Vision-based innate aversion to ants and ant mimics

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Innate vision-based aversions to model and mimic were investigated using a mimicry system in which the models were ants (Formicidae), and both the mimics and the predators were jumping spiders (Salticidae). Jumping spiders are a large group of predatory invertebrates that usually prey opportunistically on prey of similar size. We used 12 representative species from this group, the "ordinary salticids" as predators. The mimics considered belonged to another group, salticids that resemble ants. A choice arena containing an empty chamber and a stimulus chamber was used for testing predator responses to a variety of dead arthropods (ants, ant mimics, and an array of non–ant-like species) mounted in a lifelike posture. When presented with visual cues from arthropods other than ants or ant-like salticids, naive predators chose the empty chamber no more often than the stimulus chamber. However, when visual cues were from ants or from ant-like salticids, ordinary salticids chose the empty chamber significantly more often than the stimulus chamber. These findings suggest learning by the predator is not necessary in order for ant-like salticids to gain Batesian mimicry advantages. *Key words:* ants, innate aversion, mimicry, myrmecomorphy, spiders, vision. *[Behav Ecol 17:676–681 (2006)]*

In a Batesian mimicry system, palatable and safe prey individuals deceive potential predators by resembling unpalatable or dangerous models that signal their inedibility using salient cues, such as bright coloration (aposematism) (Bates 1862; Wickler 1968; Edmunds 1974). Traditionally, the extensive literature on the subject centers on the predators' (typically birds) acquisition of a learned aversion to unpalatable prey (typically butterflies), which is then generalized and extended to a palatable mimic of similar appearance (Brower 1958; Uesugi 1996; Mappes and Alatalo 1997; Ritland 1998). In contrast, relatively little attention has been given to the role of different sensory systems, the effect of different types of visual systems, and to the possibility that innate aversions might also drive the evolution of Batesian mimicry. Hypotheses about vision-based mimicry typically arise from judging how an animal appears to our eyes. Birds and other vertebrate predators may have eyes similar to our own, but it is not a foregone conclusion that what they see is similar to what we see (Cuthill and Bennet 1993). Although many arthropods (e.g., mantises; see Cleal and Prete 1996) use vision-based predatory behavior, it may be less tempting to presume that what the experimental subject sees resembles what we see when using arthropods instead of birds as predators.

Our research is atypical of the Batesian mimicry literature because we consider innate instead of learned aversion (but see Blest 1957; Smith 1975; Caldwell and Rubinoff 1983; Nelson et al. 2006), because the predators we use in our experiments are predatory arthropods instead of birds, and because the models are not traditionally aposematic. We investigate a system in which the models are ants (Formicidae), and both the mimics and the predators are jumping spiders (Salticidae). In the tropics, salticids tend to be especially abundant spiders (Coddington and Levi 1991) and ants tend to be the most abundant insects (Hölldobler and Wilson

1990). However, because of their formidable defenses (e.g., powerful mandibles, formic acid, poison-injecting stings, and the ability, as social insects, to mob potential predators; Eisner 1970; Blum 1981), ants may be unpalatable as prey for most salticids. Ants may also be among the most important predators of salticids (Nelson et al. 2004). Ability to identify ants from a distance and then avoid coming into close proximity may often be advantageous for a salticid.

For ant mimics, we chose 5 myrmecomorphic (ant-like) species (see Cushing 1997), all from the genus *Myrmarachne*. For predators, we chose representatives of the bulk of salticids, the "ordinary salticids" (defined as salticids that neither resemble nor routinely prey on ants). Ordinary salticids tend to be opportunistic predators that prey on a wide variety of insects and other arthropods, including other spiders (Foelix 1996). As one of the ordinary salticids, we chose *Portia labiata*, a species that actively chooses other spiders as preferred prey (Li et al. 1997).

Uniquely among spiders, salticids have high-acuity eyes (Williams and McIntyre 1980; Land and Nilsson 2002; Harland and Jackson 2004) and the ability to discriminate by sight between different kinds of prey (Land 1974; Harland and Jackson 2001; Jackson et al. 2005). Here we consider whether ordinary salticids have an innate aversion to ants and whether this aversion is generalized to myrmecomorphic salticids. At the same time, our experiments clarify whether, by sight alone, ordinary salticids can identify and avoid ants and whether, for salticids, ant mimics resemble ants.

