Innate aversion to ants (Hymenoptera: Formicidae) and ant mimics: experimental findings from mantises (Mantodea)

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Field data suggest that ants may be important predators of mantises which, in turn, may be important predators of jumping spiders (Salticidae). Using a tropical fauna from the Philippines as a case study, the reactions of mantises to ants, myrmecomorphic salticids (i.e. jumping spiders that resemble ants) and ordinary salticids (i.e. jumping spiders that do not resemble ants) were investigated in the laboratory. Three mantis species (*Loxomantis* sp., *Orthodera* sp., and *Statilia* sp.) were tested with ten ant species, five species of *Myrmarachne* (i.e. myrmecomorphic salticids), and 23 ordinary salticid species. Two categories of the myrmecomorphic salticids were recognized: (1) 'typical *Myrmarachne*' (four species with a strong resemblance to ants) and (2) *Myrmarachne bakeri* (a species with less strong resemblance to ants). Ants readily killed mantises in the laboratory, confirming that, for the mantises studied, ants are dangerous. In alternate-day testing, the mantises routinely preyed on the ordinary salticids, but avoided ants. The mantises reacted to myrmecomorphic salticids similarly to how they reacted to ants (i.e. myrmecomorphic salticids appear to be, for mantises, Batesian mimics of ants). Although myrmecomorphic salticids were rarely eaten, *M. bakeri* was eaten more often than typical *Myrmarachne*. Because the mantises had no prior experience with ants, ant mimics or ordinary salticids, our findings suggest that mantises have an innate aversion to attacking ants and that this aversion is generalized to myrmecomorphic salticids even in the absence of prior experience with ants. © 2006 The Linnean Society of London, *Biological Journal of the Linnean Society*, 2006, **88**, 23–32.

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INTRODUCTION

In a Batesian-mimicry system, palatable prey individuals deceive potential predators by resembling unpalatable models (Bates, 1862; Wickler, 1968; Edmunds, 1974, 1978; Vane-Wright, 1980). Although the Batesian-mimicry literature has emphased examples in which the predator learns cues by which unpalatable prey can be identified (Brower, 1958; Edmunds, 1974; Berenbaum & Miliczky, 1984; Ritland, 1995, 1998;

Uesugi, 1996; Mappes & Alatalo, 1997), examples of innate aversion comprise important potential evidence for how particular types of prey may shape the evolution of a predator's behaviour (Blest, 1957; Smith, 1975; Caldwell & Rubinoff, 1983; Roper & Cook, 1989; Brodie, 1993). In the present study, we investigated a mimicry system in which the models are ants (Formicidae), the predators are mantises (Mantidae) and the mimics are a minority group of jumping spiders (Salticidae) that resemble ants (myrmecomorphic species).

In the tropics, salticids tend to be dominant spiders (Coddington & Levi, 1991; Platnick, 2002) and ants tend to be dominant insects (Hölldobler & Wilson,

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1990). Most mantises appear to be generalist preda- tors that rely on vision for prey-capture cues (Rilling, Mittelstaedt & Roeder, 1959; Rossel, 1991, 1996; Prete *et al*., 2002), and it may not be surprising that mantises sometimes prey on salticids (Reitze, 1991; Benrekaa & Doumandji, 1997; Bruce, Herberstein & Elgar, 2001). However, ants, because of their powerful mandibles, poison-injecting stings, formic acid and ability, as social insects, to mob the predator's defences (Eisner, 1970; Blum, 1981), may present formidable challenges to many predators that routinely prey on other arthropods of a similar size. Ants are also lead- ing predators of other arthropods, including spiders and mantises (Oliveira, 1988; Hölldobler & Wilson, 1990; Elgar, 1993; Nelson *et al*., 2004). We provide evi- dence that the three mantis species in the present study are vulnerable to ants.

An ant-like appearance (myrmecomorphy) has evolved in a minority of salticid genera (Edmunds, 1974; McIver & Stonedahl, 1993; Cushing, 1997), the most extensively studied being *Myrmarachne* (Edmunds, 1974, 1978, 1993; Wanless, 1978; Jackson, 1986; Cutler, 1991; Jackson & Willey, 1994). In the present study, we examine how mantises react to *Myr- marachne*. As a case study, we use a tropical fauna from the Philippines: three mantis species, ten ant species, and 28 salticid species, five of which were myrmeco- morphic. We consider three hypotheses: (1) mantises are innately averse to attacking ants; (2) for mantises, myrmecomorphic salticids are Batesian mimics of ants; and (3) 'poor' mimics of ants are not as effective at deterring predation compared to 'good' mimics of ants.

