

1 **Conditional use of honest signaling by a Batesian mimic**

2

3 Short title: Honest communication by mimic

4

5 Ximena J. Nelson^{1*}, Robert R. Jackson¹, Daiqin Li²

6

7 ¹School of Biological Sciences, University of Canterbury, Private Bag 4800, Christchurch, New

8 Zealand

9

10 ²Department of Biological Sciences, National University of Singapore, Singapore 119260

11

12 **Current address:* Department of Psychology, Animal Behavior Laboratory, Macquarie University,

13 Sydney, NSW 2109, Australia

14 Email: ximena@galliform.bhs.mq.edu.au

15 Phone: 61-2-98509232

16 Fax: 61-2-98509231

17

17 Jumping spiders (Salticidae) usually avoid ants, but some species within this family single out ants
18 as preferred prey, while others (especially the species in the genus *Myrmarachne*) are Batesian
19 mimics of ants. Field records show that ant-eating salticids sometimes prey on *Myrmarachne*,
20 suggesting that the unwanted attention of predators that specialize on the model may be an
21 important, but poorly understood, cost of Batesian mimicry. By staging encounters in the laboratory
22 between living ant-eating salticids and *Myrmarachne*, we determined that ant-eating salticids attack
23 *Myrmarachne*. However, when *Myrmarachne* detects a stalking ant-eating salticid early enough, it
24 adopts a distinctive display posture (legs almost fully extended; elevated 45° and held out to the
25 side 45°), and this usually deters the predator. When *Myrmarachne* detects an ant-eating salticid
26 before stalking begins, *Myrmarachne* makes pre-emptive displays that appear to inhibit the
27 initiation of stalking. Using immobile lures made from dead *Myrmarachne* that were either in a
28 display posture or a non-display posture, we ascertained that specifically the display posture of
29 *Myrmarachne* deters the initiation of stalking (ant-eating salticids stalked non-displaying more
30 often than displaying lures). In another experiment, we ascertained that it is specifically the
31 interjection of display posture that deters stalking. When ant-eating salticids that had already begun
32 stalking experienced lures that switched from a non-display to a display posture, they stopped
33 stalking. Although the unwanted attentions of its models' predators may be, for *Myrmarachne*, a
34 hidden cost of Batesian mimicry, *Myrmarachne* appears to have an effective defense against these
35 predators.

36

37 *Key words:* anti-predator behavior, ants, Batesian mimicry, Salticidae, signals

38

38 Having potent defenses, which may include powerful mandibles, poison-injecting stings, formic
39 acid and the ability, as social insects, to launch communal attacks (Hölldobler and Wilson, 1990),
40 ants appear to be especially suitable model species in Batesian mimicry systems (Edmunds, 1972,
41 1993; Cushing, 1997) and ant mimicry has evolved repeatedly not only in insects but also in spiders
42 (McIver and Stonedahl, 1993). However, trading one predator for another may be a significant
43 problem for a Batesian mimic because prey that is unpalatable to one predator may be the preferred
44 prey of another (Nelson et al., in press a). This hidden cost may be especially applicable to ant
45 mimics because numerous spiders and predatory insects have evolved specialization at preying on
46 ants (Brandt and Mahsberg, 2002; Jackson et al., 1998). When the models' predators become
47 significant problems for the mimic, the evolution of effective defenses against these particular
48 predators might be expected.

49 Our hypothesis is that ant mimics sometimes defend themselves against ant-eating predators
50 by actively revealing to these predators that they are not really ants. There are other well-known
51 examples of prey defending themselves by honestly communicating with predators. For example,
52 prey may deter predators by accurately revealing their ability to defend themselves (Caro et al.,
53 2004). However, what we show here is different because it is the first detailed study of a Batesian
54 mimic defending itself by switching to honest communication during encounters with the models'
55 predators.

