

Research article

Vision-based ability of an ant-mimicking jumping spider to discriminate between models, conspecific individuals and prey

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Abstract. *Myrmarachne assimilis*, an ant-like (myrmecomorphic) jumping spider (Araneae, Salticidae) from the Philippines, is a Batesian mimic of *Oecophylla smaragdina*, the Asian weaver ant. Salticids are well known for their acute eyesight and the elaborate vision-based display behaviour they adopt during encounters with conspecific individuals, but most salticids are not myrmecomorphic. Despite its unusual morphology, *M. assimilis* adopts display behaviour during intraspecific interactions that is similar to the display behaviour of more typical salticids. The specificity with which *M. assimilis* deploys display behaviour is investigated and provides insights into this mimic's ability to differentiate, by sight alone, between models, conspecific individuals and prey. During each standardized test, an adult *M. assimilis* female was in a large cage along with a small transparent glass vial, a stimulus animal being enclosed in the vial such that potential optical cues, but not potential chemical cues, were available to the tested *M. assimilis* individual. Depending on the test, the stimulus animal was another adult *M. assimilis* female, a house fly (prey) or an ant (*Camponotus* sp. or *O. smaragdina*). Only the conspecific female consistently elicited display from *M. assimilis*, implying that *M. assimilis* is a Batesian mimic that can, when relying on vision alone, discriminate between conspecific individuals, models and prey.

Keywords: Batesian mimicry, visual discrimination, display behaviour, ants, myrmecomorphy.

Introduction

Signals can be defined as acts or structures of the sender that, because of evolutionary modification, are effective at influencing the behaviour of the receiver (Maynard Smith and Harper, 2003), with displays being sequences of signals that transmit information in a way that, on average, benefits the sender. Whether the signal is reliable or deceptive can be related to whether or not the transmitted information also benefits the receiver (Searcy and Nowicki, 2005). One of the best examples of deceptive signalling is Batesian mimicry, where predators that avoid a model (e.g., an ant) also avoid a mimic (e.g., an ant-like, or myrmecomorphic, spider). Within the largest family of spiders, the jumping spiders (Salticidae), numerous species appear to be Batesian mimics of ants (Jackson, 1982a; Edmunds, 1993; McIver and Stonedahl, 1993; Jackson and Willey, 1994; Cushing, 1997; Nelson and Jackson, 2006), with the best studied of these being in the genus *Myrmarachne* (Wanless, 1978; Cutler, 1991; Edmunds, 2000, 2006; Nelson et al., 2004, 2006a,b). Pronounced sexual dimorphism has also evolved in *Myrmarachne*, with the adult male's chelicerae being greatly elongated in comparison with the chelicerae of adult females and juveniles (Wanless, 1978; Cushing, 1997).

In nature, *Myrmarachne* is generally found in the vicinity of ants, and living near ants may be advantageous because it encourages predators to associate mimic with model. However, *Myrmarachne* may have to balance this advantage against the risk of being attacked by the model or becoming the model's prey (Nelson et al., 2004, 2006a). This may be especially true for *M. assimilis*, as this species mimics the Asian weaver ant, *Oecophylla smaragdina*

(Nelson et al., 2005), a species known for being exceptionally aggressive (Hölldobler, 1983; Hölldobler and Wilson, 1990).

Salticids are unique among because of having complex eyes and eyesight based on exceptionally high spatial acuity (Land, 1969a,b; Williams and McIntyre, 1980; Blest et al., 1990; Land and Nilsson, 2002; Harland and Jackson, 2004) and also because of the especially elaborate vision-based display behaviour that they adopt during intersexual and intrasexual encounters with conspecific individuals (Crane, 1949; Jackson and Pollard, 1997). Ant-mimicking salticids may face special problems, but surprisingly little is known about how readily these salticids discriminate by sight between conspecific individuals, prey and ants. Yet a Batesian mimic that relies on vision-based identification of conspecific individuals would have to be proficient at discriminating accurately between the mimic and the model, despite this being precisely the discrimination that, for defence, the mimic relies on its own visual predators in having difficulty achieving.