MATERIAL AND METHODS

ANTS, MANTISES AND SALTICIDS

The mantises used were *Loxomantis* sp., *Orthodera* sp., and *Statilia* sp. The ants used were *Anoplolepsis longipes* (Jerdon) (body length of worker 7 mm) (Formicinae); *Camponotus* sp. (5–8 mm) (Formicinae), *Crematogaster* sp. (3 mm) (Myrmicinae); *Diacamma rugosum* (Le Guillou) (12 mm) (Ponerinae); *Doli- choderus thoracicus* Stitz (4 mm) (Dolichoderinae); *Oecophylla smaragdina* (Fabricius) (7–10 mm) (For- micinae); *Odontomachus* sp. (10–12 mm) (Ponerinae), *Pheidologeton* sp. (4–5 mm) (Myrmicinae); *Polyrachis dives* Smith (5–6 mm) (Formicinae); and *Solenopsis geminata* (Fabricius) (4 mm) (Myrmicinae).

We use the term 'ordinary salticid' when referring to non-myrmecomorphic salticids. The ordinary salticids used were *Bavia sexpunctata* (Doleschall); *Carrhotus sannio* (Thorell); *Cosmophasis estrellaensis* Barrion & Litsinger; *Chalcotropis gulosa* (Simon); *Chalcotropis luceroi* Barrion & Litsinger; *Cytaea* sp.; *Emathis weyersi* Simon; *Epeus hawigalboguttatus* Barrion & Litsinger; *Gambaquezonia itimana* Barrion & Litsinger; *Harmochirus brachiatus* (Thorell); *Hasar- ius adansoni* (Savigny & Audouin); *Heretemita alboplagiata* (Simon); *Lepidemathis* sp.; *Menemerus bivittatus* (Dufour); *Orthrus bicolor* Simon; *Phintella piantensis* Barrion & Litsinger; *Plexipus petersi* (Kar- sch); *Portia labiata* (Thorell); *Pseudicius manillaensis* Proszynski; *Siler semiglaucus* Simon; *Telamonia mas- inloc* Barrion & Litsinger; *Thiania* sp.; and *Xenocytaea* sp.

Four of the myrmecomorphic salticids used are what Edmunds (2000) called 'good' mimics (i.e. to the human observer, they strongly resemble their model) and one was a 'poor' mimic (i.e. to the human observer, it does not strongly resemble an ant).

The poor ant mimic was *Myrmarachne bakeri* Banks and good ant mimics ('typical *Myrmarachne*') were *Myrmarachne assimilis* Banks; *Myrmarachne biden- tata* Banks; *Myrmarachne maxillosa* (C. L. Koch); and *Myrmarachne nigella* (Simon). The anterior ends of the abdomens of typical *Myrmarachne* are especially narrow, simulating the narrow waist of an ant, but the narrowing of the anterior abdomen of *M. bakeri* is less pronounced.

Our field site was the vicinity of Los Baños (Laguna Province, Luzon) in the Philippines. We collected ant workers from the field, as required, and used labora- tory cultures for mantises and salticids, with mainte- nance procedures being employed as described in earlier studies (Jackson & Hallas, 1986). The mantises had no prior experience with ants or with salticids. In all tests, the mantises used were nymphs and the ants were workers. Each salticid was either an adult female or a juvenile chosen to match the body length of the ant with which it was paired in alternate-day test- ing (see below). No individual salticid or ant was used in more than one test, but the same mantises were used in alternate-day testing.

GENERAL PROCEDURES

The testing apparatus was a clear plastic cage ($300 \times 300 \times 300$ mm). There were two holes centred in the top of the cage (diameter of each hole 20 mm; clos- est edges of the two holes 40 mm apart), one plugged with a cork (for introducing mantises, ants and spi- ders into the cage) and the other covered with fine- mesh screening (for ventilation). A hole centred in the bottom of the cage (diameter 10 mm) was plugged with a cotton roll (diameter 5 mm, length 40 mm) that pro- truded into the cage *c.* 5 mm, with the lower, longer portion protruding out of the bottom of the cage. The cage rested on a plastic water-filled pot, with the out- side portion of the cotton roll sitting in the water. The water-logged cotton roll provided humidity and drink- ing water for the arthropods during testing.

A green mango leaf (*c.* 150 mm long), still attached to its stem (*c.* 50 mm long), was placed in each cage and held upright by wedging the stem against the cotton roll and through the hole in the bottom of the cage. With the lower half of the stem sitting in the water, the leaf remained firm and green during the test. The mantis used the leaf as a perch during testing.