56 The specific example we consider is a system in which the predators and the mimics are
57 jumping spiders and the models are ants. Jumping spiders (Salticidae) are of particular interest
58 because of their exceptional eyesight (Land and Nilsson, 2002) and their intricate vision-guided
59 predatory behavior (Jackson and Pollard, 1996). Although most salticids may be generalist
60 insectivores that avoid ants (Harland and Jackson, 2001), a sizeable minority (the ant-eating
61 salticids) routinely feed on ants, adopt ant-specific prey-capture behavior and actively select ants as
62 preferred prey (Jackson et al., 1998; Jackson and Li, 2001). Another sizeable minority of the
63 Salticidae (the ant-like salticids) have a morphological and behavioral resemblance to ants

64 (Cushing, 1997). *Myrmarachne*, the largest genus of ant-like salticids (Wanless, 1978), is especially
65 diverse in tropical Asia, Africa and Australasia and ant-eating salticids tend to be common in the
66 same habitats (Jackson and Willey, 1994). Previous experimental work has shown that the ant-like
67 appearance of species in this genus is effective at deterring ant-averse predators (Harland and
68 Jackson, 2001; Nelson et al., in press b).

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

75 Salticids are renowned for the elaborate vision-based displays they adopt during courtship
76 and when threatening conspecific rivals of the same sex, but salticids do not routinely display at
77 other species (Jackson and Pollard, 1997). Ongoing research (RRJ, XJN, unpubl.) is revealing that
78 *Myrmarachne* is different because the species in this genus tend to display briefly when approached
79 head-on by another salticid, even when the other salticid belongs to a different species or genus and
80 is not ant-like in appearance. Yet *Myrmarachne* does not normally display at ants or at any
81 arthropods other than salticids.

82 In encounters with conspecifics, *Myrmarachne*'s initial display (see Jackson, 1982) is to
83 posture with its forelegs elevated 45° and held out to the side 45° , all joints distal to the femur-
84 patella being fully extended (called 'erect-legs posture'). Erect-legs postures are especially common
85 displays within the family Salticidae (Jackson and Pollard, 1997) and are very un-ant-like in
86 appearance. With conspecifics, *Myrmarachne* may display before being faced by the other spider
87 and the initial erect-legs posturing is usually followed by a complex sequence of displays (XJN,
88 RRJ, in prep.). However, when the individual encountered is not conspecific, erect-legs display
89 posture is typically adopted only when *Myrmarachne* and the other spider are face to face, usually

90 but not always with the other spider approaching, and *Myrmarachne* typically moves away, and
91 stops displaying, quickly after posturing for no more than a few seconds (RRJ, XJN, unpubl.). The
92 hypothesis that we consider here is that these momentary bouts of adopting un-ant-like posture
93 deter ant-eating salticids.

94

95 **MATERIALS AND METHODS**

96 **General**

97 All living spiders (Table 1) came from laboratory culture, with maintenance, testing procedures,
98 cage design, terminology and conventions for describing behavior being as in earlier spider studies
99 (Jackson and Hallas, 1986). Testing was carried out at the International Rice Research Institute in
100 Los Baños (The Philippines) and at the University of Canterbury (New Zealand) between 0900 h
101 and 1100 h (laboratory photoperiod 12L:12D, lights on at 0800 h). Test spiders had no prior contact
102 with any other salticids or with ants. Hunger was standardized by keeping each salticid without prey
103 for 5 days. No individual salticid was tested more than once.

104 All ant-like salticids used were juveniles and adult females of *Myrmarachne*. Adult males
105 were not used because there is pronounced sexual dimorphism in this genus (Pollard, 1994), with
106 males having greatly elongated chelicerae which, to the human eye, detract from the males' ant-like
107 appearance (but see Nelson and Jackson, 2006). We chose as predators six ant-eating species for
108 which details of prey-capture behavior are known (Jackson and van Olphen, 1992; Li and Jackson,
109 1996; Jackson et al., 1998; Jackson and Li, 2001). As the adult males of many salticids appear to
110 feed less readily than adult females and juveniles (Givens, 1978; Jackson and Pollard, 1997), we
111 used only adult females and large juveniles as test spiders in the experiments reported on here.

112 For baseline information about how predators and prey interacted, we staged encounters
113 between living ant-like and ant-eating salticids in the laboratory (live-prey tests). Taking into
114 account details about the different predatory tactics of the different ant-eating species that we used,
115 we carried out three variations on live-prey testing, standard tests, large-prey tests and bark tests

116 (see below). In each instance, testing was carried out by leaving one ant-eating and one ant-like
117 salticid together until predation occurred or until 30 min elapsed, whichever came first. Live-prey
118 testing was followed by experiments (using lures) designed to test hypotheses suggested by the
119 findings from live-prey tests.

120 In all instances, the two species paired in a test were sympatric. Data from using different
121 combinations of ant-eating and ant-like species were not significantly different (standard tests: $\chi^2 =$
122 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
123 each test. Data were analyzed using Fisher exact tests of independence and chi-square tests of
124 independence.

