in the field. (b) A photograph of *P. laudandus* (replica 1) was manipulated to create replicas that varied in colour and pattern (replicas 2–3). A replica of *Plagiotremus rhinorhynchus* (replica 4) was used as a control.

Indopacific (Moland *et al.* 2005). The bicour fangblenny, *Plagiotremus laudandus*, closely resembles the fork-tail blenny, *Meiacanthus atrodorsalis* (Losey 1972; Springer & Smith-Vaniz 1972; Moland *et al.* 2005). The colour patterns of *P. laudandus* and *M. atrodorsalis* are nearly identical; both are blue anteriorly, and yellow posteriorly (figure 1a). When threatened, *M. atrodorsalis* delivers toxic bites to predators using enlarged canine teeth with venom glands at the base of each tooth (Randall *et al.* 1997). During experiments in which living *Meiacanthus* spp. were fed to predators, the majority of individuals were taken into the predators' mouth and promptly rejected (Losey 1972; Springer & Smith-Vaniz 1972). *Plagiotremus laudandus* is therefore thought to act as a Batesian mimic benefiting from its resemblance to *M. atrodorsalis* by gaining protection from predation (Losey 1972). However, *P. laudandus* is also considered to be an aggressive mimic (Losey 1972; Moland *et al.* 2005); it attacks passing coral reef fishes to feed on scales, fins and tissue (Randall *et al.* 1997) and may benefit from associating with *M. atrodorsalis* by being undetected by potential victims.

While Batesian-type and aggressive-type benefits have been independently evaluated experimentally in coral reef fishes (Caley & Schluter 2003; Moland & Jones

2004; Cheney & Côté 2007), this study aims to provide empirical evidence that dual benefits can apply to a single mimicry system. *Plagiotremus laudandus* was assessed to determine whether it benefited in terms of (i) increased foraging success and (ii) reduced predation risk from its association with, and resemblance to, the model *M. atrodorsalis* in areas which varied in the abundance of models and mimics.

2. MATERIAL AND METHODS

(a) Behavioural observations

Observations were conducted for 30 min on 40 *P. laudandus* that were haphazardly located on 10 coral reefs around Pulau Hoga 05°28' S, 123°45' E, southeast Sulawesi, Indonesia, in July–August 2006. Individuals were located using self-contained underwater breathing apparatus (SCUBA) at depths of 2–18 m and were found at least 10 m apart, therefore the assumption was made that individuals were not observed on more than one occasion. During each observation, the following was recorded: the total number of attacks made by a mimic, defined as a mimic darting towards a potential victim; the number of successful attacks, defined as clear contact made with the victim; and the time that each

mimic spent within 30 cm of the nearest *M. atrodorsalis* model. After each observation was conducted, the abundance of all *P. laudandus* and *M. atrodorsalis* was recorded within a 5×5 m quadrat centred on each focal individual's location at first sighting. The numbers of potential victims/predators were also estimated at each site with five 5 min point counts, noting the number and species within or passing through a 3×3 m quadrat.

(b) Replicas of *P. laudandus*

The response of predatory wild fish to four fish replicas (figure 1b) during a 10 min trial was tested on reefs around Pulau Hoga and on fringing reefs off Lizard Island ($14^{\circ}39'$ S, $145^{\circ}26'$ E), Great Barrier Reef, Australia. Replicas were constructed by gluing a photograph of a fish on either side of a 2 mm thick Perspex outline and then waterproofed with boat resin. The replicas were tested at eight sites on reefs off Pulau Hoga, all of which had both *P. laudandus* and *M. atrodorsalis* present in relatively high numbers (mean $\pm$ s.d. 100 m^{-2} : *P. laudandus* 1.3 ± 0.2 ; *M. atrodorsalis* 3.2 ± 1.3), 10 sites on reefs at Lizard Island that had *P. laudandus* and *M. atrodorsalis* present in lower numbers (*P. laudandus* 0.5 ± 0.1 ; *M. atrodorsalis* 1.2 ± 1.3) and eight sites on reefs that did not have any *P. laudandus* and *M. atrodorsalis* present. Depths varied from 2 to 5 m.