In each instance, one mantis was introduced alone into a cage at 08.00 h (12 : 12 h light/dark photoperiod, lights on 08.00 h). Testing was initiated the next day by introducing a salticid, an ant, or ten ants into the cage. Intermittent observations were made during the 10-h duration of the test, but the primary data were survival records (i.e. whether a particular mantis, ant, or salticid was still alive at the end of the test period). Between tests, cages were cleaned with 80% ethanol followed by distilled water as a precaution against the possibility that chemical traces from previous ants, mantises, and salticids might have influenced test outcomes.

Survival data were compared using chi-square tests of independence. Bonferroni adjustments were used when multiple comparisons were made with the same data sets (Sokal & Rohlf, 1987).

MANTIS MORTALITY IN THE PRESENCE OF ANTS

In one-ant tests, one mantis and one ant (*O. smaragdina* or *Odontomachus* sp.) were housed together in the same cage for 10 h (each mantis species was used; $N = 20$ for all mantis-ant combinations). In two-ant tests, one mantis was housed in the same cage with ten ants (all ten ants in the cage belonged to a single species: *Camponotus* sp.; *D. rugosum*; *O. smaragdina*; *Odontomachus* sp.; or *S. geminata*) for 10 h (each mantis species was used; $N = 20$ for all mantis–ant combinations). In large-ant testing, the ant and mantis were equal in body length. In small-ant testing, the ant's body length was half that of the mantis. All ant species were used in large-ant testing, but only *S. geminata* was used for small-ant testing.

In control tests, each mantis was left for 10 h alone in a cage ($N = 20$ for each mantis species) (mantises comparable in body length to the mantises used in ten-ant testing). These control tests provide baseline information on how likely it was that mantises might die of causes unrelated to ants during a 10-h period in the testing apparatus. Another series of control tests were carried out using two of the mantis species (*Orthodera* sp. and *Statilia* sp.): one mantis housed with one large myrmecomorphic salticid (*M. assimilis*) (i.e. the salticid's body length was comparable to the mantis' body length) (one-*Myrmarachne* test, $N = 20$ for each mantis species) or one mantis was housed with ten large myrmecomorphic salticids (*M. assimilis*) (ten-*Myrmarachne* test, $N = 20$ for each mantis species). We used

this control series because, from preliminary trials, we knew that large *Myrmarachne* did not prey on mantises and mantises did not prey on large *Myrmarachne* (i.e. these control tests provide baseline information on how many mantises tend to die because of indirect influences of being in the presence of ant-like arthropods rather than directly from predation by ants).

ALTERNATE-DAY TESTING OF MANTISES WITH ANTS AND SALTICIDS

Four questions were considered using a paired-testing design (i.e. each mantis was tested once with one type of prey and once with another type of prey; $N = 30$ for each combination).

Question 1: do mantises distinguish between ants and ordinary salticids?

Each mantis was tested on one day with an ant and, on the next or the previous test day, with an ordinary salticid (sequence random). Test duration was 10 h. After the first test, the mantis was put into a new cage with a new leaf and left until the next test (48 h later). The body length of the mantis was approximately five times the body length of each of the two alternative prey, and the body length of each prey matched within the nearest millimetre the body length of the other prey.

The design adopted aimed not to test each of the three mantis species with each ant species and each salticid species. We chose instead to use one ant species (*S. geminata*) as a standard against which we tested all 28 salticid species (i.e. the 23 ordinary salticids, the four typical *Myrmarachne* and *M. bakeri*). Because there were no statistically discernible differences across the 23 ordinary salticid species or across the four species of typical *Myrmarachne*, only pooled data are presented here.

Having found that the standard responses of mantises to ordinary salticids, typical *Myrmarachne* and ants did not vary significantly among species within each category, we paired only one representative salticid species per category (*P. petersi*, a representative ordinary salticid; *M. assimilis*, a representative good mimic; *M. bakeri*, the poor mimic) with each of eight ant species in an attempt to provide general information about the responses of mantises to these three salticid categories.

Question 2: do mantises distinguish between myrmecomorphic and ordinary salticids?

Testing methods were the same as for Question 1 except that myrmecomorphic salticids were used instead of ants. As for Question 1, only pooled data are presented because no discernible differences were

found across the 23 ordinary salticid species or across the four species of typical *Myrmarachne*.

In alternate-day tests with *M. assimilis* (representative good mimic) and with *M. bakeri* (poor mimic), we tested the 23 ordinary salticids with the three mantis species. Because the particular species of ordinary salticid did not affect the outcome of the test, only *P. petersi* was used, as a representative ordinary salticid, in tests with *M. bidentata*, *M. maxillosa*, and *M. nigella*.

