

# Evolutionary implications of deception in mimicry and masquerade

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**Abstract** Aggressive mimicry occurs when an organism resembles some aspect of another organism (the model) in order to obtain prey through its deceptive resemblance. This may function either through the overt response of the receiver or through the lack of response of the receiver. Reviewing selected examples, I discuss some of the difficulties in ascribing a model for the mimic. I also discuss how a single animal can have multiple ploys in its armoury of deceptive signals, thus belonging within two or more categories of deceptive signalling. In addition to aggressive mimicry, these may include crypsis or camouflage, masquerade (mimicry of inanimate objects), and Batesian or protective mimicry. Each of these examples of deception has multiple evolutionary pathways, and some deceptive signals may be more costly to receivers than others, but no single organism is subject to a single selection pressure, leading to the reality that many evolutionary pathways contribute to the diversity we see around us. New technologies are opening new channels of investigation into deceptive signaling in many different sensory modalities, and this is reflected in the recent increase in studies investigating the structure and function of deceptive signals. In turn, these studies are beginning to expose the fascinating complexity of deceptive signaling systems, allowing us to discover the myriad, non-mutually exclusive, solutions that can be selected for to obtain prey [*Current Zoology* 60 (1): 6–15, 2014].

**Keywords** Mimicry, Masquerade, Crypsis, Deceptive communication, Cleaner fish, Pre-existing biases

## 1 Introduction

In aggressive mimicry an organism resembles some aspect of another organism (the model) in order to obtain prey through its resemblance to the model. Receivers pay a direct cost, such as injury or death (e.g., Jackson and Wilcox, 1993; Cheney and Côté, 2005), in responding to these types of deceptive signals. However, deceptive signals can evolve as long as, on balance, the suite of potential receivers don't pay a fitness cost by responding to deceptive signals. This is achieved through frequency-dependent selection, because on average the model on which the deceptive signal is based is more common than the mimic, and responding to the model confers benefits to the receiver (Bradbury and Vehrencamp, 1998; Pfennig et al., 2001; McGregor, 2004; Skelhorn et al., 2011). However, it is often difficult to determine the precise origin of these deceptive signals. Here, I argue that the deceptive signals should be considered in terms of their function. I also argue that as evolution acts on the phenotype, a signal or suite of signals may serve multiple purposes, rather than arising through a single one of the three functional evolutionary pathways (predator protection, reproduction

and finding food), which are all too often regarded separately.

A classic example of aggressive mimicry is that of firefly *femmes fatales* (Lloyd, 1965). Here, females of several species of *Photuris* fireflies mimic the bioluminescent flashes used as courtship displays by females in other genera to attract conspecific males. The timing characteristics of the bioluminescent flashes made by fireflies are used as species-specific courtship signals. Males signal a display, which is answered by a female, which in turn attracts the male to the source of the female response. The mimic, *Photuris*, uses deceptive responses to the displays of several species to lure these species' males toward them and capture them as prey (Lloyd, 1975, 1984).

In comparison to work on other types of mimicry, aggressive mimicry has received relatively little attention, and with notable exceptions, such as the firefly *femmes fatales*, it is only in the last two decades that good evidence of this widespread phenomenon has emerged. Aggressive mimics have been found in several taxa, notably among arthropods, snakes, and fish. Reviewing selected examples from these groups, I aim to tease apart some of the classification issues that have

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overwhelmed the field of deceptive signalling (e.g., Randall, 2005; Stevens and Merilaita, 2009; Skelhorn et al., 2010).

An important problem is that the word mimicry brings with it an inherent desire to search for the model that is being mimicked. While some deceptive signals of aggressive mimics are of a specific organism (e.g., a specific species of ant), or of a generic type of organism (e.g., ants in general), in other cases what is resembled is not an identifiable organism, or something else that is easily defined (such as a twig or bird dropping). The key to successful aggressive mimicry is that the receiver's response (or, in some cases, lack thereof) to the signal is repeatable, and thus can be selected for in the sender. In other words, deceptive signals can evolve through any channel that can be exploited and do not require that the signal 'resemble' an organism, merely that the target receivers' behaviour benefits the signaler.