The four replicas were constructed using the following photographs: (i) a true photograph of *P. laudandus*, (ii) and (iii) manipulated photographs of *P. laudandus* that varied in colour and patterns, and (iv) a photograph of *P. rhinorhynchus* (figure 1b). Photographs were manipulated using Adobe Photoshop CS by altering their colours to red and green (replica 2) or altering the colour information to shades of grey (replica 3). A replica of *P. rhinorhynchus* was used to control for the fact that predators could approach the manipulated replicas (2 and 3) more frequently owing to a novelty effect.

Methods for replica trials were modified from Caley & Schluter (2003). A trial involved observing a single replica placed at a fixed location for 10 min on snorkel or SCUBA. Each replica was given buoyancy by attaching one end of a section of monofilament line to a point on its upper back, and attaching a small piece of foam to the line approximately 2 m from the replica. The monofilament line was attached to a small piece of PVC pipe, around which the line could be wrapped and held by the observer. This line was used to create motion to the replica by the observer in a sequence of regular upward and downward movements. A second monofilament line was attached to the bottom of the replica and a small fishing weight was added approximately 30 cm from the replica. Separate trial sites were spaced at least 20 m apart to ensure that the same potential predators were not repeatedly exposed to the same replica. Replica type was randomized between days, sites and time. Individual sites were not visited more than once per day. All trials were conducted between 08.00 and 14.00.

The number and species of fishes approaching a replica was recorded during a 10 min trial. An approach was recorded when an individual fish swam towards the replica and either halted and visually inspected it within a distance of 2 m or actually bit the replica. Repeated approaches by the same fish were counted as a single approach. Fish species were classified as piscivores or non-piscivores (from fishbase.org). Non-piscivores were recorded approaching the replicas to

examine whether another undefined aspect of a particular replica was attracting or deterring fishes.

The Vorobyev and Osorio colour discrimination opponent theoretical vision model was used (Vorobyev & Osorio 1998; Vorobyev *et al.* 2001) to determine whether a potential fish predator that had been observed approaching the replicas (*Lutjanus bohar*) and a potential victim that had been observed being attacked by *P. laudandus* (*Acanthurus nigroris*) had the visual capabilities to distinguish between the replicas based on colour alone. The vision model estimates a 'colour distance' (ΔS) between coloured spectra within a visual space, determined by the visual system of a signal receiver. Essentially, colours that appear similar to a signal receiver either because of the nature of the visual system or because of a small difference in the reflectance spectra of colours result in small ΔS values, while those that have high chromatic contrast have large ΔS values.

The spectral reflectance of each colour patch on each replica was measured with an Ocean Optics (Dunedin, FL) USB2000 spectrophotometer with a PX-2 pulsed xenon light source, a 200 μm bifurcated fibre optic cable and a Spectralon 99 per cent white reflectance standard (Lab-Sphere, Inc., North Sutton, NH). The spectral sensitivity of *L. bohar* and *A. nigroris* is known from microspectrophotometry work performed previously (*L. bohar*: $\lambda_{\text{max}} = 424, 494$ and 518 nm ; Lythgoe *et al.* 1994; *A. nigroris*: $\lambda_{\text{max}} = 446, 514$ and 526 nm ; Losey *et al.* 2003). The proportions of spectrally distinct cone types and the Weber fraction were used as per a previous study (Cheney *et al.* 2009). Colour distances were calculated using illumination measurements at a water depth of 5 m.

(c) Statistical analyses

A multiple linear regression model was used with the success of attacks considered as the dependent variable; ratio of model : mimic, time spent with model and number of predators/victims in the local area as predictor variables. However, there was strong multicollinearity between the ratio of model : mimic and time spent with model, therefore the effects of time spent with model and ratio of model and mimic could not be disentangled without further experimentation. Correlation analyses were therefore conducted for individual variables. A repeated measures analysis of variance (ANOVA) was used to assess differences in predator and non-predator approach rates, replicas 1–4 were treated as within-subject factors, and sites (Lizard Island—no models/mimics present, Lizard Island—models/mimics present, Pulau Hoga) were between-subject factors. Statistical analyses were conducted using SPSS v. 11.0.

