

# Conditional use of honest signaling by a Batesian mimic

Ximena J. Nelson,<sup>a</sup> Robert R. Jackson,<sup>a</sup> and Daiqin Li<sup>b</sup>

<sup>a</sup>School of Biological Sciences, University of Canterbury, Private Bag 4800, Christchurch, New Zealand and <sup>b</sup>Department of Biological Sciences, National University of Singapore, Singapore 119260

Jumping spiders (Salticidae) usually avoid ants, but some species within this family single out ants as preferred prey, while others (especially the species in the genus *Myrmarachne*) are Batesian mimics of ants. Field records show that ant-eating salticids sometimes prey on *Myrmarachne*, suggesting that the unwanted attention of predators that specialize on the model may be an important, but poorly understood, cost of Batesian mimicry. By staging encounters in the laboratory between living ant-eating salticids and *Myrmarachne*, we determined that ant-eating salticids attack *Myrmarachne*. However, when *Myrmarachne* detects a stalking ant-eating salticid early enough, it adopts a distinctive display posture (legs almost fully extended, elevated 45°, and held out to the side 45°), and this usually deters the predator. When *Myrmarachne* detects an ant-eating salticid before stalking begins, *Myrmarachne* makes preemptive displays that appear to inhibit the initiation of stalking. Using immobile lures made from dead *Myrmarachne* that were either in a display posture or a nondisplay posture, we ascertained that specifically the display posture of *Myrmarachne* deters the initiation of stalking (ant-eating salticids stalked nondisplaying more often than displaying lures). In another experiment, we ascertained that it is specifically the interjection of display posture that deters stalking. When ant-eating salticids that had already begun stalking experienced lures that switched from a nondisplay to a display posture, they stopped stalking. Although the unwanted attentions of its models' predators may be, for *Myrmarachne*, a hidden cost of Batesian mimicry, *Myrmarachne* appears to have an effective defense against these predators. *Key words*: antipredator behavior, ants, Batesian mimicry, Salticidae, signals. [*Behav Ecol* 17:575–580 (2006)]

Having potent defenses, which may include powerful mandibles, poison-injecting stings, formic acid, and the ability, as social insects, to launch communal attacks (Hölldobler and Wilson 1990), ants appear to be especially suitable model species in Batesian mimicry systems (Edmunds 1972, 1993; Cushing 1997), and ant mimicry has evolved repeatedly, not only in insects, but also in spiders (McIver and Stonedahl 1993). However, trading one predator for another may be a significant problem for a Batesian mimic because prey that is unpalatable to one predator may be the preferred prey of another (Nelson et al. 2006). This hidden cost may be especially applicable to ant mimics because numerous spiders and predatory insects have evolved specialization at preying on ants (Jackson et al. 1998; Brandt and Mahsberg 2002). When the models' predators become significant problems for the mimic, the evolution of effective defenses against these particular predators might be expected.

Our hypothesis is that ant mimics sometimes defend themselves against ant-eating predators by actively revealing to these predators that they are not really ants. There are other well-known examples of prey defending themselves by honestly communicating with predators. For example, prey may deter predators by accurately revealing their ability to defend themselves (Caro et al. 2004). However, what we show here is different because it is the first detailed study of a Batesian mimic defending itself by switching to honest communication during encounters with the models' predators.

The specific example we consider is a system in which the predators and the mimics are jumping spiders and the models

are ants. Jumping spiders (Salticidae) are of particular interest because of their exceptional eyesight (Land and Nilsson 2002) and their intricate vision-guided predatory behavior (Jackson and Pollard 1996). Although most salticids may be generalist insectivores that avoid ants (Harland and Jackson 2001), a sizeable minority (the ant-eating salticids) routinely feed on ants, adopt ant-specific prey-capture behavior, and actively select ants as preferred prey (Jackson et al. 1998; Jackson and Li 2001). Another sizeable minority of the Salticidae (the ant-like salticids) have a morphological and behavioral resemblance to ants (Cushing 1997). *Myrmarachne*, the largest genus of ant-like salticids (Wanless 1978), is especially diverse in tropical Asia, Africa, and Australasia, and ant-eating salticids tend to be common in the same habitats (Jackson and Willey 1994). Previous experimental work has shown that the ant-like appearance of species in this genus is effective at deterring ant-averse predators (Harland and Jackson 2001; Nelson and Jackson, forthcoming).