Our sensory world perceives distinct objects and hence we tend to search for specific objects as models (e.g., Sazima, 2002; Randall, 2005; Reiserer and Schuett, 2008), rather than frameworks based on the sensory systems or perceptual worlds of receivers, which might be the evolutionary pathway usurped by the mimic (e.g., receiver psychology, Guilford and Dawkins, 1991; see Moore, 2013 for a similar view on host manipulation by parasites). These pre-existing biases, either at a sensory level or at a more cognitive level, exist by being beneficial to the receiver for tasks such as detecting food or mates (Basolo, 1990).

Aggressive mimics obtain food either because they resemble a precise species, a generic type of organism (such as 'ants'), or a stimulus that triggers in the sensory or cognitive make-up of a receiver a response which is beneficial to the sender but which might cost the receiver its life (even though on average it is still beneficial for the receiver to respond to the signal), such as a movement pattern characteristic of prey. The latter concept has recently been termed 'exploitation of perceptual biases', or EPB (Schaefer and Ruxton, 2010). The EPB model usefully encompasses the narrower existing definitions of 'sensory exploitation', which emphasises sensory biases, and 'sensory traps', which emphasises cognitive biases, among others (see Endler and Basolo, 1998). Ruxton and Schaefer (2011) argue that mimicry differs from EPB in that only in mimicry is misidentification (of a specific model) involved, while EPB requires only generalisation of a signal that is favourable (on average) to the receiver and, as there is no specific model, no spatiotemporal overlap between

a model and the sender is required.

Another complication with animal deception is that communication theory is based on the premise that signals elicit responses, yet there are numerous instances of animals using deception precisely so as *not* to elicit responses. For example, many animals use cryptic signals, such as colouration to match the background, that function to avoid detection by predators that otherwise might have perceived and attacked the prey. Despite the active wording of the term 'aggressive mimicry', this too can function either by eliciting an overt response from the receiver or through a lack of response (a wolf in sheep's clothing), but this distinction is rarely acknowledged. For example, a spider may mimic the chemical signature of an ant to raid ant nests undetected as an intruder (Allan and Elgar, 2001). In contrast, as mentioned, a firefly may mimic the bioluminescent signals of females of a different species to 'actively' lure males of that species to them (Lloyd, 1965). Yet, from the deceptive sender's point of view of trying to obtain a meal, the evolutionary pathways leading to overt response or lack of response by receivers are the same.

A final thorn in the mix is that aggressive mimicry, like all forms of mimicry, is not a discrete category, but lies at the very least on a continuum, sometimes with Batesian mimicry, where a mimic co-opts a signal of a well-defended model in order to deter predators, or Müllerian mimicry, where multiple organisms share a common signal to advertise their unpalatability. In the latter case, different mimetic species may vary in their level of distastefulness, and hence in the cost paid by potential predators, with the concomitant effect that some Müllerian mimics may be "quasi-Batesian" and may dilute the honesty of the signal (Speed et al., 2000). Other times this continuum is shared with masquerade, or mimicry of inanimate objects such as twigs or pebbles, and probably with other phenomena such as crypsis, which can lie on its own continuum with masquerade (Skelhorn and Ruxton, 2011a,b). In discussing camouflage and crypsis, Stevens and Merilaita (2009) argue that the best way to differentiate between the many subtle mechanisms that animals use for concealment is how each variant functions to reduce predation, acknowledging that features are likely to vary along continua. However, no single organism is subject to a single selection pressure (as selection will act on avoiding predation, finding mates and finding food), leading to the reality that many evolutionary pathways and concomitant trade-offs contribute to the diversity we see

around us. On the face of it, this makes a consideration of the function of the deceptive signal somewhat difficult to evaluate, as often these signals may serve a plurality of functions. Furthermore, preconceived ideas of what the target organism (the 'intended' receiver) might be can blinker our understanding of the scope of the phenomenon. Using examples of aggressive mimicry for the 'purpose' of obtaining prey (sometimes known as feeding or foraging mimicry), I will highlight and clarify these issues.