Despite its unusual morphology, *Myrmarachne assimilis* adopts during intraspecific interactions display behaviour that is similar to that of more typical salticids (Nelson and Jackson, unpubl.; Jackson, 1982a,b). We use the specificity of the display behaviour readily deployed by *M. assimilis* in intersexual and intrasexual encounters with conspecific individuals as an assay by which we investigate this mimic's ability to differentiate, by sight alone, between models, conspecific individuals and prey.

Materials and methods

For each test there was one 'test spider' (an adult female of *Myrmarachne assimilis*) and one 'stimulus animal' (in each test, body lengths of test spider and stimulus animal matched to within 1 mm). Our testing procedure limited the test spider to vision-based cues, and we compared how readily *M. assimilis* females displayed when the stimulus animals were conspecific females, prey (house flies; *Musca domestica*), and two different ant species, *Oecophylla smaragdina* (the specific model of *M. assimilis*) and *Camponotus* sp. (a representative ant to which *M. assimilis* had a general resemblance short of the more precise resemblance to the specific model). The rationale for using two ant species was that we might detect whether the ability of *M. assimilis* to distinguish ants from conspecific individuals depends on how similar the ant is to *M. assimilis*' own appearance.

All spiders used for testing came from a laboratory culture (spiders reared from eggs under standardized conditions: see Jackson and Hallas, 1986) started from specimens collected at the field site (Los Baños, Laguna Province, Luzon, the Philippines; 14°10'N, 121°14'E) (voucher specimens: Taxonomy Laboratory, International Rice Research Institute, Los Baños; Florida State Collection of Arthropods, Gainesville, Florida). The laboratory-rearing environment for salticids was "enriched" (spacious cages, mesh works of twigs within each cage; see Carducci and Jakob 2000). Spiders were reared on homopterans and, before testing, had no contact with ants, dipterans or, except for conspecifics in eggsacs before dispersal, spiders of any species. Ants were collected from the field site as needed and house flies came from laboratory stock. Testing was carried out between 0800 h and 1700 h (laboratory photoperiod: 12 : 12 L : D, lights on at 0800 h). No individual spider or insect was used in more than one test (N = 38 tests with each of the four stimulus animals).

A rectangular chamber (Fig. 1), as used in previous salticid studies (Harland and Jackson, 2001), was adopted for our testing apparatus. The chamber had two narrow walls, a floor and a roof, all made from wood, and two wide sides made of transparent glass (glass removable, facilitating cleaning). There were two holes (diameter 15 mm), one on each of the two wooden walls (centred 30 mm below the top of the frame), which were used for introducing the test spider and for presenting the stimulus animal.

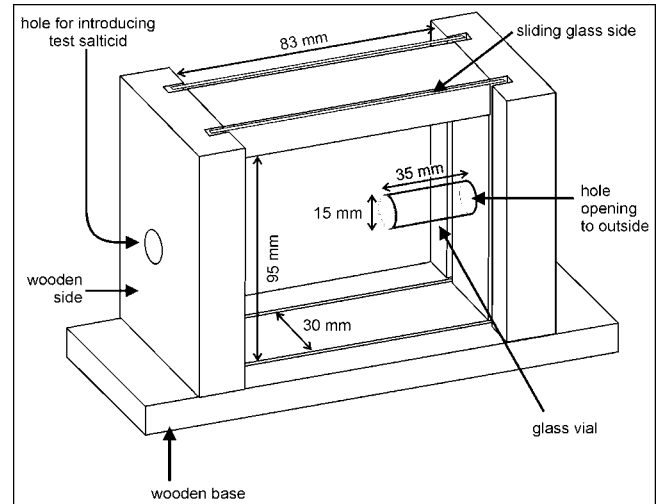


Figure 1. Apparatus used in formal tests (wooden frame with two glass sides). To start test, sealed glass vial, with stimulus animal inside, was inserted into chamber. *Myrmarachne assimilis* was introduced through hole (stoppered during test) in opposite end. Glass wall slides were taken out to allow cleaning of apparatus between tests.