Over a 20-year period (1984–2004), records have been kept of all instances in which salticids were seen feeding in the field (RR Jackson, unpublished data). Within this larger data set, there are no records of ant-eating salticids eating non-ant-like salticids and no records of *Myrmarachne* eating ants, but there are, besides several hundred records of ant-eating salticids eating ants, 14 records of ant-eating salticids eating ant-like salticids. These records suggest that the unwanted attentions of the ants' predators may sometimes impact adversely on ant mimics.

Salticids are renowned for the elaborate vision-based displays they adopt during courtship and when threatening conspecific rivals of the same sex, but salticids do not routinely display at other species (Jackson and Pollard 1997). Ongoing research (RR Jackson and XJ Nelson, unpublished data) is revealing that *Myrmarachne* is different because the species in this genus tend to display briefly when approached head-on by another salticid, even when the other salticid belongs to a different species or genus and is not ant-like in appearance.

Address correspondence to X.J. Nelson, who is now at the Department of Psychology, Animal Behavior Laboratory, Macquarie University, Sydney, New South Wales 2109, Australia. E-mail: ximena@galliform.bhs.mq.edu.au.

Received 5 August 2005; revised 27 February 2006; accepted 8 March 2006.

Table 1

Results from standard tests (body length of predator 2× body length of prey) ( $N = 225$ ) of encounters staged between ant-eating salticids (predators) and ant-like salticids (prey)

Ant-eating salticid	Ant-like salticid ( <i>Myrmarachne</i> )	Number of occurrences in which the ant-eating salticid performed the stated outcome				
		Stalked and preyed on nondisplaying <i>Myrmarachne</i>	Stalked and preyed on displaying <i>Myrmarachne</i>	Stalked displaying <i>Myrmarachne</i> but desisted before attacking	Did not stalk displaying <i>Myrmarachne</i>	No stalking and no displaying
<i>Chalcotropis gulosa</i> <sup>a</sup>	<i>M. assimilis</i> <sup>a</sup>	3	1	9	10	2
<i>Chalcotropis gulosa</i> <sup>a</sup>	<i>M. bakeri</i> <sup>a</sup>	2	0	14	8	1
<i>Chalcotropis gulosa</i> <sup>a</sup>	<i>M. bidentata</i> <sup>a</sup>	4	0	10	7	4
<i>Chalcotropis gulosa</i> <sup>a</sup>	<i>M. maxillosa</i> <sup>a</sup>	1	1	11	11	1
<i>Chrysilla lauta</i> <sup>b</sup>	<i>M. plataleoides</i> <sup>b</sup>	7	0	9	8	1
<i>Natta rufopicta</i> <sup>c</sup>	<i>M. kilifi</i> <sup>c</sup>	6	0	8	10	1
<i>Siler semiglaucous</i> <sup>b</sup>	<i>M. plataleoides</i> <sup>b</sup>	5	0	10	9	1
<i>Zenodorus orbiculatus</i> <sup>d</sup>	<i>M. lupata</i> <sup>d</sup>	4	1	11	7	2
<i>Xenocytaea</i> sp. <sup>a</sup>	<i>M. bakeri</i> <sup>a</sup>	8	0	6	9	2
Summary		40	3	88	79	15

$n = 25$  for each row. Designated footnotes provide the origins of individuals from which laboratory cultures were started.

<sup>a</sup> The Philippines.

<sup>b</sup> Sri Lanka.

<sup>c</sup> Kenya.

<sup>d</sup> Australia.

Yet *Myrmarachne* does not normally display at ants or at any arthropods other than salticids.

