

Aggressive use of Batesian mimicry by an ant-like jumping spider

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Batesian and aggressive mimicry are united by deceit: Batesian mimics deceive predators and aggressive mimics deceive prey. This distinction is blurred by *Myrmarachne melanotarsa*, an ant-like jumping spider (Salticidae). Besides often preying on salticids, ants are well defended against most salticids that might target them as potential prey. Earlier studies have shown that salticids identify ants by their distinctive appearance and avoid them. They also avoid ant-like salticids from the genus *Myrmarachne*. *Myrmarachne melanotarsa* is an unusual species from this genus because it typically preys on the eggs and juveniles of ant-averse salticid species. The hypothesis considered here is that, for *M. melanotarsa*, the distinction between Batesian and aggressive mimicry is blurred. We tested this by placing female *Menemerus* sp. and their associated hatchling within visual range of *M. melanotarsa*, its model, and various non-ant-like arthropods. *Menemerus* is an ant-averse salticid species. When seeing ants or ant mimics, *Menemerus* females abandoned their broods more frequently than when seeing non-ant-like arthropods or in control tests (no arthropods visible), as predicted by our hypothesis that resembling ants functions as a predatory ploy.

Keywords: aggressive mimicry; Batesian mimicry; ant mimicry; deceit; predation

1. INTRODUCTION

Aggressive, Batesian and Müllerian mimicry are well-known examples of interspecific resemblance. Aggressive mimics deceive their prey and Batesian mimics deceive their predators. Models for the latter have unpalatable flesh, venom, weapons or other characteristics that deter the mimic's predators. Batesian mimics dishonestly advertise to predators that they have the aversive characteristics of their models (Bates 1862; Edmunds 1974). In Müllerian mimicry, two or more species with aversive characteristics resemble each other; thus representing 'honest' signals. However, when two species have differentially aversive characteristics the Müllerian–Batesian distinction becomes ambiguous, and it is often more realistic to envisage Batesian and Müllerian mimicry as ends of a continuum (Speed 1999; Rowland *et al.* 2007).

That the distinction between Batesian and aggressive mimicry is also subject to blurring was shown in a

recent study of fangblennies (*Plagiotremus rhinorhynchos*; Côté & Cheney 2007). By resembling a cleaner fish, the fangblenny can approach a host fish and then, instead of feeding on the host's parasites, feed on the host. Côté & Cheney (2007) argue that, besides functioning as aggressive mimicry, resembling cleaner fish also has a protective (Batesian mimicry) function for the fangblenny, as host fish are reluctant to deploy full, potentially damaging retaliatory attacks against what they perceive to be a misbehaving cleaner fish.

We consider an example in which a jumping spider (Salticidae) uses Batesian mimicry as a predatory ploy. Salticids have vision based on exceptional spatial acuity (Land & Nilsson 2002), allowing them to distinguish prey and predators from a distance and making them especially suitable for experiments on mimicry.

Ants often prey on salticids (Nelson *et al.* 2004) and, although comparable in size to typical salticid prey, ants have formidable defences, and many salticids identify ants by sight and avoid them (Nelson & Jackson 2006a), as an encounter with an ant is likely to end in the salticid's death (Nelson *et al.* 2004). *Myrmarachne* is a genus of ant-like (myrmecomorphic) salticids and other salticids are also known to avoid *Myrmarachne*, apparently mistaking them for ants (Nelson & Jackson 2006a,b; Nelson & Jackson *in press a*). It is now widely accepted that myrmecomorphy functions as Batesian mimicry for *Myrmarachne* (Cushing 1997); therefore, providing further evidence of this is not our objective. We consider instead whether *Myrmarachne melanotarsa* (Wesolowska & Salm 2002), a mimic of a cocktail ant (*Crematogaster* sp. indet., hereafter *Crematogaster*), uses Batesian mimicry as an aggressive mimicry ploy. Most species in the genus *Myrmarachne* appear to be generalist predators of insects, associating with, but not preying on, ants (Jackson & Pollard 1996). 'Araneophagy', or preferentially preying on spiders, is not uncommon among salticids, but *M. melanotarsa* has the distinction of being the only known example of a myrmecomorphic salticid that is also araneophagic (Nelson & Jackson *in press b*). *Myrmarachne melanotarsa*'s strategy is to raid nests (cocoon-like silk shelters) for the eggs and 'post-embryos' (recently hatched juveniles that remain in the nest, have limited mobility and do not feed) of ant-averse non-myrmecomorphic salticids (Jackson *et al.* 2008).