3. RESULTS

(a) Behavioural observations

The total number of attacks made by a mimic ranged from 1 to 12 per 30 min (mean $\pm$ s.d.: 5.68 ± 3.06) and the number of successful attacks ranged from 0 to 9 per 30 min (mean $\pm$ s.d.: 2.98 ± 2.25). The time that each mimic spent within 30 cm of the nearest *M. atrodorsalis* model ranged from 0 to 30 min (mean $\pm$ s.d.: 13.78 ± 9.98). Both the total number of attacks and the percentage of successful attacks were positively correlated with time spent by the mimic in proximity to its model (total number of attacks: Pearson's correlation $r = 0.66$,

Figure 2. The percentage (%) of successful attacks by mimic bicour fangblennies (*P. laudandus*) in relation to (i) time spent within 30 cm of models (*M. atrodorsalis*) (white diamonds) and (ii) ratio of models to mimics (black circles); $n = 40$.

$n = 40$, $p < 0.001$; successful attacks (%): Pearson's correlation $r = 0.64$, $n = 40$, $p < 0.001$; figure 2).

The maximum number of models and mimics found in one location was four models and two mimics, and a maximum of three mimics were found in the same location. Nine individual mimics were found without a model in close proximity. The ratio of models to mimics at each location was correlated with the percentage of successful attacks (Spearman rank $r_s = 0.43$, $n = 40$, $p = 0.005$; figure 2).

The total number of potential victims/predators ranged from 5 to 81 species (mean $\pm$ s.d.: 36.0 ± 20.1). The number of potential victims/predators did not significantly account for variation in the total number of attacks ($t = 0.20$, $p = 0.84$) or the proportion of successful attacks (%) ($t = 0.34$, $p = 0.72$).

(b) Replicas of *P. laudandus*

A total of 1230 fish approached the replicas during 104 trials. Piscivores included wrasses (Labridae; mainly *Epibulus insidiator* and *Cheilinus diagrammus*), groupers (Serranidae; mainly *Cephalopholis cyanostigma*) and snappers (Lutjanidae; mainly *Lutjanus fulvivittatus*). On reefs where there were no mimics and models present (Lizard Island), there were no differences in the number of predators that approached the true replica compared with the other replicas ($F_{3,21} = 1.19$, $p = 0.34$; figure 3a). However, at locations where both *P. laudandus* and *M. atrodorsalis* were present, significantly fewer predators approached the true replica of *P. laudandus* in comparison with manipulated replicas or the control replica of *P. rhinorhynchus* (range: 0–7 per 10 min; mean $\pm$ s.d.: 2.6 ± 1.4 ; repeated measures ANOVA: Lizard Island (with models and mimics): $F_{3,27} = 3.12$, $p = 0.04$, figure 3b; Pulau Hoga: $F_{3,21} = 9.95$, $p < 0.001$, figure 3c). Non-predators included damselfish (Pomacentridae), angelfish (Pomacanthidae), wrasses (Labridae) and surgeonfish (Acanthuridae) (range: 4–23 per 10 min; mean $\pm$ s.d.: 19.2 ± 10.4).

(c) Spectral capabilities of predators/victims viewing models and mimics

There was no overlap between the colours of replicas in the chromaticity diagram, and colours were distributed across different areas of the plot (figure 4); therefore, both fish have the theoretical capability of distinguishing between the various colours of the replicas.

4. DISCUSSION

This study provides empirical evidence that the *P. laudandus*–*M. atrodorsalis* mimicry system may be best described as Batesian–aggressive mimicry, as dual benefits are received by the mimic in terms of increased success in attacking reef fishes when in the presence of a model, independent of the number of potential victims in the local area, and a reduction in predation risk owing to mimetic resemblance. The avoidance of replicas by predators could have been a function of aposematic coloration, defined as the use of conspicuous coloration to warn potential predators they are chemically or otherwise defended, or an effect of increased detectability; however, we did not find an avoidance of *P. laudandus*-type mimics on reefs where *M. atrodorsalis* was not present. The relative benefits of increased foraging versus protection—both of which provide a significant fitness advantage—remains to be determined, and may underpin our understanding of the evolution of such mimicry systems.

