

Compound mimicry and trading predators by the males of sexually dimorphic Batesian mimics

Running Title: Compound mimicry

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ABSTRACT

Sexual dimorphism is pronounced in *Myrmarachne*, a large genus of ant-like jumping spiders (Salticidae) and one of the major animal groups in which Batesian mimicry of ants has evolved. Although adult females and juveniles of both sexes are distinctly ant-like in appearance, *Myrmarachne* males have elongated chelicerae that might appear to detract from their resemblance to ants. Experimental findings suggest that the *Myrmarachne* male's solution is to adopt compound mimicry (i.e., the male's model seems to be not simply an ant worker but a combination of an ant and something in the ant's mandibles: an 'encumbered ant'). By becoming a mimic of a particular subset of worker ants, *Myrmarachne* males may have retained their Batesian-mimicry defence against ant-averse predators, but at the price of receiving the unwanted attention of predators for which encumbered ants are preferred prey. Two salticid species were used as predators in the experiments. *Portia fimbriata* is known to choose other salticids as preferred prey and to avoid un-encumbered ants and their mimics (*Myrmarachne* females). In experiments reported here, *P. fimbriata* avoided encumbered ants and *Myrmarachne* males. Ants are the preferred prey of *Chalcotropis gulosus*. In our experiments, *C. gulosus* chose safer encumbered ants in preference to more dangerous unencumbered ants, chose *Myrmarachne* males more often than *Myrmarachne* females and showed no evidence of distinguishing between *Myrmarachne* males and encumbered ants. The cost of reconciling sexual dimorphism with Batesian mimicry appears to be that *Myrmarachne* males attract the unwanted attention of specialist predators of their compound model.

Keywords: ants; Batesian mimicry; predation; Salticidae; sexual dimorphism; spiders

1. INTRODUCTION

In a Batesian-mimicry system, palatable, safe and easy-to-capture prey individuals deceive potential predators by resembling unpalatable, dangerous or hard-to-capture models (Bates 1862; Wickler 1968; Edmunds 1974; Vane-Wright 1980; Ruxton *et al.* 2004). In contrast to the extensive literature on how mimicry benefits the mimic (Rettenmeyer 1970; Mallet & Joron 1999; Caley & Schluter 2003), relatively little attention has been given to how mimicry might be costly to the mimic (see Holen & Johnstone 2004), how predators of the model respond to the mimic and how predator behaviour is influenced when the mimic is sexually dimorphic.

Here we consider a Batesian-mimicry system in which the mimics and the predators are jumping spiders (Salticidae), the models are ants and sexual dimorphism is pronounced in the mimics. One predator was *Portia fimbriata*, a salticid that selects other salticids as preferred prey (araneophagic) (Li & Jackson 1996). Although *P. fimbriata* supplements its spider diet with insects (Jackson & Blest 1982), ants are unpalatable and dangerous potential prey for many arthropods (Cott 1940; Holldobler & Wilson 1990), and *P. fimbriata* is known to avoid coming into close proximity to ants (Harland & Jackson 2001). The other predator, *Chalcotropis gulosus*, sometimes preys on other arthropods, but actively selects ants as its preferred prey (myrmecophagic) (Jackson *et al.* 1998). The mimics (myrmecomorphic salticids) were two species of *Myrmarachne*. This large genus is especially diverse in tropical regions of Africa, Asia and Australasia, with all species appearing to be Batesian mimics of ants (see Edmunds 1993; Nelson *et al.* in press) and with sexual dimorphism being pronounced in all species