In encounters with conspecifics, *Myrmarachne*'s initial display (see Jackson 1982) is to posture with its forelegs elevated 45° and held out to the side 45°, all joints distal to the femur-patella being fully extended (called "erect-legs posture"). Erect-legs postures are especially common displays within the family Salticidae (Jackson and Pollard 1997) and are very non-ant-like in appearance. With conspecifics, *Myrmarachne* may display before being faced by the other spider, and the initial erect-legs posturing is usually followed by a complex sequence of displays (XJ Nelson and RR Jackson, in preparation). However, when the individual encountered is not conspecific, erect-legs display posture is typically adopted only when *Myrmarachne* and the other spider are face to face, usually but not always with the other spider approaching, and *Myrmarachne* typically moves away and stops displaying quickly after posturing for no more than a few seconds (RR Jackson and XJ Nelson, unpublished data). The hypothesis that we consider here is that these momentary bouts of adopting non-ant-like posture deter ant-eating salticids.

## MATERIALS AND METHODS

### General

All living spiders (Table 1) came from laboratory culture, with maintenance, testing procedures, cage design, terminology, and conventions for describing behavior being as in earlier spider studies (Jackson and Hallas 1986). Testing was carried out at the International Rice Research Institute in Los Baños (The Philippines) and at the University of Canterbury (New Zealand) between 09:00 AM and 11:00 AM (laboratory photoperiod 12:12 h light:dark, lights on at 08:00 AM). Test spiders had no prior contact with any other salticids or with ants. Hunger was standardized by keeping each salticid without prey for 5 days. No individual salticid was tested more than once.

All ant-like salticids used were juveniles and adult females of *Myrmarachne*. Adult males were not used because there is pronounced sexual dimorphism in this genus (Pollard 1994),

with males having greatly elongated chelicerae that, to the human eye, detract from the males' ant-like appearance (but see Nelson and Jackson 2006). We chose as predators 6 ant-eating species for which details of prey-capture behavior are known (Jackson and van Olphen 1992; Li and Jackson 1996; Jackson et al. 1998; Jackson and Li 2001). As the adult males of many salticids appear to feed less readily than adult females and juveniles (Givens 1978; Jackson and Pollard 1997), we used only adult females and large juveniles as test spiders in the experiments reported here.

For baseline information about how predators and prey interacted, we staged encounters between living ant-like and ant-eating salticids in the laboratory (live-prey tests). Taking into account details about the different predatory tactics of the different ant-eating species that we used, we carried out 3 variations on live-prey testing, standard tests, large-prey tests, and bark tests (see below). In each instance, testing was carried out by leaving one ant-eating and one ant-like salticid together until predation occurred or until 30 min elapsed, whichever came first. Live-prey testing was followed by experiments (using lures) designed to test hypotheses suggested by the findings from live-prey tests.

In all instances, the 2 species paired in a test were sympatric. Data from using different combinations of ant-eating and ant-like species were not significantly different (standard tests:  $\chi^2 = 26.1$ ,  $P = 0.758$ ,  $df = 32$ ; large-prey tests:  $\chi^2 = 8.68$ ,  $P = 0.467$ ,  $df = 9$ ), and these data were pooled for each test. Data were analyzed using Fisher's Exact tests of independence and chi-square tests of independence.

### Standard tests using living prey

The body length of the ant-eating salticid was, to the nearest millimeter, twice the body length of the ant-like salticid. This meant that, in our tests, *Myrmarachne*'s size relative to that of the ant-eating salticids corresponded to the size of ants and other prey that ant-eating salticids have usually been seen feeding on in the field (see Jackson et al. 1998).

The 2 salticids were placed in a plastic cage made from a petri dish (diameter 140 mm) with 2 corked holes (diameter

10 mm) in its bottom surface, the center of each of these holes being 20 mm from the nearest side of the cage and 100 mm from the center of the other cork hole. The ant-like salticid was introduced into the cage through one hole, and then the ant-eating salticid was immediately introduced through the other hole to start a test.

### Large-prey tests using living prey

Methods for large-prey tests were the same as for standard tests except that only *Chalcotropis gulosa* was used as a predator. In these tests, the body lengths of *C. gulosa* and the ant-like salticids were matched for size because field records (RR Jackson, unpublished data) revealed that *C. gulosa* is an exception among ant-eating salticids in that it often preys on large ants and its ant-specific prey-capture behavior has been observed only when the ants are large (Jackson et al. 1998).