Test duration was 10 min. A test spider was first transferred from a 30 mm long plastic tube (diameter 15 mm; stoppered at one end) into the chamber by placing the open end of the tube flush with the open introduction hole and then removing the stopper from the tube and prodding the spider with a small brush until it passed through the introduction hole. Once the test spider was in the chamber, the introduction hole was plugged with a rubber stopper and the test began. There was a transparent glass vial positioned inside the stimulus-presentation hole (open end flush with outside of cage; rest of vial protruding 35 mm into chamber). During the test, the live stimulus animal was visible inside the vial, but potential chemical cues from the stimulus animal were ruled out because the vial was airtight (opening situated outside chamber plugged with rubber stopper). Between tests, the glass sides were removed and the entire chamber was washed with 80% ethanol, followed by distilled water, and then allowed to dry before subsequent testing.

We recorded whether the spider displayed at the stimulus animal during the test. A display was defined as erect-legs posturing: forelegs extended stiffly forward while the spider faced the stimulus animal. Display, when it occurred, was always brief (duration less than 3 s). Data were analysed using one-way Kruskal-Wallis tests and Mann-Whitney tests on SPSS v11, with Bonferroni adjustments being applied whenever multiple comparisons were made using the same dataset.

Although the findings we analyze came only from formal tests, we also tested *Myrmarachne assimilis* informally with each of the stimulus animals (test spider and stimulus animal placed together in clean cage (no vial) and watched for 60 min or until predation occurred; 20 tests with each stimulus animal). For each type of stimulus animal, findings from informal tests were qualitatively similar to findings from formal tests.

Results

In informal tests, when the stimulus animal was a house fly it was always captured and fed on. Only one spider displayed (briefly) before capturing the fly, but the test spider always displayed when the stimulus animal was a conspecific female, and none stalked or attacked conspecific females. No ants were stalked or attacked, but five test spiders displayed momentarily at the ant.

In formal tests, 35 individuals of *Myrmarachne assimilis* displayed at conspecifics, compared with 18 at *Oecophylla smaragdina*, 15 at *Camponotus* sp. and five at house flies. Differences in the number of displays per test were especially pronounced (Fig. 2). Stimulus animal had a significant effect on the frequency with which females displayed ($H_3 = 68.281$, $P < 0.0001$).

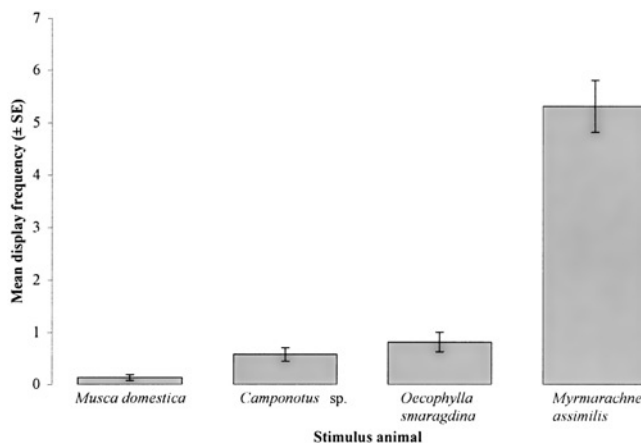


Figure 2. Number of bouts of display per test (mean \pm SE). *Myrmarachne assimilis* females tested with ants (*Camponotus* sp. and *Oecophylla smaragdina*), house flies (*Musca domestica*) and conspecifics ($N = 38$ tests with each stimulus animal)

Paired comparisons showed that *M. assimilis* females displayed toward conspecific females significantly more often than toward *O. smaragdina* ($Z = -6.232$, $P < 0.0001$), *Camponotus* sp. ($Z = -6.568$, $P < 0.0001$) and house flies ($Z = -7.206$, $P < 0.0001$). *M. assimilis* also displayed significantly more often at *O. smaragdina* ($Z = -3.404$, $P < 0.01$) and *Camponotus* sp. ($Z = -2.796$, $P < 0.05$) than at house flies, but the number of displays toward the two ant species were not significantly different ($Z = -0.702$, NS).