Pronounced sexual dimorphism has evolved in *Myrmarachne* (Wanless 1978), with the adult male's chelicerae being greatly elongated in comparison with the chelicerae of adult females (fig. 1) and with those of juveniles. To our eyes, *Myrmarachne* males may resemble

ants, but less convincingly than *Myrmarachne* females and juveniles, suggesting that, along with impaired feeding mechanics (Pollard 1994), impaired effectiveness at resembling ants has been a cost of sexual dimorphism for *Myrmarachne* males. However, the degree to which cheliceral enlargement impairs Batesian mimicry may depend on the particular predator that is encountered (see Cuthill & Bennett 1993). Our hypothesis is that, when the predator is another salticid, *Myrmarachne* males maintain Batesian mimicry by resembling a particular category of ants. Ants use their mandibles to carry a wide variety of objects, including food, larvae and other workers (Hölldobler & Wilson 1990). Perhaps the *Myrmarachne* male's long chelicerae mimic an object held by an ant worker's mandibles. Here we consider three specific hypotheses. (1) By resembling ant workers that have some unspecified objects in their mandibles ('encumbered'), *Myrmarachne* males retain the advantages of resembling ants despite their long chelicerae, but (2) mimicking encumbered ants makes *Myrmarachne* males more attractive to myrmecophagic salticids because (3) myrmecophagic salticids prefer safer encumbered to more dangerous un-encumbered ants.

These hypotheses were suggested by preliminary laboratory observations of *Myrmarachne* males and encumbered ant workers being avoided by *Portia fimbriata*, but readily eaten by *Chalcotropis gulosus*. Salticids have exceptional eyesight (Land & Nilsson 2002), and they are unique among spiders because of they readily respond to motionless lures (Jackson & Tarsitano 1993). Here, by using lures, we investigate specifically the decisions made by araneophagic and myrmecophagic salticids when using sight alone and in the absence of cues from movement and in the absence of confounding factors from prey behaviour.

2. MATERIAL AND METHODS

Laboratory cultures (F2 generation) of *Portia fimbriata* (origin: specimens collected near Cairns in Queensland, Australia) and of *Chalcotropis gulosus* (origin: Los Baños, Laguna Province, Luzon, the Philippines) were used as test spiders. The test spiders and their parents had no prior experience with ants or with spiders of any species (all were reared on dipterans). Salticid maintenance procedures, which were the same as in earlier spider studies (see Li & Jackson 1997), included ‘enriched environments’ (spacious cages and meshwork’s of twigs within the cages; see Carducci & Jakob 2000). All testing was carried out between 0900 h and 1100 h (laboratory photoperiod 12L:12D, lights on at 0800 h) at the University of Canterbury (Christchurch) and at the International Rice Research Institute (Los Baños).

As salticid males are often less responsive to prey than females (Li & Jackson 1996), we used only adult females (body length 11-12 mm) as test spiders (‘predators’). Hunger state was standardized before testing by keeping each predator without prey for 5 days before testing.

Each individual predator was used in a single simultaneous-presentation test using two stationary lures, each lure being a different prey type. Arthropods used for making lures (table 1) were collected from the field (Los Baños or Christchurch), except for dipterans, which came from laboratory cultures.

Each lure was made by immobilizing an arthropod with CO₂ and then placing it in 80% EtOH. One day later, the arthropod was mounted in a life-like posture on the centre of one side of a disc-shaped piece of cork (diameter c. 1.25 X the body length of the arthropod; thickness c. 2 mm). For preservation, the lure and the cork were next sprayed a transparent aerosol plastic adhesive (see Jackson & Tarsitano 1993).

The apparatus was a Y-shaped ramp (2 arms) (for details, see Jackson *et al.* 1998), each arm ending at a perpendicular wooden wall against which the test spider viewed a lure. The test spider was first kept until quiescent in a covered pit near the lower end of the ramp.

When testing began (i.e., when the cover was removed), the test spider walked up the stem of the ramp and viewed a lure at the end of each arm (centred 10 mm in front of the wall, facing 45° away from the pit).

Successful tests ended when the test spider oriented toward the lure (i.e., aligned its large anterior-medial eyes with the lure) and maintained this orientation while moving past the threshold (a line at the juncture of the two arms with the stem of the Y-shaped ramp, 40 mm from the centre of the pit). The test spider's choice was recorded as the prey type at the top of the arm on to which it walked when crossing the threshold. There were no instances in which the salticid crossed the threshold without first orienting toward the lure. Tests were unsuccessful if the salticid walked or leapt off the ramp before crossing the threshold, or if the salticid remained on the ramp for 30 min without crossing the threshold.