125

126 **Standard tests using living prey**

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

131 The two salticids were placed in a plastic cage made from a petri dish (diameter 140 mm)
132 with two corked holes (diameter 10 mm) in its bottom surface, the center of each of these holes
133 being 20 mm from the nearest side of the cage and 100 mm from the center of the other cork hole.
134 The ant-like salticid was introduced into the cage through one hole and then the ant-eating salticid
135 was immediately introduced through the other hole to start a test.

136

137 **Large-prey tests using living prey**

138 Methods for large-prey tests were the same as for standard tests except that only *Chalcotropis*
139 *gulosa* was used as a predator. In these tests, the body lengths of *C. gulosa* and the ant-like salticids
140 were matched for size because field records (RRJ, unpubl.) revealed that *C. gulosa* is an exception

141 among ant-eating salticids in that it often preys on large ants and its ant-specific prey-capture
142 behavior has been observed only when the ants are large (Jackson et al., 1998).

143

144 **Bark tests using living prey**

145 We used only *Zenodorus orbiculatus* in bark tests (N=50) because this species expresses distinctive
146 ant-specific prey-capture behavior only when on tree trunks (Jackson and Li, 2001). Tests were
147 carried out by placing one individual of *Myrmarachne lupata* together with one individual of *Z.*
148 *orbiculatus* (body length of *Z. orbiculatus* twice that of *M. lupata*) on a piece of *Eucalyptus* bark
149 (100 mm high X 30 mm wide). The bark was held vertical (lower end 100 mm above table top) by a
150 clamp (connected to top end of bark). The other end of the clamp was connected via a 300 mm long
151 rigid cable to a stand (sitting on a table) 300 mm behind the bark.

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

159

160 **Simultaneous-presentation tests using lures**

161 Using immobile lures made from dead *Myrmarachne* that were either in an erect-legs display
162 posture or a non-display posture, we investigated whether it is specifically the display posture of
163 *Myrmarachne* that deters the initiation of stalking by ant-eating salticids. Testing with stationary
164 lures avoids confounding variables from cues other than the arthropod's static appearance, and
165 much previous experimental work has shown that salticids respond readily to stationary lures made
166 from dead arthropods mounted in lifelike posture on cork discs (Jackson and Tarsitano, 1993;

167 Jackson et al., 2005). Here our prediction is that, given the choice between *Myrmarachne* in a
168 display and a non-display posture, ant-eating salticids more often stalk the non-displaying
169 *Myrmarachne*.

170 Each lure was made by immobilizing an adult *Myrmarachne assimilis* female with CO₂ and
171 then placing it in 80% ethanol. One day later, it was mounted in a lifelike posture in the center of a
172 disc-shaped piece of cork (diameter c. 1.25 X the length of the spider). The mounted *Myrmarachne*
173 was next sprayed with an aerosol plastic adhesive for preservation. In each test, there were two
174 lures matched for body length within the nearest millimeter (one in the erect-legs posture and one in
175 non-display posture). No individual lure was used in more than one test.

176 In these tests, a Y-shaped ramp (2 arms) was used (see Jackson et al., 1998), each arm
177 ending at a brown wooden wall (55 mm high, 40 mm wide and 15 mm thick) glued perpendicular to
178 the top end of the arm. Before testing started, the test spider was kept in a covered pit near the lower
179 end of the ramp until quiescent. Testing was begun by removing a transparent glass plate used as a
180 cover, allowing the test spider to walk up the stem of the ramp with a view of both lures (display
181 and non-display) at each end of the ramp (lure positioned on the left versus right decided at
182 random). Each lure was centered 10 mm in front of a wall and was facing the pit.

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

190

191 **Sequential-presentation tests using lures**

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

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

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

215 Testing was aborted whenever the salticid walked or leapt off the ramp without crossing the
216 threshold and whenever the salticid remained on the ramp for 30 min without crossing the

217 threshold. Aborted tests were rare (<5%). Data were analyzed using chi-square tests of
218 independence.