### Bark tests using living prey

We used only *Zenodorus orbiculatus* in bark tests ( $N = 50$ ) because this species expresses distinctive ant-specific prey-capture behavior only when on tree trunks (Jackson and Li 2001). Tests were carried out by placing one individual of *Myrmarachne lupata* together with one individual of *Z. orbiculatus* (body length of *Z. orbiculatus* twice that of *M. lupata*) on a piece of *Eucalyptus* bark (100 mm high  $\times$  30 mm wide). The bark was held vertical (lower end 100 mm above table top) by a clamp (connected to top end of bark). The other end of the clamp was connected via a 300-mm-long rigid cable to a stand (sitting on a table) 300 mm behind the bark.

Using a paintbrush, an individual of *Z. orbiculatus* was first coaxed out onto the top end of the bark. Once it became quiescent, facing downward, an individual of *M. lupata* was coaxed out onto the bottom end of the bark (same side). Testing began when *M. lupata* first came to within 50 mm of *Z. orbiculatus* (overt reactions by either spider were never witnessed at distances greater than 50 mm when *Z. orbiculatus* was quiescent on bark). Whenever *Z. orbiculatus* failed to become quiescent facing down at the top of the bark within 60 s of being coaxed onto the bark, testing was aborted.

### Simultaneous-presentation tests using lures

Using immobile lures made from dead *Myrmarachne* that were either in an erect-legs display posture or a nondisplay posture, we investigated whether it is specifically the display posture of *Myrmarachne* that deters the initiation of stalking by ant-eating salticids. Testing with stationary lures avoids confounding variables from cues other than the arthropod's static appearance, and much previous experimental work has shown that salticids respond readily to stationary lures made from dead arthropods mounted in lifelike posture on cork discs (Jackson and Tarsitano 1993; Jackson et al. 2005). Here our prediction is that, given the choice between *Myrmarachne* in a display and a nondisplay posture, ant-eating salticids more often stalk the nondisplaying *Myrmarachne*.

Each lure was made by immobilizing an adult *Myrmarachne assimilis* female with CO<sub>2</sub> and then placing it in 80% ethanol. One day later, it was mounted in a lifelike posture in the center of a disc-shaped piece of cork (diameter ca. 1.25 $\times$  the length of the spider). The mounted *Myrmarachne* was next sprayed with an aerosol plastic adhesive for preservation. In each test, there were 2 lures matched for body length within the nearest millimeter (one in the erect-legs posture and one in nondisplay posture). No individual lure was used in more than one test.

In these tests, a Y-shaped ramp (2 arms) was used (see Jackson et al. 1998), each arm ending at a brown wooden wall

(55 mm high, 40 mm wide, and 15 mm thick) glued perpendicular to the top end of the arm. Before testing started, the test spider was kept in a covered pit near the lower end of the ramp until quiescent. Testing was begun by removing a transparent glass plate used as a cover, allowing the test spider to walk up the stem of the ramp with a view of both lures (display and nondisplay) at each end of the ramp (lure positioned on the left vs. right decided at random). Each lure was centered 10 mm in front of a wall and was facing the pit.

Successful tests ended when the spider, after leaving the pit, oriented toward the lure (i.e., when it aligned its large anterior-medial eyes with the lure) and maintained this orientation while moving past the "threshold," the threshold being a line at the juncture of the 2 arms with the stem of the Y-shaped ramp (40 mm from the center of the pit). The test spider's choice was recorded as the lure at the top of the arm onto which it walked when crossing the threshold. There were no instances in which the salticid walked across the threshold without first orienting toward the lure. Data were analyzed using chi-square tests of goodness of fit.

### Sequential-presentation tests using lures

Another experiment was carried out using lures, with the rationale this time being to determine whether it is specifically *Myrmarachne's* interjection of display posture that deters the stalking behavior of ant-eating salticids. In this experiment, after an ant-eating salticid had already begun stalking, it experienced lures that switched from a nondisplay to a display posture (experimental tests) or did not switch posture (control).