For data analysis, we used tests of goodness of fit. Yates' correction was not applied, as this correction is unduly conservative. However, applying this correction would not make any of our significant findings NS.

3. TESTING AN ARANEOPHAGIC PREDATOR

Portia fimbriata was tested simultaneously with a lure made from an ordinary salticid or a house fly paired with a lure made from an encumbered ant (table 2) ('encumbered': ant with a 'parcel', the parcel being a vinegar fly, *Drosophila melanogaster*, or the head and thorax (abdomen removed) of another ant, *Monomorium antarcticum*). The posterior end of the parcel was pressed against the ant's mandibles. The parcel's head extended in the same direction as the ant's head.

In each test, the two lures were of matching length (length of ant plus parcel matched to the nearest millimetre length of ordinary salticid or house fly). Our prediction was that *Portia fimbriata* would choose the ordinary salticid or the fly instead of the encumbered ant,

regardless of the identity of the object with which the ant was encumbered (i.e., we predicted that *P. fimbriata* would be influenced primarily by what was behind the parcel). We also tested *P. fimbriata* with a lure made from a *Myrmarachne assimilis* male paired with a lure made from *Plexippus paykulli* and, in addition, with a lure made from a *Myrmarachne maxillosa* male paired with a lure made from *Musca domestica*. In each instance, the body-plus-chelicerae length of the *Myrmarachne* male matched the body length of the other lure. Based on our hypothesis that, for *P. fimbriata*, *Myrmarachne* males resemble encumbered ant workers, we predicted that *P. fimbriata* would choose the ordinary salticid (*P. paykulli*) and choose the fly (*M. domestica*) more often than the *Myrmarachne* male.

Regardless of the ant's parcel, *Portia fimbriata* chose lures made from ordinary salticids and house flies significantly more often than it chose lures made from encumbered ants (table 2). *P. fimbriata* also chose ordinary salticids significantly more often than *Myrmarachne assimilis* ($\chi^2=15.00$; $P<0.001$) and chose house flies significantly more often than *Myrmarachne maxillosa* ($\chi^2=15.00$; $P<0.001$). In fact, *P. fimbriata* never chose ants or *Myrmarachne*.

4. TESTING A MYRMECOPHAGIC PREDATOR

Chalcotropis gulosus was tested with two ant lures (table 3), one encumbered and the other unencumbered. Depending on the test, the parcel was a vinegar fly, a beetle, or the head and thorax of another ant (*Monomorium antarcticum*). We predicted that *C. gulosus* would choose the encumbered, instead of the unencumbered, ant.

The rationale for using these three parcel types was to ascertain whether *Chalcotropis gulosus* made decisions based on seeing that the ant worker's mandibles were encumbered independent of whether it was attracted to the object used as a parcel (ant workers are *C.*

gulosus' preferred prey; flies are eaten, but not preferred; *C. gulosus* does not normally eat beetles: Jackson *et al.* 1998). In each test, the lengths of the lures matched to the nearest millimetre.

Chalcotropis gulosus chose encumbered ants significantly more often than unencumbered ants, regardless of the parcel's identity (table 3).

Chalcotropis gulosus was also tested with a lure made from a *Myrmarachne assimilis* male or a *Myrmarachne maxillosa* male (table 4) paired with a lure made from a conspecific female (*Myrmarachne* species held constant, but lure size varied because of the male's elongated chelicerae) and with a lure made from a *M. maxillosa* male paired with a lure made from a *M. assimilis* female (*Myrmarachne* species varied, but lure size constant). Our prediction was that, regardless of differences in prey size, *C. gulosus* would choose the *Myrmarachne* male instead of the *Myrmarachne* female.

C. gulosus chose *Myrmarachne* males significantly more often than conspecific females (different size) and significantly more often than same-size *Myrmarachne* females (different species) (table 4).

We also paired lures made from ants with lures made from *Myrmarachne* (table 5). From our hypothesis that *Myrmarachne* females are mimics of unencumbered ants and *Myrmarachne* males are mimics of encumbered ants, we predicted that *Chalcotropis gulosus* would choose *Myrmarachne* males more often than unencumbered ants and it would choose encumbered ants more often than *Myrmarachne* females, but show no choice between *Myrmarachne* males and encumbered ants.