Question 3: do mantises distinguish between ants and myrmecomorphic salticids?
Testing methods were the same as for Question 1 except that myrmecomorphic instead of ordinary salticids were used. *Solenopsis geminata* was used as a representative ant paired with each of the five myrmecomorphic salticids. However, because there was no significant difference across species of typical *Myrmarachne*, the results were pooled. The seven remaining ant species were tested with *M. assimilis* (representative good mimic) and with *M. bakeri* (the poor ant mimic).

Question 4: do mantises distinguish between M. bakeri and typical Myrmarachne?
Testing methods were the same as for Question 1 except that one prey was always an individual of *M. bakeri* and the other was an typical *Myrmarachne* (*M. assimilis*, *M. bidentata*, and *M. maxillosa; M. nigella* was not tested) ($N = 45$ for each mantis–*Myrmarachne* combination). Because the results for the different species of typical *Myrmarachne* were not significantly different, they were pooled for comparison with the results for *M. bakeri*.

Whenever prey died during a test, we recorded whether it was intact, had been masticated, or had been entirely consumed by the mantis. Intact remains of prey were rare, and they were not recorded as eaten by the mantis because all mantises thoroughly masticated prey when observed feeding, with little or nothing remaining of the prey afterwards. However, relaxing this rule and recording all instances of prey death never changed significant outcomes from nonsignificance.

RESULTS

OBSERVATIONS IN THE FIELD

On three occasions, mantises were seen in the field eating ordinary salticids: a nymph of *Orthodera* sp. eating *Carrhotus sannio*; a nymph of *Orthodera* eating an unidentified salticid; and adult female of *Statilia* sp. eating *Phintella piatensis*. On five occasions, ants were seen eating mantises in the field: *Diacamma rug-* *osum* eating *Loxomantis* sp.; *Oecophylla smaragdina* eating *Orthodera* sp.; *Oecophylla smaragdina* eating an unidentified mantis; *Solenopsis geminata* eating an unidentified mantis ($\times 2$). Mantises were never seen in the field eating ants or eating myrmecomorphic salticids.

MANTIS MORTALITY IN THE PRESENCE OF ANTS
No mantises died during any of the control tests, but at least some of the mantises died in all tests with ants (Fig. 1).

ALTERNATE-DAY TESTING WITH ANTS AND SALTICIDS
Most ants survived testing, and the ants that died were never masticated. However, almost all salticids that died during testing had been thoroughly masticated, or else completely consumed. Ordinary salticid species were eaten significantly more often than ants ($P < 0.001$ for each salticid species and for all species of mantis) and, within each salticid category (ordinary salticid and typical *Myrmarachne*), mortality did not differ significantly between species. To simplify the presentation of these data, we pooled, for each species of mantis, data from all ordinary salticids and from all typical *Myrmarachne*. Regardless of mantis species, survival of ants was not significantly different from survival of typical *Myrmarachne*. However, with *Statilia* sp. (Fig. 2) and with *Orthodera* sp. (Fig. 3), but not with *Loxomantis* sp. (Fig. 4), there were some instances in which the poor ant mimic, *M. bakeri*, had significantly lower survival than ants.
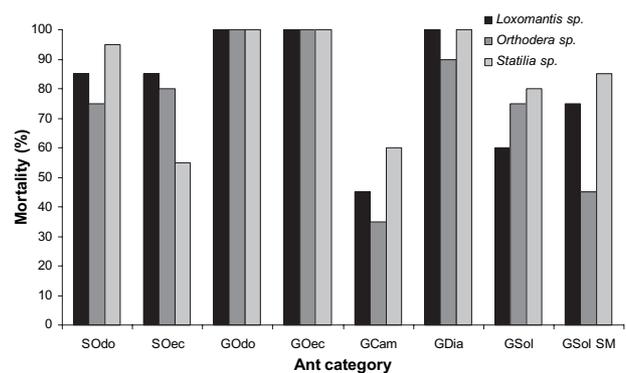