MATERIALS AND METHODS

Ants and other insects were collected as needed from our field site (Los Baños, Laguna Province, Luzon) in the Philippines, but all salticids came from laboratory cultures (bred to F2 generation from specimens collected in the field). Before testing, the ordinary salticids used as test spiders, and their parents, had no prior experience with ants, with allospecific spiders, or with any of the other arthropods used for making lures. Salticid maintenance procedures, which were the same as in numerous earlier spider studies (see Jackson and Hallas 1986), included "enriched environments" (spacious cages and meshwork of twigs within each cage; see Carducci and Jakob
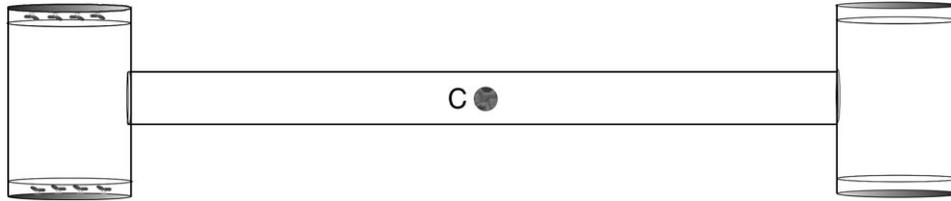
Figure 1
Schematic view of apparatus (cylindrical walkway and 2 cylindrical chambers made from clear Perspex) used for testing responses of 12 ordinary salticid species to the appearance of motionless lures made from ants, *Myrmarachne* (myrmecomorphic salticids), and non–ant-like arthropods. Test spider introduced through cork hole (C) into walkway and allowed to settle in stimulus chamber (lures on paper) or blank chamber (no lures present).

2000). No individual salticid was used in more than one test. Wilcoxon signed-rank tests and Kruskal–Wallis tests were carried out using JMP software (SAS Institute Inc., Cary, North Carolina), with Bonferroni adjustments applied whenever multiple comparisons were made using the same data sets (Sokal and Rohlf 1995).

The test apparatus (Figure 1) was a transparent Perspex tube (diameter, 30 mm; length, 320 mm) (called the "walkway") that connected at each end to a wider transparent Perspex tube (diameter, 90 mm; length, 100 mm) (called a "chamber") perpendicular to the walkway. Each end of each chamber was sealed by the bottom of a clear plastic petri dish (diameter, 90 mm). A round piece of white blotting paper (diameter, 90 mm) was taped inside the top of each petri dish which was itself taped to the bottom of the petri dish that sealed the chamber (i.e., the side of the dish farthest from the inside of the chamber was white). The 2 petri dishes on the ends of the blank chamber contained only blotting paper. However, there were 4 lures made from dead arthropods in each of the stimulus chamber's 2 dishes. Each lure was made by first immobilizing an arthropod with carbon dioxide and then placing it in 80% ethanol at least 24 h prior to each test. The 4 lures in any one petri dish were always made from individuals of the same size, sex, and species. Lures were glued in lifelike posture to the blotting paper. Each lure was positioned equidistant from its 2 nearest neighbors, facing the center of the blotting paper and with its posterior end approximately 20 mm from the outer edge of the paper.

Whether the stimulus chamber was on the left or right side of the walkway was decided at random for each test. Each test consisted of 4 successive trials with 20 individual salticids. Tests began at 08:00 AM and lasted for 10 h (laboratory photoperiod, 12:12 h light:dark, lights on at 07:00 AM). The 10-h period gave the spider time to explore the chambers and build a silk nest in the chamber in which it settled. A 10-mm wide cork hole in the center of the top surface of the walkway was used for introducing a test spider at the beginning of each test. The test spider was first taken into a 40-mm long (diameter, 8 mm) clear glass tube (each end plugged by a cork) and transferred 10 min later to the walkway by removing the corks from the tube and from the hole in the top of the walkway, placing one open end of the tube against the open hole in the walkway and inserting a soft brush through the opposite end of the tube. If the test spider did not immediately enter the walkway, the brush was used as a plunger for gently pushing the salticid out of the tube and into the walkway. The salticid's location was recorded at 06:00 AM, by which time most salticids had built a silken nest in 1 of the 2 chambers (settled). Testing was aborted on rare occasions when a test spider did not settle or else settled in the walkway instead of a chamber.