Aggressive and Batesian mimics are typically understood to be in an evolutionary arms race (Dawkins & Krebs 1979) with signal receivers: mimics are under selection pressure to appear more similar to the models to prevent detection, while signal receivers are under selection to improve discrimination between models and mimics. In Batesian–aggressive mimicry, the selective agents driving the mimicry system are both predators and victims of attack, causing additional evolutionary pressures on the mimic to exist compared with either types of mimicry alone. Mimics may therefore evolve a more accurate resemblance to their models to ensure that they are not detected by a wide range of signal receivers with varying visual and perceptual capabilities. Reef fishes certainly vary in their visual capabilities (Losey *et al.* 2003), and therefore mimics may have to appear visually similar to each type of system to prevent discrimination. Indeed, the seemingly exact mimicry of *P. laudandus*–*M. atrodorsalis* could be a result of simultaneous defence from predators and foraging selection by prey.

In both Batesian and aggressive mimicry systems, mimics benefit from their resemblance to the model, while models incur costs (Huheey 1988; Côté & Cheney 2004, but see Rowland *et al.* 2007). In Batesian mimicry, models typically display a warning signal which predators learn to avoid. If predators come into contact with palatable Batesian mimics displaying similar warning signals, then predator learning is disrupted and models incur costs in the form of increased attack rates from predators. Similarly, in aggressive mimicry systems, mimics impose costs on their models including reduction in foraging rates (Côté & Cheney 2004), reduced reproductive opportunities and/or death (Lloyd 1965). However, in the *P. laudandus*–*M. atrodorsalis* system, predators will receive an adverse stimulus from aggressive

Figure 3. The mean number of approaches by predators and non-predators towards replicas at (a) Lizard Island (no models/mimics present), (b) Lizard Island (models/mimics present), and (c) Pulau Hoga (models/mimics present). Error bars represent 1 s.e.m. Asterisk indicates significant difference from other bars (least significant difference post hoc, $p < 0.05$).

mimics (in terms of being attacked), and therefore models could potentially benefit from the presence of mimics, as predators will learn to avoid both models and mimic. Thus, this mimicry system could also include aspects of Müllerian mimicry, defined as two or more defended species that evolve to resemble one another to enhance predator learning (Müller 1879). Instead of *M. atrodorsalis* models evolving new colour patterns to escape its mimic, the model and mimic may evolve to resemble one another. However, whether *P. laudandus* mimics do benefit *M. atrodorsalis* in this mimicry system remains to be determined.

Plagiotremus laudandus may enhance their foraging success as a Batesian mimic if they alter their behaviour in the presence of a model, for example, by spending more time in the open or less time engaging in anti-predator behaviour. However, behavioural observations

of *P. laudandus* suggest that there is no difference in such activities between individuals that spend a lot of time with models compared to those that do not (K. L. Cheney 2006–2007, unpublished data). Further observations should be conducted to confirm this.

Empirical data should be collected on other types of putative Batesian–aggressive mimicry systems. For example, the false cleanerfish (*Aspidontus taeniatus*) closely resembles cleaner wrasse (*Labroides dimidiatus*) (Wickler 1968). Instead of removing ectoparasites from client reef fishes, these mimics have also been observed to attack fishes to remove scales, fins and body tissue. The mimic is reported to use its resemblance to cleaner fish in order to attract clients. However, recent studies have shown that the fangblenny mimic is rarely observed attacking fishes (K. L. Cheney 2006–2008, unpublished data; Moland *et al.* 2005). Indeed, fish eggs and demersal

Figure 4. The trichromatic visual system of *L. bohar* (predator), dark circles, and *A. nigroris* (victim) open circles, represented by a two-dimensional chromaticity diagram corresponding to the photoreceptor noise-limited colour opponent model. The colours from the replica models were plotted according to eqn (B5) in Kelber *et al.* (2003). Chromaticity values that plot at a distance of less than one unit are unlikely to be discriminable along that axis. As plots increase in distance from one another, colours are more distinguishable. The origin corresponds to all achromatic colours including white, black and grey.

material are found more frequently in their diet (Kuwamura 1981). Therefore, fangblennies may also benefit from protection from predation by resembling the cleaner fish, which is thought to be generally immune from predation (Côté 2000).