## 2 Aggressive Mimicry through Overt Receiver Response: The Classic Phenomenon

Ambush predators require prey to wander past them sufficiently close for an attack, and because they don't actively seek prey, these predators may be subject to a lower frequency of encounters with prey than active predators. In fish (the only group in which fitness parameters associated with encounter rates of ambush phenotypes versus more active phenotypes have been measured), this is partially compensated for by the lower metabolic costs of inactivity (Kobler et al., 2009). Other mechanisms used by ambush predators to compensate for reduced encounter rates are morphological or behavioural attributes that function to lure prey within striking distance (e.g., Gawryszewski et al., 2012)

Famously, anglerfish lure prey by twitching a prey-like modified dorsal fin spine, sometimes containing bioluminescent bacteria within it, extended in front of the mouth (Wilson, 1937; Pietsch and Grobecker, 1978). However, the details of this classic example of aggressive mimicry remain poorly understood. Better understood is caudal luring, an analogous phenomenon found in many snake families. This behaviour consists of a distinct wriggling or twitching of the distal portion of the tail, which attracts the attention of nearby animals, such as frogs and lizards (Neill, 1960; Heatwole and Davison, 1976; Sazima, 1991; Leal and Thomas, 1994; Reiserer, 2002; Hagman et al., 2008; Reiserer and Schuett, 2008), seemingly lured towards the snake due to the possibility of the signal emanating from one of their own prey (notably arthropods). If the 'target' frog or lizard is unlucky, this approach leads to a successful strike by the snake.

In a spider example of *femmes fatales*, late instar juveniles and adult female bolas spiders (*Mastophora* spp.) hunt using a web reduced to a sticky ball (the bolas)

suspended on the end of a short vertical thread that is attached to a single horizontal line strung between twigs. An allomone emitted by the spider mimics the sex pheromones of female moths and attracts male moths upwind toward the source of the smell (Eberhard, 1977; Stowe et al., 1987). Once a moth is within striking range, the spider, which in the predatory position holds the thread connected to the bolas with one of her two anteriormost pairs of legs, swings the bolas to snare the moth before drawing it in or climbing down the thread to paralyze it. Yet another sensory modality is used by the jumping spider (Salticidae) *Portia fimbriata*, which lures females of the salticid *Euryattus* sp. out of their nests in rolled-up leaves by imitating the vibrations made by courting male *Euryattus*. Once exposed, *Portia* then attacks the vulnerable female *Euryattus* (Jackson and Wilcox, 1990).

In these examples we have apparently clear-cut cases of predators luring potential prey toward them using a deceptive signal in any one of a number of different sensory modalities. In each of these cases the signal produces an overt behavioural response from the receiver, the potential prey. The signal sender - the mimic - in these instances clearly benefits from the receiver's active response to the deception. The receiver in these instances pays with its life, but under more common and less Machiavellian circumstances would benefit from finding a mate (bolas spider; *Euryattus* sp.) or prey (fish; lizards and toads). Thus, on average, it pays for the receiver to respond to these signals.

## 3 Aggressive Mimicry through Non-Response of Receivers

For those predators that can survive their defences, ants provide an inexhaustible source of food, and as they rely primarily on chemoreception to discriminate between nestmates and non-nestmates (Hölldobler and Wilson, 1990), they are vulnerable to chemical mimics. Aggressive mimicry of ants is found among spiders, arthropods of a similar size and sharing a similar niche and habitat to ants. Usually this is achieved through posing as an ant so as to avoid the defensive behaviour typically invoked by intruders. The jumping spider *Cosmophasis bitaeniata* is a chemical mimic of the weaver ant *Oecophylla smaragdina*. This spider does not biosynthesise the cuticular hydrocarbons of its model, but instead, by eating ant larvae, acquires the colony-specific chemical signature that allows it to penetrate its host nest to steal its larvae as prey (Allan and Elgar, 2001; Elgar and Allan, 2004), in a 'wolf in