Myrmarachne melanotarsa belongs to a minority of species (the 'communal salticids') that live in individually occupied nests connected to each other by silk. *Myrmarachne melanotarsa*'s nests are often embedded within those of other communal salticids (Jackson *et al.* 2008). Two of these species, *Menemerus* sp. indet. and *Pseudicius* sp. indet. (hereafter *Menemerus*, *Pseudicius*), were used in our experiments.

Ants appear to have difficulty moving through spider nest complexes, and eggs and post-embryos left unattended for a short time in a nest complex may often be safe from ants, but *M. melanotarsa*, being a salticid, has little difficulty negotiating silk. Our hypothesis is that *M. melanotarsa* blurs the distinction between Batesian and aggressive mimicry by using its resemblance to ants as a predatory ploy. We predict that *Menemerus* females in nests with post-embryos will flee when they see ants and that, not distinguishing between ants and ant mimics, they will also flee when they see *M. melanotarsa*.

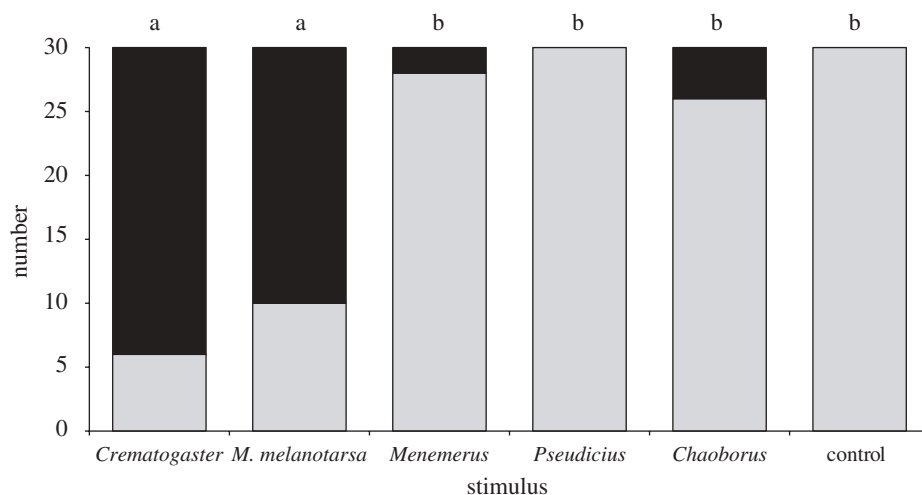


Figure 1. Frequency of test spider (*Menemerus* sp.) females remaining inside nest with hatchlings or vacating nest when surrounded by groups of 20 individual ants (*Crematogaster* sp.), ant-like salticids (*M. melanotarsa*), non-ant-like salticids (*Menemerus* sp. and *Pseudicius* sp.), midges (*Chaoborus* sp.) and empty stimulus chambers (control). All $n = 30$. Prior to test commencement all test spiders were within their nests. Letters denote significant differences ($p < 0.001$). Black, outside nest; grey, inside nest.

2. MATERIAL AND METHODS

Our field site and laboratory were in western Kenya (Thomas Odhiambo Campus of the International Center of Insect Physiology and Ecology). All spiders were from laboratory cultures (F2 generation, standard spider-laboratory procedures adopted, see Jackson *et al.* 2008). Insects were field-collected as needed. Work was carried out in 2007.

Before testing began, mated *Menemerus* females that had not yet laid eggs ('test spiders') were individually maintained in 'test chambers' (Petri dish, diameter 140 mm). In the test chamber, each test spider built a nest and oviposited in its nest. These spiders remained with the eggs and later with the post-embryos. Test chambers were checked daily and the morning after first seeing post-embryos in the nest, testing began (08.00) by placing one 'stimulus chamber' (Petri dish, diameter 55 mm) above, and another below, the test chamber, each centred on the nest. In control tests both stimulus chambers were empty. In experimental tests there were 10 individuals of one of the following per chamber (always the same species in each chamber): ant workers (*Crematogaster*, body length 3 mm); adult female ant mimic (*M. melanotarsa*, 3 mm); conspecific adult female (*Menemerus*, 5–6 mm); heterospecific adult female (*Pseudicius*, 5–6 mm), adult female midge (*Chaoborus* sp. indet., 4–5 mm, common prey of *Menemerus*; hereafter *Chaoborus*). Thirty test spiders were randomly assigned to each of the six treatments. Testing ended at 19.00, when we recorded the number of test spiders found away from their nests ('frequency of vacating nest'). The rationale for using *Menemerus*, *Pseudicius* and *Chaoborus*, all of these being sympatric non-ant-like arthropods similar in size to the mimic and the ant, was to ascertain whether *Menemerus*' decision to leave the nest was based on seeing a myrmecomorphic arthropod. Test spiders' vacate-or-remain decisions were compared across treatments using $2 \times 2 \chi^2$ and Fisher's exact tests of independence (using Bonferroni adjustments for multiple comparisons). All tests were two-tailed.