C. gulosus chose *Myrmarachne* males significantly more often than unencumbered ants (table 5). *C. gulosus* chose encumbered ants more often than *Myrmarachne* females, but how often it chose *Myrmarachne* males was not significantly different from how often it chose encumbered ants (table 5).

5. DISCUSSION

Although *Myrmarachne* is one of the major animal groups in which Batesian mimicry of ants has evolved (Edmunds 1974; Cushing 1997), it is the juveniles and the adult females that, to humans, particularly resemble ants. *Myrmarachne* males have enlarged chelicerae that might seem incompatible with ant resemblance. Cheliceral enlargement probably evolved as a sexually-selected trait (Pollard 1994), and perhaps reduced efficacy of Batesian mimicry has been a cost of sexual dimorphism in this genus. Our findings suggest a somewhat different conclusion. Instead of sacrificing mimicry, *Myrmarachne* males may be the first experimentally demonstrated example of a Batesian mimic with a compound model (i.e., instead of simply mimicking an ant, the *Myrmarachne* male seems to mimic an ant plus a parcel in the ant's mandibles). Ants tend to be extraordinarily abundant in the tropical habitats of *Myrmarachne* (Hölldobler & Wilson 1990). Even if the percentage of ant workers that are encumbered is low, the sheer numbers of ants in *Myrmarachne*'s habitat probably ensures that encumbered ants are numerous. By adopting this alternative model, the *Myrmarachne* male may retain protection against ant-averse predators, but concomitantly become more attractive to myrmecophagic predators.

Araneophagic and myrmecophagic salticids have in common that the mouthparts of their preferred prey tend to be weapons. Besides having venom and fangs, and ability to bite, there are even a few spiders (the species in the genus *Scytodes*) that spit a sticky gum over would-be predators (Li *et al.* 1999). With mouthparts occupied, the spider and the ant may become safer prey for the araneophagic and myrmecophagic salticid, respectively (Jackson *et al.* 2002), and *Portia* has been shown to choose spitting spiders that have their mouthparts encumbered with eggs in preference to more dangerous unencumbered spitting spiders (Li &

Jackson 2003). By preferring ants with encumbered mandibles *C. gulosus* apparently adopts a similar strategy.

Evidently, our data reveal the predator's innate prey-choice decisions (no individuals that we tested had prior experience with ants or with ant mimics). Having used second-generation spiders from laboratory rearing under standardized conditions, maternal effects (Wade, 1998) and other indirect genetic effects (Moore *et al.* 1998) are unlikely alternative explanations for these findings.

Whether encumbered (this study) or not (Harland & Jackson 2001), ants were not attacked by *Portia fimbriata*. Likewise, neither the males nor the females of *Myrmarachne* were attacked, suggesting that *P. fimbriata* is innately predisposed to avoid ants, encumbered or not, and that this innate aversion to ants repels attacks on *Myrmarachne*, whether the individual of *Myrmarachne* is a male or a female. As an alternative hypothesis, perhaps encumbered ants and *Myrmarachne* males are ignored because they do not resemble anything identifiable to *P. fimbriata*, but this seems unlikely because, knowing that *Portia* readily preys on encumbered spiders (Jackson *et al.* 2002), and this alternative hypothesis requires an explanation for why *Portia* can identify a spider behind a parcel but not an ant. Besides, we showed that *Chalcotropis gulosus* distinguishes between encumbered and un-encumbered ants, choosing the encumbered ant, and the alternative hypothesis requires an explanation for why *Portia*'s vision-based ability fails where *C. gulosus*' succeeds.

We call the *Myrmarachne* male a 'compound mimic' because its model seems to be not simply an ant but an ant-parcel combination. By becoming a mimic of a particular subset of worker ants, *Myrmarachne* males may have retained their Batesian-mimicry defence against ant-averse predators and, in the process, they may receive the unwanted attentions of predators that single out the *Myrmarachne* male's specific model (encumbered ants) as preferred prey.