sheep's clothing' approach. Normally, penetration of the nest by an intruder would provoke attack by the ants, but under the guise of a colony member, the spider is able to do this unharmed, although how *C. bitaeniata* enters the nest to eat larvae in the first place is unclear. A similar approach is taken by the zodariid spiders *Zodarion germanicum* and *Z. rubidium*. These spiders kill an ant and then walk through a group of ants holding the dead ant in front of it. The ant's body transmits the odour cue that allows *Zodarion* to continue foraging (Pekár and Král, 2002).

These examples illustrate that animals also use deceitful signals that rely on the non-response of receivers in order to gain access to prey. Often these cases rely on the deceptive signal enabling the predator to move among prey because the predator is misidentified by the model, which is also the target receiver for aggressive mimicry, as one of its own.

#### 4 The Elusive Search for A Model

While snake caudal luring has often been described as vermiform (Green and Campbell, 1972; Heatwole and Davison, 1976; Shine, 1980; Chiszar et al., 1990; Sazima, 1991; Rabastky and Farrell, 1996), suggesting caterpillars or insect larvae as models, specific experiments addressing this hypothesis are lacking. Lack of experimental work designed to search for what constitutes the model and how the deceptive signal actually functions is not uncommon (e.g., see Skelhorn et al., 2011), with intuition based on our perception seeming to be taken as evidence even to this day (e.g., Lev-Yadun, 2009).

Caudal luring often seems to have more than one distinct movement characteristic (Rabastky and Farrell, 1996; Hagman et al., 2008) and in fact, for each of the different types of movement the only evidence so far suggests that a specific, humanly identifiable, model may be unimportant (Nelson et al., 2010). Lizards are particularly effective at eliciting luring behaviour by death adders, *Acanthophis antarcticus*, and are especially prone to respond to the signal by approach when compared with frogs (Hagman et al., 2008). Recent results suggest that death adders mimic the motion characteristics of invertebrates, rather than resembling specifically a caterpillar or worm (Nelson et al., 2010). Nelson et al. (2010) collected all invertebrates found in the territories of the jacky lizard *Amphibolurus muricatus*. These were then filmed in order to extract velocity characteristics of different prey types during locomotion, resulting in a bimodal distribution of potential prey ve-

locity. Experiments using 3D animation of a single prey item ('cybercricet') moving at different speeds showed that jacky lizards attacked cybercricet when it moved at the speeds of the most frequently found invertebrates, again showing a bimodal distribution. Based on footage of death adder luring behaviour with both fast and slow lures, as exhibited in the different motion patterns of the lures of these snakes (Carpenter et al., 1978; Hagman et al., 2008), 'cybersnake' was presented to jacky lizards and elicited predatory responses. The velocity characteristics of each of the two luring movements overlapped with the two peaks in the bimodal prey distribution (Fig. 1). Here, perhaps we could define the model as two distinct movement patterns characteristic of common prey; this seems entirely plausible and highlights the limitations of basing our conclusions on our own perception (e.g., Moore, 2013).

Caudal-luring in several species of snakes from different taxa (e.g., Australian death adders, American copperheads, massasauga rattlesnakes, African horned adders) appears to be triggered by some prey types and not others. Furthermore, there are interspecific (Reiserer, 2002) as well as intraspecific differences based on geographical distribution (Reiserer and Schuett, 2008), and luring is elicited most readily by prey taxa that are most likely to respond to it. All of these factors suggest that aggressive mimicry, rather than EPB, is the possible evolutionary origin of a signal that is evidently not classically mimetic in the sense that a conceivable entity is the model. Were caudal luring solely due to EPB, we would expect species to be successfully lured without the presence of the putative model (e.g., matching prey movement) in the field, but comparative research in this area is lacking.