219

220 **RESULTS**

221 **Live-prey testing**

222 On the whole, test outcomes were similar across the three variations of live-prey testing. Ant-eating
223 salticids stalked *Myrmarachne* and, as predicted, *Myrmarachne* frequently responded by displaying
224 at the stalking predator. As predicted, once displayed at, the predator stopped stalking and almost
225 never attacked. There were also instances of *Myrmarachne* displaying at ant-eating salticids that
226 were facing head on but had not begun stalking. Once displayed at, these salticids never began
227 stalking. Displays never lasted for more than a few seconds, after which *Myrmarachne* moved
228 rapidly away, and there were no instances of *Myrmarachne* attacking the ant-eating salticid.

229

230 **Standard tests using living prey**

231 The ant-eating salticid stalked *Myrmarachne* in 131 (58%) of 225 standard tests, but captured
232 *Myrmarachne* in only 43 (19%) (Table 1). *Myrmarachne* displayed at the stalking ant-eating
233 salticid in 170 of 225 tests (76%) and the ant-eating salticid preyed on *Myrmarachne* in only three
234 (2%) of these tests (Table 1). In each of these three instances, the *Myrmarachne*, having stopped
235 displaying and moved away, was stalked many minutes later by the ant-eating salticid and captured
236 while facing away and without displaying again. In 79 (35%) tests, *Myrmarachne* displayed and the
237 ant-eating salticid failed to stalk or attack (Table 1). *Myrmarachne* failed to display in 55 (24%) of
238 the 225 tests and was captured in 40 (73%) of these 55 tests. There were significantly more
239 instances of predation on *Myrmarachne* that failed to display (40 out of 55) than on those that did
240 display (3 out of 170) ($\chi^2 = 135.37$; $P < 0.001$; $df = 1$).

241

242 **Large-prey tests using living prey**

243 *Chalcotropis gulosa* stalked *Myrmarachne* (Table 2) in 51 of 100 tests. *Myrmarachne* displayed at
244 the ant-eating salticid in 82 tests. In these 82 tests, if *C. gulosa* was stalking it always desisted and if
245 it had not yet begun *C. gulosa* remained the rest of the test period without initiating stalking.
246 *Myrmarachne* failed to display in 18 tests and was captured in 10 of these 18 tests. As in standard
247 tests, there were significantly more instances of predation on *Myrmarachne* that failed to display
248 (10 out of 18) than on those that did display (0 out of 82) ($\chi^2 = 58.82$; $P < 0.001$; $df = 1$).

249

250 **Bark tests using living prey**

251 *Zenodorus orbiculatus* made ambushing attacks and captured *Myrmarachne lupata* in nine tests
252 (N=50). *M. lupata* did not display in any of these nine tests. In 20 tests, *M. lupata* displayed at the
253 quiescent *Z. orbiculatus* and then walked away without being attacked. In another 21 tests, *M.*
254 *lupata* walked past *Z. orbiculatus* without displaying and *Z. orbiculatus* remained quiescent. There
255 were no instances of predation on displaying *M. lupata* and there were significantly more instances
256 of predation on *M. lupata* that failed to display (9 out of 30) than on *M. lupata* that did display (0
257 out of 20) ($\chi^2 = 10.92$; $P < 0.001$; $df = 1$).

258

259 **Simultaneous-presentation tests with lures**

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

263

264 **Sequential-presentation tests with lures**

265 During experimental trials (i.e., when a displaying lure was substituted for a non-displaying lure),
266 18 of 20 ant-eating salticids discontinued stalking. Significantly fewer (4 out of 25) ant-eating
267 salticids discontinued stalking during control tests (i.e., when another non-displaying lure was
268 substituted) ($\chi^2 = 24.35$; $P < 0.001$; $df = 1$).

269

270 **DISCUSSION**

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

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

284 However, here we have shown another factor that may sometimes ameliorate the problem,
285 for a Batesian mimic, of attracting the unwanted attentions of the models' predators. *Myrmarachne*
286 appears to be an ant mimic that can, either before or after the models' predators initiate predatory
287 behavior, actively defend itself by adopting an un-ant-like posture (i.e., by displaying with erect
288 legs).

289 Our field data confirm that ant-mimicking salticids are at least sometimes subject to fatal
290 encounters with ant-eating salticids, but witnessing predation on any salticid species in the field is
291 exceedingly rare and we cannot estimate how often *Myrmarachne* encounters ant-eating salticids in
292 nature. Nor do we know whether displaying might be, for ant-like salticids, an effective defense
293 against any other ant-eating predators besides ant-eating salticids. However, in this study, our goal
294 has been primarily to illustrate that a Batesian mimic might sometimes defend itself against its

295 models' predators by revealing to these predators that it is not, in fact, an individual of the model
296 species.