Discussion

We were interested in the ability of *Myrmarachne assimilis* to classify stimulus animals by sight alone, and our tests can be envisaged as letting *M. assimilis* tell us, by displaying or not, when it has classified a stimulus animal as a conspecific individual instead of something other than a conspecific individual. By consistently displaying

at conspecific individuals but not at flies, *M. assimilis* demonstrated its ability to discriminate readily between normal prey and conspecific individuals, a conclusion that is not particularly surprising. However, other findings suggest that *M. assimilis*, a Batesian mimic of *Oecophylla smaragdina*, does something more interesting: it readily distinguishes, by sight, between conspecific individuals and ants. When discriminating between ants and conspecific individuals, whether or not the ant is *M. assimilis*' specific model, *O. smaragdina*, appears to be unimportant, as *M. assimilis* readily discriminated between conspecific individuals and ants, regardless of whether the ant was *O. smaragdina* or *Camponotus* sp. As a Batesian mimic, *M. assimilis* has evidently evolved a special facility for solving the very mimic-model discrimination problem that it depends on being difficult for other predators with good eyesight.

We currently have only a poor understanding of the cues by which any salticid makes vision-based identifications. Interest in this topic began especially with Drees (1952) who performed experiments in which models (2-D drawings and 3-D models made of plasticene and wire) were presented to males of *Salticus scenicus*, a common wall-dwelling salticid in Europe. Attacking a model was interpreted as evidence of having classified the model as prey (i.e., in the context of Drees' study, an insect) and display behaviour was interpreted as evidence of having classified the model as a conspecific individual (i.e., in the context of Drees' study, a salticid). Leg characteristics (thickness, density and a particular angle to vertical, $25^\circ - 30^\circ$) were shown to be critical cues by which *S. scenicus* identified salticids, with just about any other object of appropriate size being, by default, accepted as prey.

More recent research has shown that vision-based classification by salticids must often be considerably more intricate than Drees' (1952) findings would suggest. In particular, *Portia* is a genus of spider-eating salticids that, by sight, discriminates between different types of spiders and adopts different prey-specific tactics depending on how it classifies the spider it sees (Harland and Jackson, 2004). *P. fimbriata* from Queensland is of particular interest because it adopts a special tactic, called 'cryptic stalking', for preying on other salticids (Jackson and Blest, 1982). However, unlike *Salticus scenicus*, *P. fimbriata* relies primarily on cues from the salticid's large forward-facing anterior medial eyes, instead of cues from legs, when classifying a prey item as a salticid (Harland and Jackson, 2002). Furthermore, because *P. fimbriata* displays at conspecifics, instead of adopting cryptic stalking (Jackson, 1982c), it is evident that, for *P. fimbriata*, identifying a conspecific individual is more than simply confirming that the other animal is a salticid.

It is probably common for salticids to distinguish between ants and other insects, and to respond to *Myrmarachne* in much the same way as they respond to ants (see Nelson and Jackson, 2006). *Portia fimbriata*, being a salticid that specializes at preying on other

salticids, avoids getting close either to ants or to *Myrmarachne*, and does not adopt cryptic stalking when the other salticid it encounters is *Myrmarachne* (Harland and Jackson, 2001; Nelson and Jackson, 2006).

Classifying the arthropods it encounters is, evidently, for *Myrmarachne assimilis*, a more demanding task than Drees' (1952) study would suggest. For *M. assimilis*, some insects, but not ants, are prey. As for many non-myrmecomorphic salticids, ants tend to be dangerous neighbours (James et al. 1999; Nelson et al., 2004, 2005), but simply to avoid ant-like arthropods is not a realistic option for *M. assimilis*, as this would imply avoiding conspecific individuals. *M. assimilis*' solution to this problem has apparently included the evolution of special perceptual abilities that facilitate rapid vision-based discrimination between mimic and model, the very type of discrimination that it depends being, for other visual predators, not so readily achieved.

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