In addition to models being somewhat problematic to define, a given animal may use any one of a number of different approaches based on deception to obtain prey. Possibly the best example of this are jumping spiders in the genus *Portia*. These spider-eating salticids invade other spiders' webs and lure the resident spider towards them. To achieve this without eliciting an attack from the resident, *Portia* either uses species-specific innate plucking routines using a combination of the abdomen, legs and pedipalps, or trial-and-error to derive an effective plucking scheme (Jackson and Blest, 1982; Jackson and Wilcox, 1993; Tarsitano et al., 2000; Jackson and Nelson, 2011). The resident spider is slowly drawn to investigate, whereupon *Portia* pounces on it. This is a clear example of aggressive mimicry by overt response, although the 'model' is simply a display that produces a

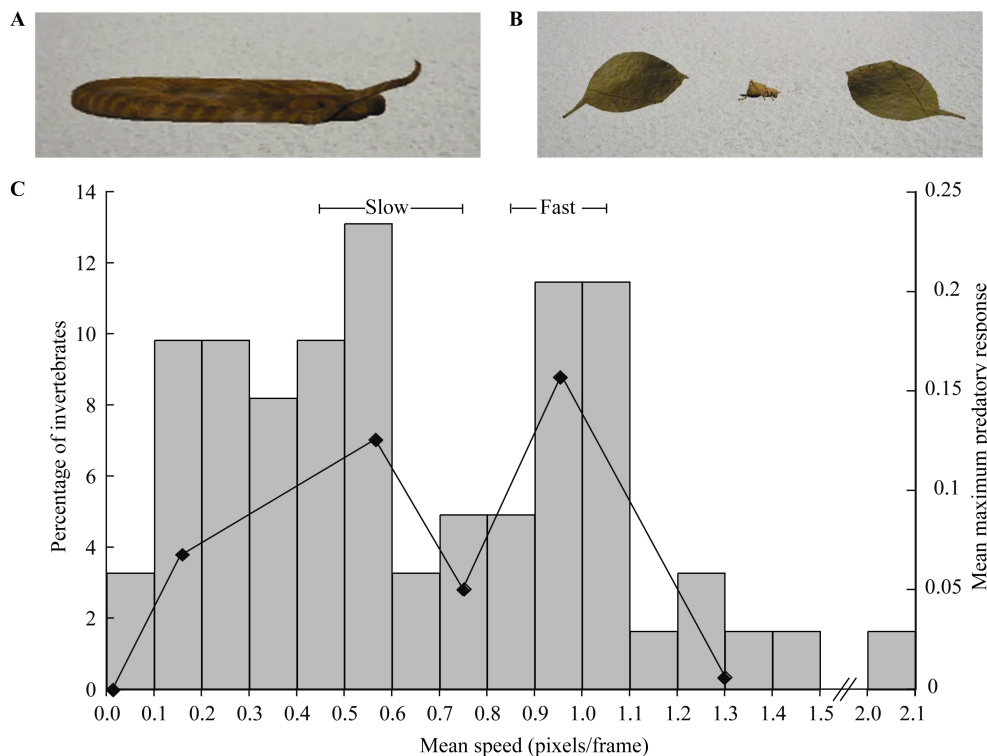
safe overt luring response, rather than something more specific (Tarsitano et al., 2000).

## 5 Aggressive Masquerade and Aggressive Mimicry

Animals that resemble either parts of objects, or whole objects found in the environment that a potential predator might find inedible, such as leaves, twigs, bird droppings or stones, and as a consequence are misclassified by potential predators or prey (receivers), are said to be using masquerade. In contrast to mimicry, any change in the population or evolutionary dynamics of the model will be through the direct action of the masquerador (such as leaf masquerading insects eating the leaves of their host plant), rather than through changes in the behaviour of the receiver that may have evolutionary implications on both model and mimic, such as in mimicry. Masquerade can be defensive or ‘aggressive’ when the resemblance serves to increase the mas-

querador’s access to prey (Skelhorn et al., 2010).