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

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

319 Although Batesian mimicry may miscarry when mimics elicit the unwanted attentions of
320 their models' predators, our findings suggest that it may be interesting to look for other examples

321 where mimics do not suffer this cost passively but instead actively defend themselves by revealing
322 their true identity to these predators. *Myrmarachne* appears to have a conditional anti-predator
323 strategy that is based on maintaining Batesian mimicry during encounters with most potential
324 predators but turning Batesian mimicry off (i.e., adopting erect-legs posturing) when faced by ant-
325 eating salticids. The primary cues that trigger *Myrmarachne*'s adoption of erect-legs posturing may
326 be seeing any salticid approaching head on. However, this does not alter the basic conclusion about
327 a conditional anti-predator strategy because, based on earlier work, we know that most salticids
328 avoid getting close to ants or to ant-like salticids (Nelson and Jackson, provisional acceptance). If a
329 non-conspecific salticid is approaching, it is most likely to be an ant-eating salticid species.
330

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

334

334 **REFERENCES**

335

336 Brandt M, Mahsberg D, 2002. Bugs with a backpack: the function of nymphal camouflage in the
337 West African assassin bugs *Paredocla* and *Acanthaspis* spp. *Anim Behav* 63: 277-284.

338

339 Caro TM, Graham CM, Stoner CJ, Vargas JK, 2004. Adaptive significance of antipredator behavior
340 in artiodactyls. *Anim Behav* 67: 205-228.

341

342 Cushing PE, 1997. Myrmecomorphy and myrmecophily in spiders: A review. *Fla Entomol* 80: 165-
343 193.

344

345 Edmunds ME, 1972. Defensive behavior in Ghanaian preying mantids. *Zool. J Linn Soc* 51: 1-32.

346

347 Edmunds ME, 1993. Does mimicry of ants reduce predation by wasps on salticid spiders? *Mem*
348 *Queensland Mus* 33: 507-512.

349

350 Forster LM, 1977. A qualitative analysis of hunting behavior in jumping spiders (Araneae:
351 Salticidae). *N Z J Zool* 4: 51-62.

352

353 Givens RP, 1978. Dimorphic foraging strategies of a salticid spider (*Phidippus audax*). *Ecology* 59:
354 309-21.

355

356 Harland DP, Jackson RR, 2001. Prey classification by *Portia fimbriata*, a salticid spider that
357 specializes at preying on other salticids: Species that elicit cryptic stalking. *J Zool Lond* 255:
358 445-460.

359

360 Hölldobler B, Wilson EO, 1990. The ants. Heidelberg: Springer-Verlag.
361
362 Jackson RR, 1982. The biology of ant-like jumping spiders: Intraspecific interactions of
363 *Myrmarachne lupata* (Araneae, Salticidae). Zool J Linn Soc 76: 293-319.
364
365 Jackson RR, Hallas SEA, 1986. Comparative studies of *Portia*, araneophagic web-building jumping
366 spiders (Araneae, Salticidae): Predatory versatility, utilisation of silk, and intraspecific
367 interactions of *P. africana*, *P. albimana*, *P. fimbriata*, *P. labiata*, and *P. Schultzzi*. N Z J Zool
368 13: 423-489.
369
370 Jackson RR, Li D, 2001. Prey-capture techniques and prey preferences of *Zenodorus durvillei*, *Z.*
371 *metallescens* and *Z. orbiculata* tropical ant-eating jumping spiders (Araneae: Salticidae) from
372 Australia. N Z J Zool 28: 299-341.
373
374 Jackson RR, Pollard SD, 1996. Predatory behavior of jumping spiders. Annu Rev Entomol 41: 287-
375 308.
376
377 Jackson RR, Pollard SD, 1997. Jumping spider mating strategies: Sex among cannibals in and out
378 of webs. In: The evolution of mating systems in insects and arachnids (Choe JC, Crespi BJ,
379 eds.), Cambridge: Cambridge University Press; 340-351
380
381 Jackson RR, Tarsitano MS, 1993. Responses of jumping spiders to motionless prey. Bull Br
382 Arachnol Soc 9: 105-109.
383

384 Jackson RR, van Olphen A, 1992. Prey-capture techniques and prey preferences of *Chrysilla*, *Natta*
385 and *Siler*, ant-eating jumping spiders (Araneae, Salticidae) from Kenya and Sri Lanka. J Zool
386 Lond 227: 163-170.