This is the first study, to my knowledge, to provide empirical evidence that dual benefits can be bestowed on a mimic, and may demonstrate a system in which multiple selective agents can drive the evolution of a mimetic species. Despite the intuitive appeal of classifying mimicry systems under discrete, mutually exclusive headings such as Batesian, Müllerian, aggressive, or reproductive mimicry, such a classification system appears to be too simplistic. Indeed, a number of recent papers have questioned the classification of mimicry systems. For example, traditional Batesian versus Müllerian mimicry classification has been challenged by the quasi-Batesian mimicry theory (Speed 1999; Speed & Turner 1999). Mimicry systems are perhaps not such a clear dichotomy as has been previously supposed, and many examples may lie on a mimicry spectrum in which there is overlap between mimicry categories.

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REFERENCES

- Bates, H. W. 1862 Contributions to an insect fauna of the Amazon Valley. Lepidoptera: Heliconidae. *Trans. Linn. Soc. Lond.* **23**, 495–566. (doi:10.1111/j.1096-3642.1860.tb00146.x)
- Bateson, W. 1892 The alleged ‘aggressive mimicry’ of *Volucellæ*. *Nature (Lond.)* **46**, 585–586. (doi:10.1038/046585d0)
- Caley, M. J. & Schluter, D. 2003 Predators favour mimicry in a tropical reef fish. *Proc. R. Soc. Lond. B* **270**, 667–672. (doi:10.1098/rspb.2002.2263)
- Cheney, K. L. & Côté, I. M. 2007 Aggressive mimics profit from a model-signal receiver mutualism. *Proc. R. Soc. B* **274**, 2087–2091. (doi:10.1098/rspb.2007.0543)
- Cheney, K. L., Skogh, C., Hart, N. S. & Marshall, N. J. 2009 Mimicry, colour forms and spectral sensitivity of the blue-striped fangblenny, *Plagiotremus rhinorhynchus*. *Proc. R. Soc. B* **276**, 1565–1573. (doi:10.1098/rspb.2008.1819)
- Côté, I. M. 2000 Evolution and ecology of cleaning symbioses in the sea. *Ocean. Mar. Biol. Ann. Rev.* **38**, 311–355.
- Côté, I. M. & Cheney, K. L. 2004 Distance-dependent costs and benefits of aggressive mimicry in a cleaning symbiosis. *Proc. R. Soc. Lond. B* **271**, 2627–2630. (doi:10.1098/rspb.2004.2904)
- Cott, H. B. 1940 *Adaptive coloration in animals*. London, UK: Methuen.
- Dawkins, R. & Krebs, J. R. 1979 Arms races between and within species. *Proc. R. Soc. Lond. B* **205**, 489–511. (doi:10.1098/rspb.1979.0081)
- Evans, H. E. & Eberhard, M. J. W. 1970 *The wasps*. Ann Arbor, MI: University of Michigan Press.
- Huheey, J. E. 1988 Mathematical models of mimicry. *Am. Nat.* **131**, S22–S41. (doi:10.1086/284765)
- Kelber, A., Vorobyev, M. & Osorio, D. 2003 Animal colour vision: behavioural tests and physiological concepts. *Biol. Rev.* **78**, 81–118. (doi:10.1017/S1464793102005985)
- Kuwamura, T. 1981 Mimicry of the cleaner wrasse *Labroides dimidiatus* by the blennies *Aspidontus taeniatus* and *Plagiotremus rhinorhynchus*. *Nanki Seibutu* **23**, 61–70.
- Lloyd, J. E. 1965 Aggressive mimicry in *Photuris*: firefly females fatales. *Science* **149**, 653–654. (doi:10.1126/science.149.3684.653)
- Loosey, G. S. 1972 Predation protection in the poison-fang blenny *Meiacanthus atrodorsalis*, and its mimics, *Ecsenius bicolor* and *Rumula laudandus* (Blenniidae). *Pac. Sci.* **26**, 129–139.
- Loosey, G. S., McFarland, W. N., Loew, E. R., Zamzow, J. P., Nelson, P. A. & Marshall, N. J. 2003 Visual biology of Hawaiian coral reef fishes. I. Ocular transmission and visual pigments. *Copeia* **2003**, 433–454. (doi:10.1643/01-053)
- Lythgoe, J. N., Muntz, W. R. A., Partridge, J. C., Shand, J. & Williams, D. M. 1994 The ecology of the visual pigments of snappers (Lutjanidae) on the Great Barrier Reef. *J. Comp. Physiol.* **174**, 461–467. (doi:10.1007/BF00191712)
- Malcolm, S. B. 1990 Mimicry: status of a classical evolutionary paradigm. *Trends. Ecol. Evol.* **5**, 57–62. (doi:10.1016/0169-5347(90)90049-J)
- Moland, E. & Jones, G. P. 2004 Experimental confirmation of aggressive mimicry by a coral reef fish. *Oecologia (Berl.)* **140**, 676–683. (doi:10.1007/s00442-004-1637-9)
- Moland, E., Eagle, J. A. & Jones, G. P. 2005 Ecology and evolution of mimicry in coral reef fishes. *Ocean. Mar. Biol. Ann. Rev.* **43**, 455–482.
- Müller, F. 1879 Ituna and Thyridia: a remarkable case of mimicry in butterflies. *Proc. Entomol. Soc. Lond.* **1879**, 20–29. [R. Meldola, Transl.]
- Pasteur, G. 1982 A classificatory review of mimicry systems. *Ann. Rev. Ecol. Syst.* **13**, 169–199. (doi:10.1146/annurev.es.13.110182.001125)
- Pfennig, D. W., Harcombe, W. R. & Pfennig, K. S. 2001 Frequency-dependent Batesian mimicry. *Nature* **410**, 323. (doi:10.1038/35066628)
- Pough, F. H. 1988 Mimicry of vertebrates: are the rules different? *Am. Nat.* **131**, S67–S102. (doi:10.1086/284767)