In these tests, a linear ramp was used (for details, see Jackson et al. 1998) (100 mm long, wall at top, pit at bottom). Two lures (lure-making methods same as in simultaneous-presentation tests) were held behind a wall on a sliding rack. There was a square window centered at the base of the wall. By moving the rack side to side, one or the other lure could be positioned so that it was visible through the window. As in tests with the Y-shaped ramp, the predator was kept in a covered pit until quiescent, and the cover was removed to start a test. The predator walked up the ramp and viewed the lure that was positioned behind the window. The threshold was a line on the ramp 50 mm from the window.

When testing began, the lure that was visible was a nondisplaying *M. assimilis*. When the predator crossed the threshold, the rack was moved so that the other lure became visible. In experimental tests, the lure that now became visible was a displaying *M. assimilis*. In control tests, it was another nondisplaying *M. assimilis*. After switching lures, we recorded whether the predator crossed a line 25 mm from the window (continued stalking) or stopped stalking and failed to reach the line 25 mm from the window (discontinued stalking). Although details vary among species, salticid stalking behavior is readily identifiable (see Forster 1977; Jackson and Pollard 1996). With the gaze of its anterior-medial eyes fixated on the prey, its palps stationary in front of the chelicerae, and its body lowered, the salticid makes a slow, distinctive approach toward its potential prey.

Testing was aborted whenever the salticid walked or leapt off the ramp without crossing the threshold and whenever the salticid remained on the ramp for 30 min without crossing the threshold. Aborted tests were rare (<5%). Data were analyzed using chi-square tests of independence.

## RESULTS

### Live-prey testing

On the whole, test outcomes were similar across the 3 variations of live-prey testing. Ant-eating salticids stalked *Myrmarachne*

Table 2

Results from large-prey tests (predator and prey matched in body length) ( $N = 100$ ) of encounters staged between *Chalcotropis gulosa*, an ant-eating salticid (predator), and antlike salticids (prey)

Antlike salticid ( <i>Myrmarachne</i> )	Number of occurrences in which the ant-eating salticid performed the stated outcome			
	Stalked and preyed on nondisplaying <i>Myrmarachne</i>	Stalked displaying <i>Myrmarachne</i> but desisted before attack	Did not stalk displaying <i>Myrmarachne</i>	No stalking and no displaying
<i>M. assimilis</i>	1	9	13	2
<i>M. bakeri</i>	4	10	7	4
<i>M. bidentata</i>	2	12	9	2
<i>M. maxillosa</i>	3	10	12	0
Summary	10	41	41	8

$n = 25$  for each row. There were no instances of predator stalking and capturing prey that had displayed during an earlier bout.

and, as predicted, *Myrmarachne* frequently responded by displaying at the stalking predator. As predicted, once displayed at, the predator stopped stalking and almost never attacked. There were also instances of *Myrmarachne* displaying at ant-eating salticids that were facing head-on but had not begun stalking. Once displayed at, these salticids never began stalking. Displays never lasted for more than a few seconds, after which *Myrmarachne* moved rapidly away, and there were no instances of *Myrmarachne* attacking the ant-eating salticid.

#### Standard tests using living prey

The ant-eating salticid stalked *Myrmarachne* in 131 (58%) of 225 standard tests but captured *Myrmarachne* in only 43 (19%) (Table 1). *Myrmarachne* displayed at the stalking ant-eating salticid in 170 of 225 tests (76%), and the ant-eating salticid preyed on *Myrmarachne* in only 3 (2%) of these tests (Table 1). In each of these 3 instances, the *Myrmarachne*, having stopped displaying and moved away, was stalked many minutes later by the ant-eating salticid and captured while facing away and without displaying again. In 79 (35%) tests, *Myrmarachne* displayed, and the ant-eating salticid failed to stalk or attack (Table 1). *Myrmarachne* failed to display in 55 (24%) of the 225 tests and was captured in 40 (73%) of these 55 tests. There were significantly more instances of predation on *Myrmarachne* that failed to display (40 out of 55) than on those that did display (3 out of 170) ( $\chi^2 = 135.37$ ,  $P < 0.001$ ,  $df = 1$ ).