387

388 Jackson RR, Willey MB, 1994. The comparative study of the predatory behavior of *Myrmarachne*,
389 ant-like jumping spiders (Araneae: Salticidae). Zool J Linn Soc 110: 77-102.

390

391 Jackson RR, Nelson, XJ, Sune GO, 2005. A spider that feeds indirectly on vertebrate blood by
392 choosing female mosquitoes as prey. Proc Nat Acad Sci USA 102: 15155–15160.

393

394 Jackson RR, Li D, Barrion AT, Edwards GB, 1998. Prey-capture techniques and prey preferences
395 of nine species of ant-eating jumping spiders (Araneae: Salticidae) from the Philippines. N Z
396 J Zool 25: 249-272.

397

398 Land MF, Nilsson DE, 2002. Animal eyes. Oxford: Oxford University Press.

399

400 Li D, Jackson RR, 1996. Prey-specific capture behavior and prey preferences of ant-eating and
401 araneophagic jumping spiders (Araneae: Salticidae). Rev Suisse Zool h ser: 423-436.

402

403 McIver JD, Stonedahl G, 1993. Myrmecomorphy: Morphological and behavioral mimicry of ants.
404 Annu Rev Entomol 38: 351-379.

405

406 Nelson XJ, Jackson RR, Provisional acceptance. Vision-based innate aversion to ants and ant
407 mimics. Behav Ecol.

408

409 Nelson XJ, Jackson RR, 2006. Compound mimicry and trading predators by the males of sexually
410 dimorphic Batesian mimics. Proc R Soc Lond B 273: 367-372.
411

412 Nelson XJ, Li D, Jackson RR, In press a. Out of the frying pan and into the fire: A novel trade-off
413 for Batesian mimics. Ethology.
414

415 Nelson XJ, Jackson RR, Li D, Barrion AT, Edwards GB, In press b. Innate aversion to ants
416 (Hymenoptera: Formicidae) and ant mimics: experimental findings from mantises
417 (Mantodea). Biol J Linn Soc.
418

419 Pollard SD, 1994. Consequences of sexual selection on feeding in male jumping spiders (Araneae:
420 Salticidae). J Zool Lond 324: 203-208.
421

422 Wanless FR, 1978. A revision of the genera *Belippo* and *Myrmarachne* (Araneae: Salticidae) in the
423 Ethiopian region. Bull Br Mus Nat Hist (Zool) 33: 1-139.

Table 1. Results from standard tests (body length of predator 2X body length of prey) (N = 225). Encounters staged between ant-eating salticids (predators) and ant-like salticids (prey). N=25 for each row. Footnotes: origins of individuals from which laboratory cultures were started.

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 non-displaying <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> ¹	<i>M. assimilis</i> ¹	3	1	9	10	2
<i>Chalcotropis gulosa</i> ¹	<i>M. bakeri</i> ¹	2	0	14	8	1
<i>Chalcotropis gulosa</i> ¹	<i>M. bidentata</i> ¹	4	0	10	7	4
<i>Chalcotropis gulosa</i> ¹	<i>M. maxillosa</i> ¹	1	1	11	11	1
<i>Chrysilla lauta</i> ²	<i>M. plataleoides</i> ²	7	0	9	8	1
<i>Natta rufopicta</i> ³	<i>M. kilifi</i> ³	6	0	8	10	1
<i>Siler semiglaucous</i> ²	<i>M. plataleoides</i> ²	5	0	10	9	1
<i>Zenodorus orbiculatus</i> ⁴	<i>M. lupata</i> ⁴	4	1	11	7	2
<i>Xenocytaea</i> sp. ¹	<i>M. bakeri</i> ¹	8	0	6	9	2
Summary		40	3	88	79	15

¹The Philippines. ²Sri Lanka. ³Kenya. ⁴Australia.

Table 2. Results from large-prey tests (predator and prey matched in body length) (N = 100). Encounters staged between *Chalcotropis gulosa*, an ant-eating salticid (predator), and ant-like salticids (prey). N=25 for each row. There were no instances of predator stalking and capturing prey that had displayed during an earlier bout.

Ant-like salticid (<i>Myrmarachne</i>)	Number of occurrences in which the ant-eating salticid performed the stated outcome			
	Stalked and preyed on non-displaying <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