On the day before the first trial, the test spider was fed to satiation. After the first trial, the spider was returned to its cage, fed to satiation again the next day, and then tested again 1 day later. This procedure was repeated until a total of 4 trials had been completed by each of the 20 test spiders (each test spider from a different brood). As a precaution against the possibility that chemical traces from previous ants and salticids might influence test outcomes, the apparatus, transfer tubes, and corks were cleaned between trials with 80% ethanol followed by distilled water and then allowed to dry.

Over the 4 trials, each test spider accumulated a score that ranged from 0 for when it never settled in the blank chamber to 4 for when it settled in the blank chamber in 4 out of 4 trials (i.e., test spiders with higher scores more often avoided the stimulus chamber). The null hypothesis was that the test spider's decision to settle on one side or the other was not influenced by what it saw from inside the stimulus chamber (scores = 2).

For test spiders, we used juveniles (body length 3–4 mm) of 12 ordinary salticid species: *Bavia sexpunctata, Cosmophasis estrellaensis, Epeus hawigalboguttatus, Gambaquezonia itimana, Lagnus* sp., *Mantisatta longicauda, Menemerus bivittatus, Orthrus bicolor, Plexippus petersi, P. labiata, Telamonia masinloc,* and *Thiania* sp.

For lures, we used workers of 8 ant species (each belonging to a different genus) and adult females of 5 myrmecomorphic salticid species (all from the genus *Myrmarachne*) (Figure 2). Body lengths of the specimens used for making lures are given below.

Four of the ants were formicines: *Camponotus* sp. (6 mm), *Oecophylla smaragdina* (8 mm), *Polyrachis* sp. (6 mm), and *Solenopsis geminata* (4 mm). Two were ponerines: *Diacamma rugosum* (12 mm) and *Odontomachus* sp. (5 mm). One was an aneuretinine: *Dolichoderus thoracicus* (4 mm). There was 1 myrmicine: *Crematogaster* sp. (3 mm). The myrmecomorphic salticids were *Myrmarachne assimilis* (8 mm), *Myrmarachne bakeri* (6 mm), *Myrmarachne bidentata* (9 mm), *Myrmarachne maxillosa* (7 mm), and *Myrmarachne nigella* (6 mm).

With the body lengths of ants and myrmecomorphic salticids varying considerably (3–12 mm), we wanted to rule out the possibility that the test spider was simply avoiding arthropods of particular sizes rather than specifically avoiding ants and myrmecomorphic salticids. For this reason, we carried out another series of tests using other arthropods that were not ants and were not myrmecomorphic but matched the body lengths of the various ants and myrmecomorphic salticids used as lures. Two of the "other arthropods" were large ordinary salticids, the rationale being to discern whether the test spider was simply avoiding salticids rather than specifically avoiding the myrmecomorphic salticids. Adult females of *Bavia sexpunctata* (12 mm) were the ordinary salticids used for making lures except that, when the test spiders were also *B. sexpunctata*, the ordinary salticid lures were made from adult females of *Telamonia masinloc* (12 mm). The other lures were made from adult beetles, *Epilacha* sp. (Coleoptera,
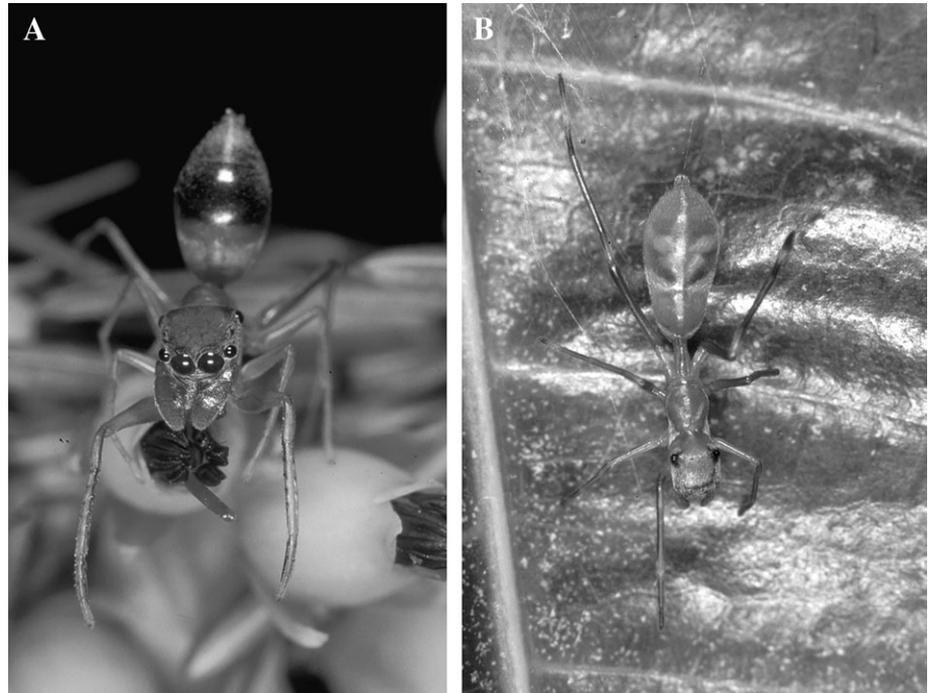
Figure 2
Representative ant-like salticids.
(A) *Myrmarachne bakeri* and (B)
Myrmarachne assimilis.