#### Large-prey tests using living prey

*Chalcotropis gulosa* stalked *Myrmarachne* (Table 2) in 51 of 100 tests. *Myrmarachne* displayed at the ant-eating salticid in 82 tests. In these 82 tests, if *C. gulosa* was stalking, it always desisted, and if it had not yet begun, *C. gulosa* remained the rest of the test period without initiating stalking. *Myrmarachne* failed to display in 18 tests and was captured in 10 of these 18 tests. As in standard tests, there were significantly more instances of predation on *Myrmarachne* that failed to display (10 out of 18) than on those that did display (0 out of 82) ( $\chi^2 = 58.82$ ,  $P < 0.001$ ,  $df = 1$ ).

#### Bark tests using living prey

*Zenodorus orbiculatus* made ambushing attacks and captured *M. lupata* in 9 tests ( $N = 50$ ). *Myrmarachne lupata* did not display in any of these 9 tests. In 20 tests, *M. lupata* displayed at the quiescent *Z. orbiculatus* and then walked away without being attacked. In another 21 tests, *M. lupata* walked past *Z. orbiculatus* without displaying, and *Z. orbiculatus* remained

quiescent. There were no instances of predation on displaying *M. lupata*, and there were significantly more instances of predation on *M. lupata* that failed to display (9 out of 30) than on *M. lupata* that did display (0 out of 20) ( $\chi^2 = 10.92$ ,  $P < 0.001$ ,  $df = 1$ ).

#### Simultaneous-presentation tests with lures

As predicted, when given the choice between a displaying and a nondisplaying *Myrmarachne* lure, *C. gulosa* chose the nondisplaying *Myrmarachne* lure ( $n = 27$ ) significantly more often ( $\chi^2 = 10.31$ ,  $P = 0.001$ ,  $df = 1$ ) than the displaying *Myrmarachne* lure ( $n = 8$ ).

#### Sequential-presentation tests with lures

During experimental trials (i.e., when a displaying lure was substituted for a nondisplaying lure), 18 of 20 ant-eating salticids discontinued stalking. Significantly fewer (4 out of 25) ant-eating salticids discontinued stalking during control tests (i.e., when another nondisplaying lure was substituted) ( $\chi^2 = 24.35$ ,  $P < 0.001$ ,  $df = 1$ ).

## DISCUSSION

During live-prey tests, *Myrmarachne* typically survived encounters with ant-eating salticids, and displaying appeared to be the deciding factor. Experimental findings from testing with lures corroborated our hypotheses that it is specifically *Myrmarachne*'s display behavior that inhibits the initiation of stalking by ant-eating salticids and that it is specifically *Myrmarachne*'s display behavior that causes stalking ant-eating salticids to desist.

Although rarely considered in the literature, it may be common for Batesian mimics to trade one set of predators for another. More specifically, an earlier study (Nelson et al. 2006) suggested that ant mimicry may be advantageous for *Myrmarachne* when the predator is an ant-averse salticid but disadvantageous when the predator is a salticid that specializes on ants as prey. Presumably, for a successful mimic, the advantage of becoming unattractive to predators that are averse to the model outweighs the cost of becoming attractive to predators that specialize on the model. Perhaps the most obvious factor might be that encounters with ant-averse predators are considerably more frequent than encounters with the models' predators.

However, here we have shown another factor that may sometimes ameliorate the problem, for a Batesian mimic, of attracting the unwanted attentions of the models' predators.

*Myrmarachne* appears to be an ant mimic that can, either before or after the models' predators initiate predatory behavior, actively defend itself by adopting a non-antlike posture (i.e., by displaying with erect legs).

Our field data confirm that ant-mimicking salticids are at least sometimes subject to fatal encounters with ant-eating salticids, but witnessing predation on any salticid species in the field is exceedingly rare and we cannot estimate how often *Myrmarachne* encounters ant-eating salticids in nature. We also do not know whether displaying might be, for ant-like salticids, an effective defense against any other ant-eating predators besides ant-eating salticids. However, in this study, our goal has been primarily to illustrate that a Batesian mimic might sometimes defend itself against its models' predators by revealing to these predators that it is not, in fact, an individual of the model species.