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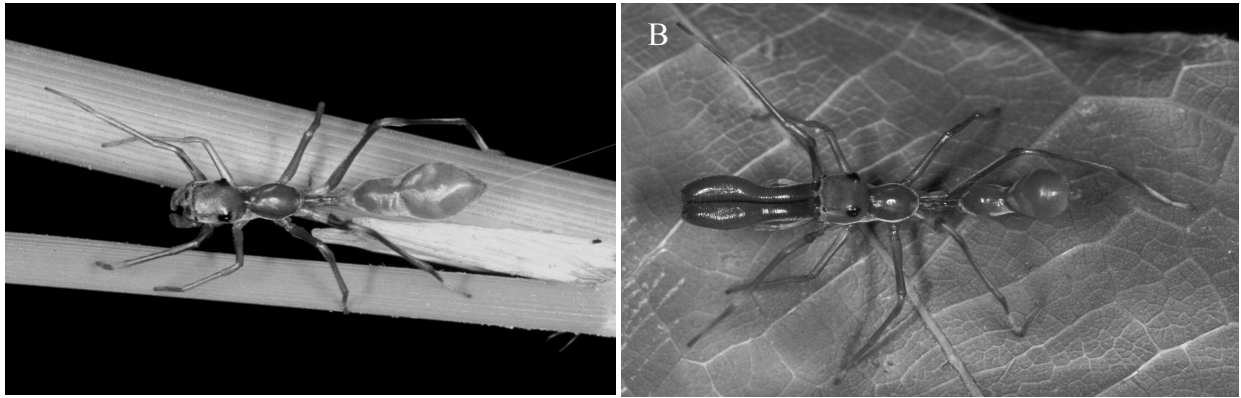


Figure 1. *Myrmarachne assimilis*, a myrmecomorphic jumping spider (Salticidae). A. Adult female (small chelicerae) (mimics unencumbered ant worker). B. Adult male (elongated chelicerae) (mimics encumbered ant worker).

Table 1. Arthropods used for making lures in simultaneous presentation tests in laboratory.

group and family	arthropods used for making lures	size (mm)	origin
Ant workers (Formicidae)	<i>Camponotus</i> sp.	5-6	Philippines
	<i>Doleromyrma darwiniana</i>	2	New Zealand
	<i>Monomorium antarcticum</i>	3	New Zealand
	<i>Oecophylla smaragdina</i>	7-9	Philippines
	<i>Solenopsis geminata</i>	4	Philippines
Beetles (Coccinellidae)	<i>Scymnus</i> sp.	3	Philippines
House Flies (Muscidae)	<i>Musca domestica</i>	5 and 7	Laboratory
Vinegar flies (Drosophilidae)	<i>Drosophila melanogaster</i>	2-3	Laboratory
Ordinary salticids*	<i>Plexippus paykulli</i> juveniles	7 and 9	Philippines
Myrmecomorphic salticids**	<i>Myrmarachne assimilis</i> females	7	Philippines
	<i>Myrmarachne assimilis</i> males	9	Philippines
	<i>Myrmarachne maxillosa</i> females	5	Philippines
	<i>Myrmarachne maxillosa</i> males	7	Philippines

*species not known to associate with ants and are not predators of ants nor ant mimics

**species that resemble ants

Table 2. *Portia fimbriata* (araneophagic predator) tested with lure simulating an encumbered ant (lure 2) (dead ant mounted with another arthropod pressed against its mandibles) paired with lure made from non-ant-like arthropod (lure 1). N=12 for each row.

lure length	lure 1	lure 2	chose lure 1	test of goodness of fit*
9 mm	<i>Plexippus paykulli</i>	<i>Camponotus</i> sp. (6 mm) + <i>Drosophila melanogaster</i> (3 mm)	12	$\chi^2=12.00$, P<0.001
7 mm	<i>Musca domestica</i>	<i>Solenopsis geminata</i> (4 mm) + <i>Drosophila melanogaster</i> (3 mm)	12	$\chi^2=12.00$, P<0.001
5 mm	<i>Musca domestica</i>	<i>Monomorium antarcticum</i> (3 mm) + head-thorax of <i>Monomorium antarcticum</i> (2 mm)	12	$\chi^2=12.00$, P<0.001