Figure 1. Mantis mortality in the presence of ants. $N = 20$ for each mantis–ant combination. SM indicates an ant that was half the size of the mantis. In all other tests, large ants (i.e. the same size as the mantis) were used. G, Group of ten ants (all species); S, single ant (only *Oecophylla smaragdina* and *Odontomachus* sp.); Cam, *Camponotus* sp.; Dia, *Diacamma rugosum*; Odo, *Odontomachus* sp.; Oec, *Oecophylla smaragdina*; Sol, *Solenopsis geminata*.
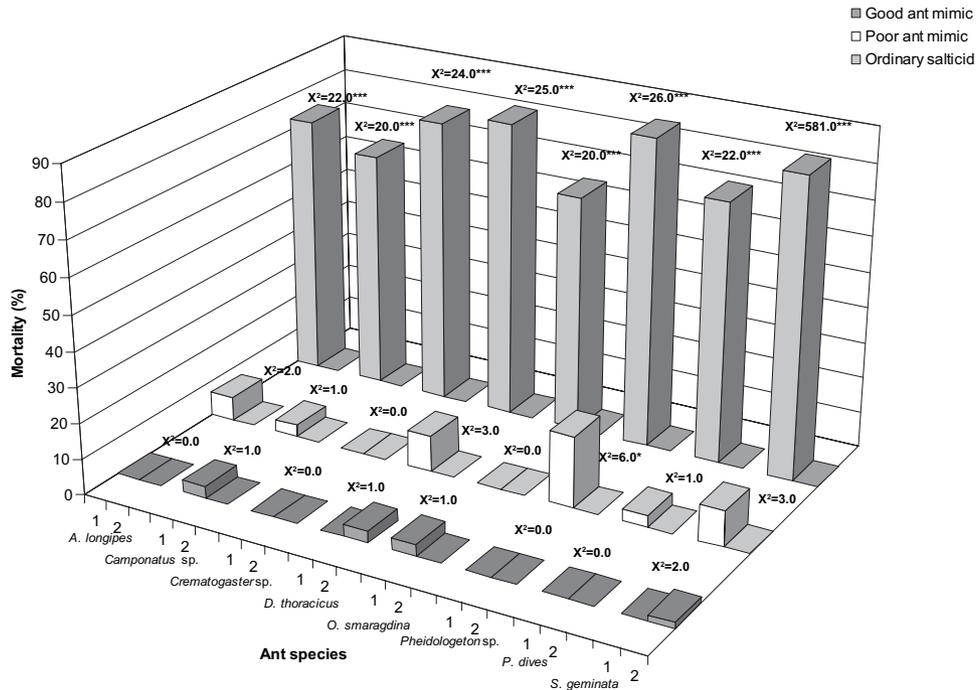
Figure 2. Alternate-day testing of *Statilia* sp. Each mantis was tested once with ant and once with salticid (good ant-mimic, *Myrmarachne bakeri*, and ordinary salticid). $N = 30$ for each ant–salticid combination (*Solenopsis geminata* tested with all salticids: $N = 120$ with good ant mimics and $N = 690$ with ordinary salticids). Mantis body length was five times that that of salticid. Salticids match in body length. 1 ate salticid but not ant (%). 2 ate ant but not salticid (%). *$P < 0.05$. ***$P < 0.001$.

When tested with an ant and with an ordinary salticid, all three mantis species discriminated strongly, often eating the salticid but seldom eating the ant. However, regardless of mantis species, ant survival was not significantly different from the survival of typical *Myrmarachne* (Figs 2–4).

When tested with an ordinary salticid and a myrmecomorphic salticid, the mantises discriminated strongly, eating the ordinary, but not the myrmecomorphic, salticid (Fig. 5). When tested with an individual of *M. bakeri* and with a typical *Myrmarachne*, the mantises usually ate neither prey, but ate *M. bakeri* more often than they ate the typical *Myrmarachne* (Fig. 6).

DISCUSSION

We avoid drawing conclusions about how the three mantis species might differ in their level of susceptibility to being killed by ants or about how the ant species differ in how readily they kill mantises. The present study was not concerned specifically with these comparisons for which conditions more closely simulating the natural environment might be needed. The conclusion drawn is simpler and more restricted:

evidently the ants we used are dangerous to the three mantis species studied.

It appears that the mantis species studied are innately averse to eating ants. In alternate-day tests, the same individual mantis that failed to eat an ant usually ate an ordinary salticid spider (i.e. a salticid that did not resemble an ant). These were our findings despite rearing the mantises under standardized conditions and denying them any prior experience with ants (i.e. what 'innate' means here is that the individual mantis' aversion to ants was not shaped by prior experience specifically with ants).