For ant-eating salticids, a nondisplaying *Myrmarachne* seems to resemble preferred prey (i.e., ants) (Nelson et al. 2006) and a displaying *Myrmarachne* seems to be identified as not something to treat as preferred prey. In at least this limited sense, we might conclude that, by displaying, the ant mimic honestly advertises its true identity to its models' predators. This does not necessarily mean that the ant-eating salticid identifies *Myrmarachne* as something more specific (e.g., as another salticid), but we might consider the possibility that *Myrmarachne's* display, being so similar to that of many other salticids (Jackson and Pollard 1997), identifies *Myrmarachne* as not simply non-ant but as a salticid making a threat display. Having never seen *Myrmarachne* attack an ant-eating salticid, we have no evidence that *Myrmarachne* actually is dangerous to the ant-eating salticid, and it might be that, if the ant-eating salticid identifies a displaying *Myrmarachne* as a potentially dangerous rival salticid, then *Myrmarachne* is communicating dishonestly with respect to whether it is dangerous or not. Yet this does not appear to change the basic conclusion that, by displaying, *Myrmarachne* reveals accurately that it is not an ant (i.e., ants do not adopt the posture of a displaying *Myrmarachne*).

The findings from testing with lures show that, for the ant-eating salticid, specifically the appearance of a displaying *Myrmarachne* can inhibit ant-eating salticids' predatory behavior. The simultaneous-presentation tests simulated preemptive displays by *Myrmarachne*, and in these tests, as predicted, the ant-eating salticid more often initiated stalking of the nondisplaying rather than the displaying lure. The sequential-presentation tests simulated *Myrmarachne* displaying in response to being stalked by an ant-eating salticid, and in these tests, as predicted, we found that ant-eating salticids that had been stalking a nondisplaying lure of *Myrmarachne* usually desisted when suddenly faced by a displaying *Myrmarachne*.

Although Batesian mimicry may miscarry when mimics elicit the unwanted attentions of their models' predators, our findings suggest that it may be interesting to look for other examples where mimics do not suffer this cost passively but instead actively defend themselves by revealing their true identity to these predators. *Myrmarachne* appears to have a conditional antipredator strategy that is based on maintaining Batesian mimicry during encounters with most potential predators but turning Batesian mimicry off (i.e., adopting erect-legs posturing) when faced by ant-eating salticids. The primary cues that trigger *Myrmarachne's* adoption of erect-legs posturing may be seeing any salticid approaching head-on. However, this does not alter the basic conclusion about a conditional antipredator strategy because, based on earlier work, we know that most salticids avoid getting close to ants or to ant-like salticids (Nelson and Jackson forthcoming). If a non-conspecific salticid is approaching, it is most likely to be an ant-eating salticid species.

Work in the Philippines was assisted by the International Rice Research Institute. We are especially grateful to Alberto Barrion, Kong Luen Heong, Tom W. Mew, Elpic Hernández, Errol Rico, Glicerio Javier, Josie Lynn Catindig, and Clod Lapis. This research was assisted in part by grants to RRJ from the Marsden Fund of the Royal Society of New Zealand.