This distinction can also be illustrated by *Portia*, as species in this genus resemble detritus. This morphology is especially important to *P. fimbriata* because it preys on other jumping spiders - and being jumping spiders they have excellent vision (Harland and Jackson, 2004). When stalking a salticid, *Portia* adopts a particular gait, known as cryptic stalking, in which it moves in a choppy stop-and-start manner. If the salticid turns to face detected movement, *Portia* freezes in mid-step until the salticid, presumably ‘thinking’ that the movement detected was light funnelling through the canopy and bouncing off detritus, turns around again (Harland and Jackson, 2001). It seems that *Portia* is an aggressive masquerador when stalking other salticids, or an aggressive mimic when simulating the courtship vibrations of male *Euryattus* or when luring alien web spiders by simulating the vibrations of a struggling insect caught in the web.



**Fig. 1** A. Frame from ‘cybersnake’ movie. B. Frame from ‘cybercricket’ movie with two ‘cyberleaves’ for the cricket to turn around for another transect across the screen. C. Close correspondence of prey speeds, lizard predatory responses and death adder caudal luring speed

Histogram of the distribution of speeds for 61 invertebrate prey items found in jacky dragon territories. Speed bins are 0.10 pixels/frame (25 fps). Lines above histogram depict speed ranges for the two caudal lure speeds of death adders. Solid line represents the mean maximum predatory response of jacky dragons ( $n = 31$ ) toward cybercricket moving at six different speeds (0, 3.35, 12.26, 16.83, 20.77, and 28.32  $\text{mm s}^{-1}$ ) within the range found in invertebrates. Predatory responses were scored as no response, visual orienting, hesitant approach and substrate licking, and rapid approach or lunging toward the screen scored using a 0 (no response) to 3 on an ordinal scale. Note clear bimodal pattern of predatory response matching that of prey speed distribution, which is overlapped by caudal luring speeds. Adapted from Nelson et al. (2010).

## 6 The Batesian-Aggressive Mimicry Continuum

Traditionally, aggressive mimicry has been classified as resemblance to another organism in order to obtain food, and Batesian mimicry as resemblance to another organism for protection from predators averse to the model (Cott, 1940; Edmunds, 1974). As we learn the intricacies of predator prey interactions in more detail, we find more and more exceptions and difficulties with this and related mimicry terminology (see Schaefer and Ruxton, 2010; Skelhorn et al., 2010). While conceptually Batesian and aggressive mimicry seem poles apart, recent evidence suggests that this might not always be the case. This is not surprising, as nature is not discrete and selection pressure is manifold, and highlights the need to acknowledge that an individual can belong in two (or more) categories, as suggested over twenty years ago by Malcolm (1990). As illustrated below, it is entirely plausible that the same signal, or suite of signals, may be useful to the sender in different contexts, such as protection from predators and to obtain food. These may not always be on a sliding gradient, and may simply be two functions based on the same signal, but certainly this is a testable hypothesis in much need of work.

*Photuris femmes fatales* are textbook examples of aggressive mimics, but it turns out that the predator sequesters defensive steroids (lucibufagins) produced by *Photinus* males mistakenly attracted to *Photuris*' deceptive bioluminescent flashes. Through ingestion of *Photinus* males, *Photuris* obtains lucibufagins which it can not produce itself and which are aversive to potential predators, such as jumping spiders (Eisner et al., 1997). This may not be a model case of Batesian-aggressive mimicry, but it shows that multiple functions or benefits may be achieved by a single mechanism.