Evidently, the mantis' aversion to ants is generalized to myrmecomorphic (i.e. ant-like) salticids from the genus *Myrmarachne*. An alternative hypothesis is that the mantis perceives ants and myrmecomorphic salticids as two distinctly different categories, has an innate aversion for ants, and also has a separate innate aversion for myrmecomorphic salticids. This is a more difficult hypothesis to defend. Reluctance to eat myrmecomorphic salticids does not appear to be a consequence of a general reluctance to eat salticids because these same mantises readily preyed on ordinary salticids in alternate-day tests. Prey-size preferences cannot easily account for the findings because,
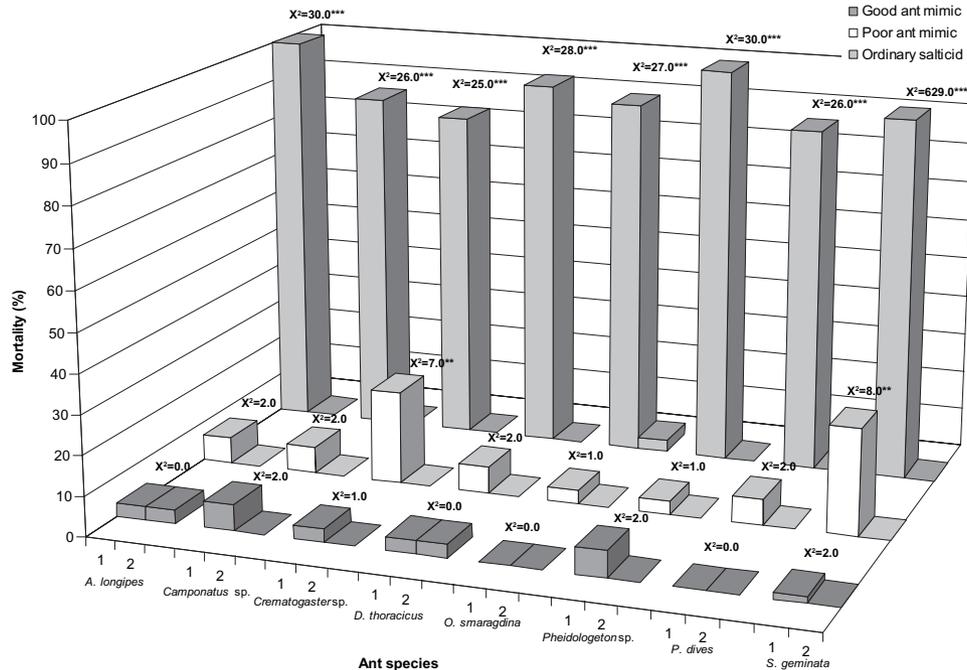
Figure 3. Alternate-day testing of *Orthodera* sp. Each mantis tested once with ant and once with salticid (good ant-mimic, *Myrmarachne bakeri*, and ordinary salticid). $N = 30$ for each ant–salticid combination (*Solenopsis geminata* tested with all salticids: $N = 120$ with good ant mimics and $N = 690$ with ordinary salticids). Mantis body length was five times that of salticid. Salticids match in body length. 1 ate salticid but not ant (%). 2 ate ant but not salticid (%). **$P < 0.01$. ***$P < 0.001$. All other results are non-significant.

despite the body lengths of ordinary salticids, myrmecomorphic salticids, and ants always being comparable, it was specifically the myrmecomorphic salticids (not ordinary salticids) that mantises avoided during alternate-day testing.

Although our mantis-survival experiment suggests that ants are potentially dangerous for a mantis, there is no evidence that myrmecomorphic salticids are, for a mantis, particularly dangerous. No mantises died in our control tests where large myrmecomorphic salticids were substituted for large ants (i.e. there is a clear rationale for expecting innate aversion to ants, but no clear rationale for expecting innate aversion specifically to myrmecomorphic salticids).

Myrmecomorphic salticids survived in the presence of mantises, despite ordinary salticids being readily eaten, and this appears to be a consequence of mantises mistaking myrmecomorphic salticids (palatable prey) for ants (unpalatable prey). As such, mrymecomorphic salticids are evidently, for mantises, Batesian mimics of ants.

Hypotheses about mimicry typically arise from judging how animals appear to our vertebrate eyes, but it is not a foregone conclusion that other animals see similarly to how we see (Cuthill & Bennet, 1993). This is only partly because animal eyes vary considerably in spatial acuity and spectral sensitivity (Land & Nilsson, 2002). Besides being sensory input through an animal's eyes to its brain, 'seeing' is also the product of cognitive processes (Schiffman, 1996; Blough & Blough, 1997; Shettleworth, 1998; Palmer, 1999).

Although our experiments were not designed to rule out sensory modalities other than vision by the mantis, our findings suggest some correspondence between how closely, for us, a salticid resembles an ant and how closely, for a mantis, a salticid resembles an ant. Even within the genus *Myrmarachne*, our own judgement of the degree of resemblance appears to be applicable to the mantis. *Myrmarachne bakeri* resembles ants, but not so strongly as typical *Myrmarachne*, and mantises also ate *M. bakeri* more often than they ate typical *Myrmarachne*.