Coccinellidae) (6 mm); cockroach nymphs, *Blatella* sp. (Blattodea, Blatellidae) (5 mm); adult mosquitoes, *Toxorhynchites nephenthis* (Diptera, Culicidae) (12 mm); termite soldiers, *Heterotermes* sp. (Isoptera, Rhinotermitidae) (3 mm); and moths, *Parasa* sp. (Lepidoptera, Limacodidae) (7 mm).

RESULTS

When the stimulus chamber contained arthropods other than ants or myrmecomorphic salticids (beetles, cockroaches, mosquitoes, termites, moths, and an ordinary salticid), there was no evidence that the ordinary salticid's settling decision was influenced by seeing the lures in the stimulus chamber. The median score in all tests for each of the 12 species used as test spiders was 2 (minimum 1st quartile = 0.25, maximum 3rd quartile = 3), and there was no significant deviation from this score. However, scores were significantly higher than 2 when the stimulus chamber contained ants and when the stimulus chamber contained myrmecomorphic salticids (Table 1).

For each of the 12 salticid species used as test spiders, a Kruskal–Wallis test was used to compare scores from using different ant species and scores from using different stimulus categories (ants, *Myrmarachne*, and nonmyrmecomorphic arthropods) ($P > 0.1$ for each category for each test spider species). Data for each of the 3 categories (ants, *Myrmarachne*, and non–ant-like arthropods) were next pooled, leaving 3 data sets for each test spider species. We then used the pooled data to compare the scores of test spiders when tested with ants with the scores of test spiders when tested with *Myrmarachne* and when tested with nonmyrmecomorphic arthropods.

Kruskal–Wallis analyses showed that, for all 12 salticid species studied, scores from tests in which the lures were ants and from tests in which the lures were myrmecomorphic salticids were not significantly different to each other ($\chi^2_{min} = 0.02$, $\chi^2_{max} = 4.41$; all NS; df = 1) and were significantly higher than scores in tests in which the lures were nonmyrmecomorphic arthropods ($\chi^2_{min} = 29.24$, $\chi^2_{max} = 95.51$; all $P < 0.001$; df = 1).

DISCUSSION

Our findings suggest that ant mimicry provides ordinary salticids with visual cues that correspond closely to the visual cues they get from ants and that ordinary salticids are innately averse to both ants and their mimics. Ordinary salticids avoided chambers surrounded by lures made from ants and ant-like salticids, but they had no evident aversion to chambers surrounded by lures made from arthropods that are not, to our eyes, ant-like in appearance. Moreover, as scores from tests with lures made from *Myrmarachne* and from ants did not differ, there was no evidence to suggest that ordinary salticids discriminated between lures made from ants or lures made from *Myrmarachne*. Even *P. labiata*, a salticid that prefers other spiders as prey (Li et al. 1997), reacted to *Myrmarachne* as though it were an ant instead of a spider.