## REFERENCES

- Brandt M, Mahsberg D. 2002. Bugs with a backpack: the function of nymphal camouflage in the West African assassin bugs *Paredocla* and *Acanthaspis* spp. *Anim Behav* 63:277–84.
- Caro TM, Graham CM, Stoner CJ, Vargas JK. 2004. Adaptive significance of antipredator behavior in artiodactyls. *Anim Behav* 67:205–28.
- Cushing PE. 1997. Myrmecomorphy and myrmecophily in spiders: a review. *Fla Entomol* 80:165–93.
- Edmunds ME. 1972. Defensive behavior in Ghanaian preying mantids. *Zool J Linn Soc* 51:1–32.
- Edmunds ME. 1993. Does mimicry of ants reduce predation by wasps on salticid spiders? *Mem Queensl Mus* 33:507–12.
- Forster LM. 1977. A qualitative analysis of hunting behavior in jumping spiders (Araneae: Salticidae). *N Z J Zool* 4:51–62.
- Givens RP. 1978. Dimorphic foraging strategies of a salticid spider (*Phidippus audax*). *Ecology* 59:309–21.
- Harland DP, Jackson RR. 2001. Prey classification by *Portia fimbriata*, a salticid spider that specializes at preying on other salticids: species that elicit cryptic stalking. *J Zool Lond* 255:445–60.
- Hölldobler B, Wilson EO. 1990. *The ants*. Heidelberg, Germany: Springer-Verlag.
- Jackson RR. 1982. The biology of ant-like jumping spiders: intraspecific interactions of *Myrmarachne lupata* (Araneae, Salticidae). *Zool J Linn Soc* 76:293–319.
- Jackson RR, Hallas SEA. 1986. Comparative studies of *Portia*, araneophagic web-building jumping spiders (Araneae, Salticidae): predatory versatility, utilisation of silk, and intraspecific interactions of *P. africana*, *P. albimana*, *P. fimbriata*, *P. labiata*, and *P. schultzei*. *N Z J Zool* 13:423–89.
- Jackson RR, Li D. 2001. Prey-capture techniques and prey preferences of *Zenodorus durvillei*, *Z. metallescens* and *Z. orbiculata* tropical ant-eating jumping spiders (Araneae: Salticidae) from Australia. *N Z J Zool* 28:299–341.
- Jackson RR, Li D, Barrion AT, Edwards GB. 1998. Prey-capture techniques and prey preferences of nine species of ant-eating jumping spiders (Araneae: Salticidae) from the Philippines. *N Z J Zool* 25:249–72.
- Jackson RR, Nelson XJ, Sune GO. 2005. A spider that feeds indirectly on vertebrate blood by choosing female mosquitoes as prey. *Proc Natl Acad Sci USA* 102:15155–60.
- Jackson RR, Pollard SD. 1996. Predatory behavior of jumping spiders. *Annu Rev Entomol* 41:287–308.
- Jackson RR, Pollard SD. 1997. Jumping spider mating strategies: sex among cannibals in and out of webs. In: Choe JC, Crespi BJ, editors. *The evolution of mating systems in insects and arachnids*. Cambridge: Cambridge University Press. p 340–51.
- Jackson RR, Tarsitano MS. 1993. Responses of jumping spiders to motionless prey. *Bull Br Arachnol Soc* 9:105–9.
- Jackson RR, van Olphen A. 1992. Prey-capture techniques and prey preferences of *Chrysilla*, *Natta* and *Siler*, ant-eating jumping spiders (Araneae, Salticidae) from Kenya and Sri Lanka. *J Zool Lond* 227:163–70.
- Jackson RR, Willey MB. 1994. The comparative study of the predatory behavior of *Myrmarachne*, ant-like jumping spiders (Araneae: Salticidae). *Zool J Linn Soc* 110:77–102.
- Land MF, Nilsson DE. 2002. *Animal eyes*. Oxford: Oxford University Press.
- Li D, Jackson RR. 1996. Prey-specific capture behavior and prey preferences of ant-eating and araneophagic jumping spiders (Araneae: Salticidae). *Rev Suisse Zool* h ser:423–36.
- McIver JD, Stonedahl G. 1993. Myrmecomorphy: morphological and behavioral mimicry of ants. *Annu Rev Entomol* 38:351–79.
- Nelson XJ, Jackson RR. Vision-based innate aversion to ants and ant mimics. *Behav Ecol*. Forthcoming.
- Nelson XJ, Jackson RR. 2006. Compound mimicry and trading predators by the males of sexually dimorphic Batesian mimics. *Proc R Soc Lond B Biol Sci* 273:367–72.

- Nelson XJ, Jackson RR, Li D, Barrion AT, Edwards GB. Innate aversion to ants (Hymenoptera: Formicidae) and ant mimics: experimental findings from mantises (Mantodea). *Biol J Linn Soc.* Forthcoming.
- Nelson XJ, Li D, Jackson RR. 2006. Out of the frying pan and into the fire: a novel trade-off for Batesian mimics. *Ethology* 112:270–77.
- Pollard SD. 1994. Consequences of sexual selection on feeding in male jumping spiders (Araneae: Salticidae). *J Zool Lond* 324: 203–8.
- Wanless FR. 1978. A revision of the genera *Belipho* and *Myrmarachne* (Araneae: Salticidae) in the Ethiopian region. *Bull Br Mus Nat Hist (Zool)* 33:1–139.