*null hypothesis: choose each prey type equally often

Table 3. *Chalcotropis gulosus* (myrmecophagic predator) tested with lure simulating an encumbered ant worker (dead ant mounted with another arthropod pressed against its mandibles) paired with lure made from unencumbered ant worker (mandibles free). Length of two lures matched. N=30 for each row.

lure length	unencumbered ant	encumbered ant	chose ant	test of goodness of fit*
4 mm	<i>Solenopsis geminata</i>	<i>Doleromyrma darwiniana</i> (2 mm) + <i>Drosophila melanogaster</i> (2 mm)	27	$\chi^2=19.20$, P<0.001
5 mm	<i>Camponotus</i> sp.	<i>Monomorium antarcticum</i> (3 mm) + <i>Drosophila melanogaster</i> (2 mm)	25	$\chi^2=13.33$, P<0.001
6 mm	<i>Camponotus</i> sp.	<i>Monomorium antarcticum</i> (3 mm) + <i>Drosophila melanogaster</i> (3 mm)	29	$\chi^2=26.13$, P<0.001
7 mm	<i>Oecophylla smaragdina</i>	<i>Solenopsis geminata</i> (4 mm) + <i>Drosophila melanogaster</i> (3 mm)	23	$\chi^2=8.53$, P<0.01
8 mm	<i>Oecophylla smaragdina</i>	<i>Camponotus</i> sp. (5 mm) + <i>Drosophila melanogaster</i> (3 mm)	27	$\chi^2=19.20$, P<0.001
6 mm	<i>Camponotus</i> sp.	<i>Monomorium antarcticum</i> (3 mm) + <i>Scymnus</i> sp. (3 mm)	26	$\chi^2=16.13$, P<0.001
5 mm	<i>Camponotus</i> sp.	<i>Monomorium antarcticum</i> (3 mm) + head-thorax of <i>Monomorium antarcticum</i> (2 mm)	26	$\chi^2=16.13$, P<0.001

*null hypothesis: choose each prey type equally often

Table 4. *Chalcotropis gulosus* (myrmecophagic predator) tested with lure made from *Myrmarachne* male paired with lure made from *Myrmarachne* female. Lure length in brackets. N=30 for each row.

<i>Myrmarachne</i> male	<i>Myrmarachne</i> female	chose <i>Myrmarachne</i> male	test of goodness of fit*
<i>M. assimilis</i> (9 mm)	<i>M. assimilis</i> (7 mm)	22	$\chi^2=6.53$, P<0.05
<i>M. maxillosa</i> (7 mm)	<i>M. maxillosa</i> (5 mm)	25	$\chi^2=13.33$, P<0.001
<i>M. maxillosa</i> (7 mm)	<i>M. assimilis</i> (7 mm)	23	$\chi^2=8.53$, P<0.01

*null hypothesis: choose each prey type equally often

Table 5. *Chalcotropis gulosus* (myrmecophagic predator) tested with lure made from ant worker (encumbered or unencumbered) paired with lure made from *Myrmarachne* (male or female). Lure length in brackets (matched lure lengths in each test). N=30 for each row.

Ant	<i>Myrmarachne</i>	chose ant	chose <i>Myrmarachne</i>	test of goodness of fit*
<i>Oecophylla smaragdina</i> (9 mm)	<i>M. maxillosa</i> male (9 mm)	8	22	$\chi^2=6.53$, P<0.05
<i>Solenopsis geminata</i> (4 mm) + <i>Drosophila melanogaster</i> (3 mm)	<i>M. assimilis</i> female (7 mm)	27	3	$\chi^2=19.20$, P<0.001
<i>Solenopsis geminata</i> (4 mm) + <i>Drosophila melanogaster</i> (3 mm)	<i>M. maxillosa</i> male (7 mm)	17	13	$\chi^2=0.53$, NS

*null hypothesis: choose each prey type equally often