Clearer examples of the “kill two birds with one stone” approach to mimicry can again be found among jumping spiders, a group in which mimicry is unusually well-studied. Ant mimicry, or myrmecomorphy, has evolved multiple times in the Salticidae (Cushing, 1997). Myrmecomorphic spiders are typically characterised by a thin, elongated body, the creation of an antennal ‘illusion’ by waving the forelegs, and an erratic style of locomotion (Reiskind, 1977; Ceccarelli, 2008) and there is now considerable evidence that at least the genus *Myrmarachne* consists primarily, if not exclusively, of Batesian ant mimics that are avoided by ant-averse predators (reviewed in Jackson and Nelson, 2012). Ants

often prey on salticids (Nelson et al., 2004) and many salticids identify ants by sight and avoid both them (Nelson and Jackson, 2006) and *Myrmarachne*, apparently mistaking them for ants (Nelson and Jackson, 2006; Nelson et al., 2006).

*Myrmarachne melanotarsa* belongs to a minority of species (communal salticids) that live in individually occupied nests connected to each other by silk. *M. melanotarsa*'s nests are often embedded within those of other communal salticids (Jackson et al., 2008), that avoid proximity either with *M. melanotarsa* or its model, *Crematogaster* sp. (Nelson and Jackson, 2009a). *M. melanotarsa* often raids the nests of these ant-averse communal salticids to prey on their eggs and recently hatched juveniles (Jackson et al., 2008). Resembling ants functions as a predatory ploy for *M. melanotarsa*, as females of the communal salticids are significantly more likely to abandon their broods in the presence of *M. melanotarsa* or *Crematogaster* than in the presence of other heterospecific non-ant-like communal salticids (Nelson and Jackson, 2009b). Why communal salticids live in heterospecific groups that include *M. melanotarsa* is unknown, but it seems likely that the non-myrmecomorphic salticids gain secondary defensive advantages by living near to ants and their mimics through deterrence of ant-averse predators.

The blurred distinction between Batesian and aggressive mimicry has also been shown in cleaner fish and their mimics. Many reef areas are visited by fish that are attended to by other, smaller, fish that remove the ectoparasites from the ‘clients’. These ‘cleaning stations’ are by and large mutually beneficial to the client, whose parasite load is reduced, and to the cleaner fish, which obtains a meal. Consequently, clients are remarkably tolerant of small cleaner fish (Grutter, 1999; Bshary, 2001), and the system is subject to exploitation by mimics. This is particularly true if host parasite loads are high (Cheney and Côté, 2007), illustrating that the success of aggressive mimicry is influenced by the potential benefits accrued to the receiver, in addition to the frequency-dependence (apostatic selection) of mimic to model.

Through both morphological and behavioural mimicry of the cleaner wrasse *Labroides dimidiatus*, fangblennies *Plagiotremus rhinorhynchus* can approach a host fish and then, instead of feeding on the host's parasites, feed on its tissue and scales (Côté and Cheney, 2004). The resemblance of these two species, as objectively measured through spectral reflectance (Cheney et al., 2008; Cheney and Marshall, 2009), is uncanny. Côté

and Cheney (2007) argue that, besides functioning as aggressive mimicry, there is a Batesian mimicry component to the system because host fish are reluctant to chase and attack what they might perceive as a misbehaving cleaner fish. Additionally, this may be an example of the continuum between camouflage and mimicry, as *P. rhinorhynchos* use visual cues (Cheney et al., 2009) to also rapidly change colour such that they can blend in with a shoal of reef fish (typically *Pseudanthias* spp. and *Leptojulius cyanopleura*), but be facultatively mimetic with *L. dimidiatus* (Côté and Cheney, 2005; Cheney et al., 2008). This may allow the camouflaged fish to change colour in the presence of *L. dimidiatus* and suddenly emerge from a shoal to attack passers-by in the guise of a cleaner fish.

Another convincing coral reef example is that of the fangblenny *P. laudandus*, which is a mimic of the blenny *Meiacanthus atrodorsalis*. When attacked, the blenny can inflict a toxic bite to the attacker and is also promptly released by the predator when taken into the mouth. Consequently, mimicry by the fangblenny is thought to be defensive (Losey, 1972). Because *P. laudandus* can also attack passing fish to feed on scales, fins and tissue by blending in with a group of *M. atrodorsalis*, it is also an aggressive mimic (Losey, 1972; Cheney, 2010), but there is potentially a Müllerian mimicry component to this system. In contrast to Batesian mimicry, in Müllerian mimicry two or more species with aversive characteristics resemble each other (thus being relatively honest signal senders). In this case, some benefits might also accrue to the model, as predators may learn not to attack them (Cheney, 2010), potentially making this an example of a Batesian-aggressive-Müllerian mimicry system.