- Poulton, E. B. 1904 The mimicry of Aculeata by the Asilidae and *Vohucella*, and its probable significance. *Trans. Entomol. Soc. Lond.* **1904**, 661–665.
- Randall, J. E., Allen, G. R. & Steene, R. 1997 *Fishes of the Great Barrier Reef and Coral Sea*. Bathurst, New South Wales, Australia: Crawford House.
- Rettenmeyer, C. W. 1970 Insect mimicry. *Annu. Rev. Entomol.* **15**, 43–74. (doi:10.1146/annurev.en.15.010170.000355)
- Rowland, H. M., Ihalainen, E., Lindström, L., Mappes, J. & Speed, M. P. 2007 Co-mimics have a mutualistic relationship despite unequal defences. *Nature* **448**, 64–67. (doi:10.1038/nature05899)
- Speed, M. P. 1999 Batesian, quasi-Batesian or Mullerian mimicry? Theory and data in mimicry research. *Evol. Ecol.* **13**, 755–776. (doi:10.1023/A:1010871106763)
- Speed, M. P. & Turner, J. R. G. 1999 Learning and memory in mimicry. II. Do we understand the mimicry spectrum? *Biol. J. Linn. Soc.* **67**, 281–312. (doi:10.1111/j.1095-8312.1999.tb01935.x)
- Springer, V. G. & Smith-Vaniz, W. F. 1972 Mimetic relationships involving fishes of the family Blenniidae. *Smithson. Contrib. Zool.* **112**, 1–36.
- Starrett, A. 1993 Adaptive resemblance: a unifying concept for mimicry and crypsis. *Biol. J. Linn. Soc.* **48**, 299–317. (doi:10.1111/j.1095-8312.1993.tb02093.x)
- Vorobyev, M. & Osorio, D. 1998 Receptor noise as a determinant of colour thresholds. *Proc. R. Soc. Lond. B* **265**, 351–358. (doi:10.1098/rspb.1998.0302)
- Vorobyev, M., Brandt, R., Peitsch, D., Laughlin, S. B. & Menzel, R. 2001 Colour thresholds and receptor noise: behaviour and physiology compared. *Vision Res.* **41**, 639–653. (doi:10.1016/S0042-6989(00)00288-1)
- Wickler, W. 1968 *Mimicry in plants and animals*. New York, NY: McGraw-Hill.
- Zabka, H. & Tembrock, G. 1986 Mimicry and crypsis: a behavioral approach to classification. *Behav. Process.* **13**, 159–176. (doi:10.1016/0376-6357(86)90023-9)