Our experimental design ruled out odor and contact chemical cues. This was not only because the lures were made from specimens that had been in kept in ethanol but also because, during testing, the lures were placed outside the chamber enclosing the test spider. Using motionless lures also ruled out sound or substrate vibration cues, as well as cues from differences in movement pattern as a basis on which the salticid made settling decisions. Clearly, in our laboratory experiments, the salticids based their decisions solely on the static appearance of the lures. Nevertheless, this has not ruled out the possibility that *Myrmarachne*'s behavior (see Cushing 1997) and odor may, in the field, contribute to the *Myrmarachne*'s success as a Batesian mimic. However, by avoiding confounding variables from odor and movement, we seem to have revealed something remarkable about what salticids see.

Besides depending on sensory input through an animal's eyes to its brain, "seeing" is also the product of cognitive processes (Blough DS and Blough PM 1997; Shettleworth 1998). To us, with our human eyes and our human brains, *Myrmarachne* strongly resemble ants (Figure 2). Unless experienced at detecting the differences, we tend to "see" an ant when we look at *Myrmarachne*. Yet, despite their very different eyes (Land and Nilsson 2002) and very different brains (see Bullock

Table 1
Median scores for the number of trials in which each of 12 ordinary salticid species settled in blank chamber instead of chamber containing ants or myrmecomorphic salticids (see Figure 1)

Stimulus category	Stimulus species	*Bavia sexpunctata* Median	Test statistic	*Cosmophasis estrellaensis* Median	Test statistic	*Epeus hawigalboguttatus* Median	Test statistic
Ants	*Camponotus* sp.	3	60.0***	3	80.5***	4	69.5***
	Crematogaster sp.	3.5	68.5***	3	52.5***	3	55.0**
	Diacamma rugosum	3.5	64.5***	3	46.5**	3	62.5***
	Dolichoderus thoracicus	3	47.5**	3	48.5**	3	39.5**
	Odontomachus sp.	3.5	76.5***	3	39.5**	3	68.0***
	Oecophylla smaragdina	3.5	52.5***	3	34.5**	4	68.0***
	Polyrachis sp.	3	56.5***	3	39.0***	3	70.0***
	Solenopsis geminata	3	62.5***	3	71.0***	3	52.5***
Ant-like salticids	*Myrmarachne assimilis*	3	52.5***	3	30.0*	3	40.0**
	Myrmarachne bakeri	3	47.5**	3	39.0***	3	60.0***
	Myrmarachne bidentata	3	45.5***	2.5	33.5*	3	62.0***
	Myrmarachne maxillosa	3	45.5***	2.5	30.0**	3	38.5**
	Myrmarachne nigella	3	40.0*	3	40.5*	3	45.5***

Stimulus category	Stimulus species	*Gambaquezonia itimana* Median	Test statistic	*Lagnus* sp. Median	Test statistic	*Mantisatta longicauda* Median	Test statistic
Ants	*Camponotus* sp.	3	43.0**	3	40.5**	3	41.5**
	Crematogaster sp.	3	45.5***	3	33.0**	3	45.5***
	Diacamma rugosum	2.5	45.5**	3	33.5**	3	49.0**
	Dolichoderus thoracicus	3	68.0***	3	30.0**	3	42.5*
	Odontomachus sp.	3	60.0***	3	39.0***	3	64.0***
	Oecophylla smaragdina	3	36.0**	3	68.0***	4	81.5***
	Polyrachis sp.	3	68.0***	3	60.0***	3	52.5***
	Solenopsis geminata	3	45.5***	3	40.5**	3	52.5***
Ant-like salticids	*Myrmarachne assimilis*	3	52.5***	2	18.0**	3	60.0***
	Myrmarachne bakeri	3	60.0***	3	28.5**	3	34.5**
	Myrmarachne bidentata	3	37.5**	3	39.0***	3	85.5***
	Myrmarachne maxillosa	4	65.5***	3	60.0***	3	60.0***
	Myrmarachne nigella	3	71.5***	3	35.5*	3	47.5**