Often aggressive mimicry is described as the resemblance of harmless models, which allows the mimic to approach and prey on the model itself or on deceived third parties (Wickler, 1968, Malcolm, 1990). However, in the context of feeding, ‘aggressive mimicry’ seems an appropriate label for *M. melanotarsa* because, by relying on other salticids mistaking them for ants and fleeing, they gain foraging access to nests containing eggs and young. *Myrmarachne melanotarsa* resembles *Photuris* or caudal luring snakes by evoking overt responses from other animals, with the critical difference that the target receiver that responds to *M. melanotarsa*’s aggressive mimicry signals is not *M. melanotarsa*’s prey but, instead, the prey’s guardian. While fireflies, *Portia*, and snakes mimic something other than predators to obtain a meal, *M. melanotarsa* mimics the parental sal-

ticid’s predator. This mimicry is not based on lulling the receiver into a false sense of security (either because it resembles harmless prey or one of its own kind), but by causing alarm.

It has been suggested that aggressive mimicry differs from Batesian mimicry in the relationship between model and target receiver because Batesian mimics “insert themselves into an antagonistic predator–prey interaction (where the models are the unpalatable prey)” whereas aggressive mimics “insert themselves into cooperative interactions” (Cheney and Côté, 2005). Later work with myrmecomorphic spiders and with reef fish (Nelson and Jackson, 2009b, Cheney, 2010) shows that this is not always the case. Furthermore, the idea that aggressive mimicry is selected by the “sexual or foraging behaviour of their prey” (Malcolm, 1990) is also not attested by these recent studies (Nelson and Jackson, 2009b, Cheney, 2010), nor in the numerous cases of mimicry among coral reef cleaner mimics (Sazima, 2002; Côté and Cheney, 2004; Moland and Jones, 2004; Randall, 2005), to name but a few examples. It has long been recognised that when two species have differentially aversive characteristics, the Müllerian-Batesian distinction becomes ambiguous and should be envisaged as ends of a continuum (Speed, 1999; Rowland et al., 2007). Perhaps Batesian, Müllerian and aggressive mimicry should in fact be envisioned as a triangle, as exemplified by the fangblenny *P. laudandus*, or, adding masquerade and crypsis, a pentahedron of mimicry space.

## 7 Concluding Remarks

When multiple trophic levels, from parasitism to outright predation, and several selective pressures are taken into account, the primary cause for the evolution of a signal may not be discernable. Deceptive signals do not require that the signal resemble an organism, and require simply that the target receivers’ behaviour benefits the signaler. Consequently, deceptive signals will evolve through any channel that can be exploited to this end. Current nomenclature is heavily based on function, which may be manifold (as shown here), context-dependent, and is all too often assumed or inferred (e.g., Lev-Yadun, 2009, see alternative explanations in Ruxton and Schaefer, 2011). It seems timely to start thinking about novel ways of testing the structure and function of deceptive signals, and indeed, in the last few years there has been a very positive trend toward testing hypotheses about function rather than assuming them based on our own perceptions (e.g., Niskanen and

Mappes, 2005; Skelhorn and Ruxton, 2010, 2011b; Halpin et al., 2012). We now have models of the visual systems of several taxa, as well as vibrometers, spectrometers, affordable mass spectrometry such as GC-MS to obtain chemical profiles, and other sophisticated equipment which for the first time truly allow us to test hypotheses concerning not only deceptive signaling in the visual domain (see Stoddard 2012), but in other modalities. If we drop preconceived notions and begin with an open mind, there seems little doubt we would advance further, and in a more unified manner produce interesting results across the board.

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