In a Batesian mimicry system, we expect the model, the mimic, and the predator to be sympatric, and the participants in the system may be subject to interesting consequences of frequency-dependent selection (Joron & Mallet, 1998; Lindstrom, Alatalo & Mappes, 1997). An especially common hypothesis is that the palatable Batesian mimic normally needs to be experienced by the predator as rare relative to the palatable model (Turner, Kearney & Exton, 1984).
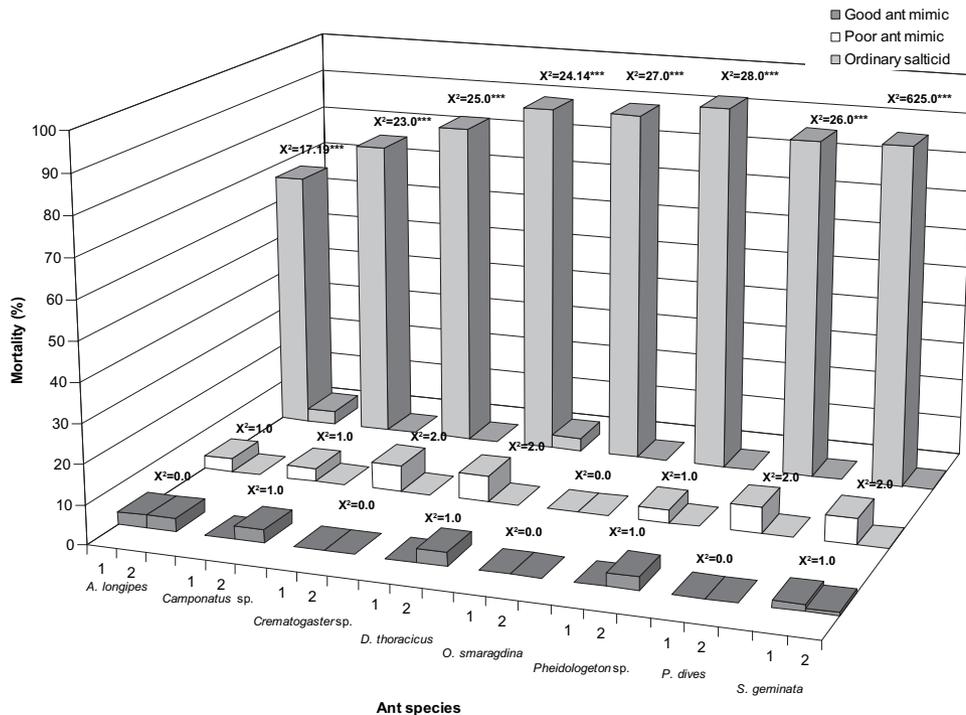
Figure 4. Alternate-day testing of *Loxomantis* sp. Each mantis tested once with ant and once with salticid (good ant-mimic, *Myrmarachne bakeri*, and ordinary salticid). *N* = 30 for each ant–salticid combination (*Solenopsis geminata* tested with all salticids: *N* = 120 with good ant mimics and *N* = 690 with ordinary salticids). Mantis body length was five times that of salticid. Salticids match in body length. 1 ate salticid but not ant (%). 2 ate ant but not salticid (%). ***$P < 0.001$. All other results are non-significant.

There appear to be two basic ideas behind this hypothesis: (1) when mimics are rarely encountered, there may be little for the predator to gain by discriminating accurately between mimic and model (i.e. it does not miss many feeding opportunities by mistaking mimics for models) and (2) mistaken identification (attacking the unpalatable model by mistake instead of a mimic) is dangerous (costly), but this cost is more often avoided when the mimic is more common.

Theory concerning the relationship between Batesian mimicry and frequency-dependent selection most often assumes learned, instead of innate, aversion (Howarth, Edmunds & Gilbert, 2004). The same basic argument may apply for both, but perhaps not with the same force. For example, the rate at which an individual predator's learned aversion might be altered by shifting the relative abundance of the model and mimic is likely to be rapid compared with the rate at which selection alters innate aversion in a population over evolutionary time.