Stimulus category	Stimulus species	*Menemerus bivittatus* Median	Test statistic	*Orthrus bicolor* Median	Test statistic	*Plexippus petersi* Median	Test statistic
Ants	*Camponotus* sp.	3	76.5***	3	76.5***	3	52.5***
	Crematogaster sp.	3	71.0***	3	45.5***	3	68.0***
	Diacamma rugosum	3	49.5**	3	54.5**	3	88.0***
	Dolichoderus thoracicus	3	68.0***	3	52.5***	3	57.0**
	Odontomachus sp.	3	52.5***	3	88.0***	3	52.5***
	Oecophylla smaragdina	3	45.5***	3	47.0**	3	89.0***
	Polyrachis sp.	3	88.5***	3	52.5***	3	60.0***
	Solenopsis geminata	3	60.0***	3	62.0***	3	79.0***
Ant-like salticids	*Myrmarachne assimilis*	3	58.5**	3	60.0***	3	52.5***
	Myrmarachne bakeri	3	60.0***	3	68.0***	3	45.5***
	Myrmarachne bidentata	3	60.0***	3	45.5***	3	68.0***
	Myrmarachne maxillosa	3	60.0***	3	63.0***	3	52.5***
	Myrmarachne nigella	3	70.5**	3	68.0***	3	63.5***

Stimulus category	Stimulus species	*Portia labiata* Median	Test statistic	*Telamonia masinloc* Median	Test statistic	*Thiania* sp. Median	Test statistic
Ants	*Camponotus* sp.	3	70.00***	3	68.0***	3	53.0*
	Crematogaster sp.	3	63.0**	3	39.0***	3	56.0**
	Diacamma rugosum	3	41.5**	3	48.5**	3	51.5**
	Dolichoderus thoracicus	3	52.5***	3	63.0***	3	50.0**
	Odontomachus sp.	3	76.5***	3	59.0**	3.5	57.0**
	Oecophylla smaragdina	3	95.0***	3.5	85.5***	3	80.5***
	Polyrachis sp.	3	70.5***	3	71.0***	3.5	54.0**
	Solenopsis geminata	3	76.5***	3	71.5***	3.5	68.0***
Ant-like salticids	*Myrmarachne assimilis*	3	79.5***	3	76.5***	3	47.5**
	Myrmarachne bakeri	3	53.5**	3	76.5***	3	56.0**
	Myrmarachne bidentata	3	54.5**	3	68.0***	3	29.0*
	Myrmarachne maxillosa	3	79.5***	3	68.0***	3	48.5**
	Myrmarachne nigella	3	89.0***	3	68.0***	3	41.5**

Four successive trials for each individual test spider. Test statistic and P value from Wilcoxon signed-rank test (null hypothesis: score of 2) ($N = 20$ in each instance). *$P < 0.05$, **$P < 0.01$, ***$P < 0.001$.

and Horridge 1965; Babu 1985), the salticids we tested may also see an ant when they look at *Myrmarachne*.

An alternative hypothesis is that the ordinary salticid readily perceives ants and *Myrmarachne* as 2 distinct categories, has an innate aversion for ants, and has a separate innate aversion for *Myrmarachne*. This hypothesis is improbable. We know that ants are potentially dangerous to ordinary salticids (Nelson et al. 2004), but there is no evidence that coming close to *Myrmarachne* is particularly dangerous. It might be argued that *Myrmarachne* is avoided because ordinary salticids simply avoid close proximity with other salticids. However, having found no evidence that the settling decisions of ordinary salticids' were influenced by seeing lures made from other ordinary salticids, this hypothesis seems unlikely.

Our findings suggest that it may be common for salticids to have innate aversion to ants and that this aversion is generalized to myrmecomorphic salticids. Variation in experience, maternal effects, and other indirect genetic effects were minimized (see Moore et al. 1998; Roff 1998; Wade 1998) because all individuals tested were laboratory reared to second generation under standardized conditions and had no prior experience with the arthropods used for making lures.

In classic examples of Batesian mimicry, aversion is learned, not innate. Another distinction is that, in classic examples of Batesian mimicry, the model is aposematic, honestly advertising its unpalatability to the predator, whereas the Batesian mimic is palatable but deceptively advertises in a manner like the model. Although ants may be unpalatable prey for ordinary salticids, aposematism may be an inappropriate description as it seems unlikely that the ant's distinctive appearance evolved as an advertisement of unpalatability. Perhaps more significant for the salticid, ants are potential predators (Nelson et al. 2004), and the threat of predation, rather than unpalatability, may have been the stronger selection factor driving the evolution of innate aversion of ants in ordinary salticids. The issue of advertisement seems to be clearer with *Myrmarachne*. By resembling an ant, *Myrmarachne* seems to be advertising, deceptively, that it is something ordinary salticids, and probably many other vision-based predators, avoid. "Batesian mimic" appears to be an appropriate term for these myrmecomorphic salticids.

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