3. RESULTS

More test spiders vacated nests when ants or ant mimics were visible than when non-myrmecomorphic arthropods were visible or in the control (ants and ant mimics versus *Menemerus*, *Pseudicius*, *Chaoborus* and control, all $p < 0.001$, Fisher's exact tests) (figure 1). However, there was no significant difference between the number of test spiders that vacated nests when they could see any of the three non-myrmecomorphic arthropods and the number that vacated nests in the control (Fisher's exact test, $p = 0.335$, $n = 120$), and the number that vacated nests when

they could see any one of the non-myrmecomorphic arthropods was never significantly different from the number that vacated nests when they could see either one of the other non-myrmecomorphic arthropods (figure 1). There was also no difference between the number of test spiders that vacated nests when they could see ants and the number that vacated nests when they could see ant mimics ($\chi^2 = 1.36$, $p = 0.24$, $n = 60$). Overall, test spiders were significantly more likely to vacate their nests when they saw ants or ant mimics instead of non-myrmecomorphic arthropods ($\chi^2 = 72.0$, $p < 0.001$, $n = 150$).

4. DISCUSSION

'Aggressive mimicry' appears to be an appropriate label for *M. melanotarsa* because, by relying on other salticids mistaking them for ants and fleeing, groups of these myrmecomorphic, araneophagic salticids gain access to nests containing eggs and post-embryos. Other araneophagic salticids practise aggressive mimicry by invading webs and, by manipulating silk lines, simulating signals that normally come from courting males or ensnared insects (Jackson & Pollard 1996). 'Femmes fatale' fireflies that lure heterospecific males by mimicking the flashing pattern of females of the deceived species (Lloyd 1965) and snakes that lure lizards by simulating movements resembling those of their own prey, such as insects (Hagman *et al.* 2008; Reiserer & Schuett 2008, X.J. Nelson unpublished data) are other examples of aggressive mimics eliciting overt responses. *Myrmarachne melanotarsa* resembles these aggressive mimics by evoking overt responses from other animals, with the critical difference that the target animal that responds to *M. melanotarsa*'s aggressive mimicry signals is not *M. melanotarsa*'s prey but, instead, the parental salticid that guards *M. melanotarsa*'s prey—the salticid's progeny. While fireflies, web-invading aggressive-mimic salticids, and snakes mimic something other than predators, *M. melanotarsa* mimics the parental salticid's predator.

It is also noteworthy that Batesian mimics rely on an overt response on being perceived (but misidentified) by the receiver (the predator), as in each of these examples of aggressive mimicry. However, aggressive mimicry is also used to describe strategies in which the mimetic signal works through not being salient to receivers (i.e. being perceived and misidentified, but not eliciting an overt response). For example, the salticid *Cosmophasis bitaeniata* preys on ant larvae and, while not particularly resembling its model (the ant *Oecophylla smaragdina*) visually, it acquires the ant's cuticular hydrocarbon signature. Using these acquired odours, *C. bitaeniata* can enter the ants' nest unmolested and prey on ants' eggs, larvae and pupae (Allan *et al.* 2002). Unlike *M. melanotarsa*, an aggressive mimic that relies on eliciting an overt response to its deceptive signal, *C. bitaeniata* depends on blending in as a colony member. *C. bitaeniata*, like comparable examples from insects (Eisner *et al.* 1978; Lucas & Brodeur 2001), can be likened to a wolf in sheep's clothing (e.g. Eisner *et al.* 1978). These predators practise aggressive mimicry by making it easy for prey to misidentify the predator as just another member of a prey group, as though lulling the prey into a false sense of security. By doing the opposite, and causing alarm, *M. melanotarsa* appears to be more akin to a black sheep in wolf's clothing.

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