Finding evidence that mantises are innately averse to eating ants and to eating myrmecomorphic salticids does not rule out the possibility that learn-

ing is important in this mantis–ant–spider system. On first encounter, the three mantises that we studied were disinclined to eat the mimic. We have not investigated whether mantises might become more discriminating over successive trials. Indeed, learning in mantises is well documented (Gelperin, 1968; Maldonado & Tablante, 1975; Berenbaum & Miliczky, 1984; Bowdish & Bultman, 1993), suggesting that the mantis might improve discrimination over time.
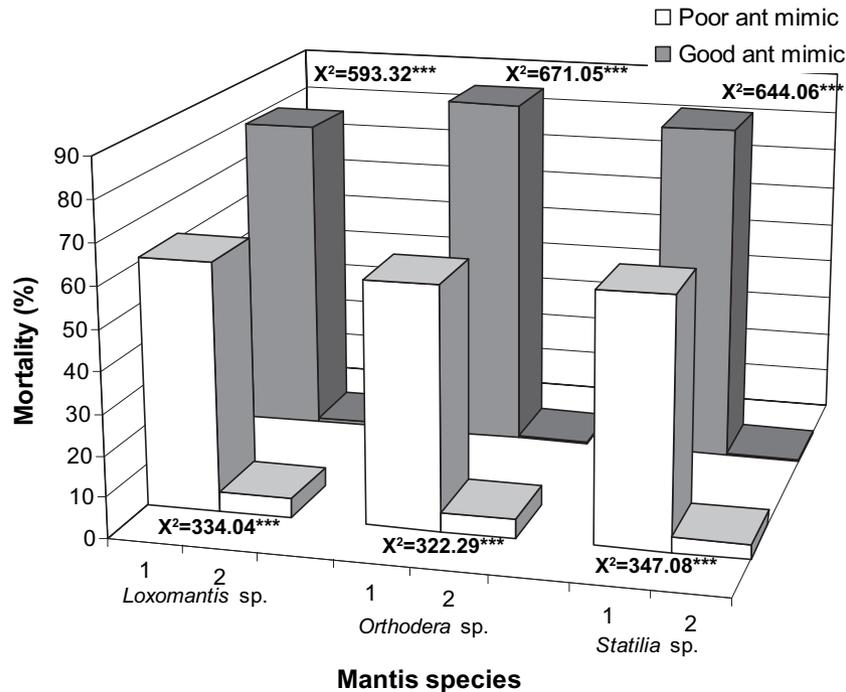
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Figure 5. Alternate-day testing with good and poor ant mimics. $N = 30$ for each combination. Each mantis tested once with a myrmecomorphic salticid and once (48 h before or after) with and ordinary salticid. Mantis body length was five times that of salticid. Salticids match in body length. 1 ate ordinary salticid but not myrmecomorphic salticid (%). 2 ate myrmecomorphic salticid but not ordinary salticid (%). ***$P < 0.001$.
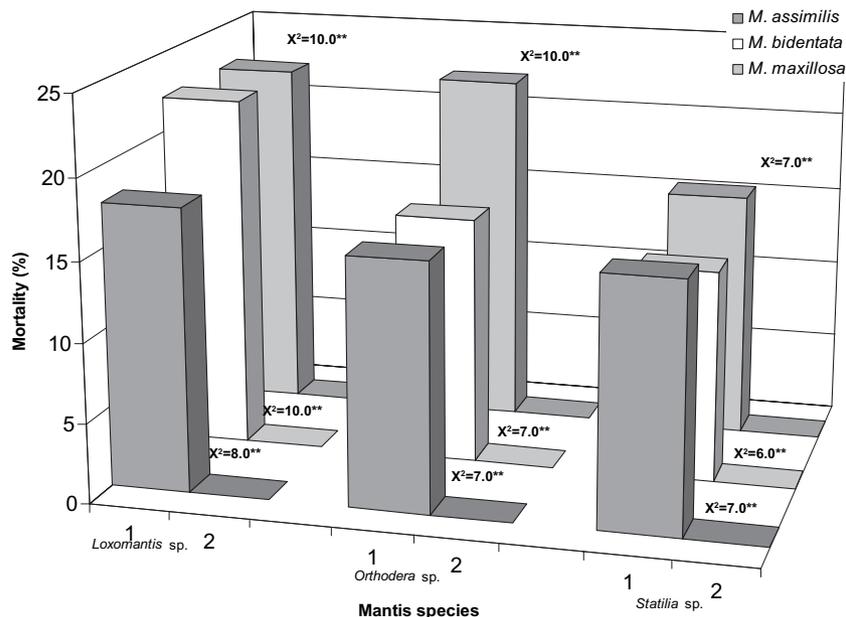

Figure 6. Alternate-day testing with good (*Myrmarachne assimilis*, *Myrmarachne bidentata*, and *Myrmarachne maxillosa*) and poor (*Myrmarachne bakeri*) ant mimics. $N = 45$ for each combination. Each mantis tested once with good ant-mimic and once (48 h before or after) with *M. bakeri*. Mantis body length was five times that of salticid. Salticids match in body length. 1 ate *M. bakeri* but not good ant mimic (%). 2 ate good ant mimic but not *M. bakeri* (%). **$P < 0.01$.

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