

Out of the Frying Pan and into the Fire: a Novel Trade-Off for Batesian Mimics

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Abstract

A mimicry system was investigated in which the models were ants (Formicidae) and both the mimics and the predators were jumping spiders (Salticidae). By using motionless lures in simultaneous-presentation prey-choice tests, how the predators respond specifically to the static appearance of ants and ant mimics was determined. These findings suggest a rarely considered adaptive trade-off for Batesian mimics of ants. Mimicry may be advantageous when it deceives ant-averse potential predators, but disadvantageous in encounters with ant-eating specialists. Nine myrmecophagic (ant-eating) species (from Africa, Asia, Australia and North America) and one araneophagic (spider-eating) species (*Portia fimbriata* from Queensland) were tested with ants (five species), with myrmecomorphic (ant-like) salticids (six species of *Myrmarachne*) and with non-ant-like prey (dipterans and ordinary salticids). The araneophagic salticid chose an ordinary salticid and chose flies significantly more often than ants. *Portia fimbriata* also chose the ordinary salticid and chose flies significantly more often than myrmecomorphic salticids. However, there was no significant difference in how *P. fimbriata* responded to ants and to myrmecomorphic salticids. The myrmecophagic salticids chose ants and chose myrmecomorphic salticids significantly more often than ordinary salticids and significantly more often than flies, but myrmecophagic salticids did not respond significantly differently to myrmecomorphic salticids and ants.

Introduction

Batesian mimics are palatable prey that resemble unpalatable or dangerous models (Bates 1862; Wickler 1968), with the most thoroughly studied examples being terrestrial arthropods. Here we consider whether, besides deceiving potential predators that are averse to preying on the model, Batesian mimics also deceive predators that specialize on the model (maladaptive for the mimic). This is an especially interesting question because it is adaptive for the mimic to deceive ant-averse predators but maladaptive to deceive predators that specialize on eating ants.

Ants are especially often the models (Edmunds 1974, 1978; Hölldobler & Wilson 1990) in Batesian-mimicry systems. Yet many predators, including various spiders and predatory insects (Allan et al. 1996; Jackson et al. 1998; Brandt & Mahsberg 2002; Cushing & Santangelo 2002; Pierce et al. 2002; Elgar & Allan 2004), specialize at preying on ants, suggesting that adaptive tradeoffs might be particularly serious for Batesian mimics of ants because of the prevalence of ant-eating specialists. This is the first study to consider the susceptibility of mimics to predators that specialize on the model.

Jumping spiders (Salticidae) are especially appropriate as a case study. Having large eyes, acute vision

and intricate vision-guided predatory behaviour (Land 1969a,b; Forster 1982; Blest et al. 1990; Jackson & Pollard 1996), and being the largest spider family (more than 5000 described species: Coddington & Levi 1991; Proszynski 2003; Platnick 2005), salticids are a dominant and diverse group of predatory arthropods (Jackson & Pollard 1996). Most salticids may be generalist insectivores (Richman & Jackson 1992; Foelix 1996), but most salticids also appear to be averse to preying on ants. However, there is sizeable minority (the myrmecophagic species) within this large family that actively selects ants as preferred prey (Edwards et al. 1974; Cutler 1980; Jackson & van Olphen 1991, 1992; Jackson et al. 1998). Within the Salticidae, a sizeable minority (the myrmecomorphic species) are Batesian mimics of ants (Edmunds 1974, 1993; Cutler 1991; Nelson et al. in press) (Fig. 1). There is yet another minority within the Salticidae (the araneophagic species) that actively selects other spiders as preferred prey, and the members of one particular population of one of these species (*Portia fimbriata* from Queensland) chooses other salticids in preference to other kinds of spiders (Li & Jackson 1996), yet is averse to ants (Harland & Jackson 2001). When its prey is an ordinary salticid, the Queensland *P. fimbriata* adopts a special tactic, 'cryptic stalking': walks in exceptionally slow, choppy gait, pulls palps back beside chelicerae and, if faced, freezes until the prey turns away (Jackson & Blest 1982; Jackson & Hallas 1986).

Cryptic stalking appears to be a prey-specific predatory behaviour because it is not adopted when stalking non-salticid prey (Harland & Jackson 2001).

Mirroring the success of ants, myrmecomorphic salticids tend to be common in the same habitats in which myrmecophagic salticids are common (Jackson & Willey 1994; Nelson et al. 2004, in press). Myrmecomorphic salticids are also common in the Queensland habitat of *P. fimbriata*. However, little is known about *P. fimbriata*'s interactions with myrmecomorphic salticids or about interactions between myrmecomorphic and myrmecophagic salticids.

Among spiders, salticids have the unique ability to discriminate by sight alone between different kinds of prey and respond readily to stationary lures made from mounted specimens of prey presented in life-like posture (Jackson & Tarsitano 1993; Harland & Jackson 2000, 2001). Here we consider whether, by sight alone, myrmecophagic and araneophagic salticids can distinguish between myrmecomorphic salticids and ants.

Methods

Study Animals

We used juveniles and adult females of the Queensland *P. fimbriata* and of nine myrmecophagic species (*Aelurillus aeruginosus* from Israel; *Chalcotropis gulosa*, the Philippines; *Chrysilla lauta*, Sri Lanka; *Corythalia*

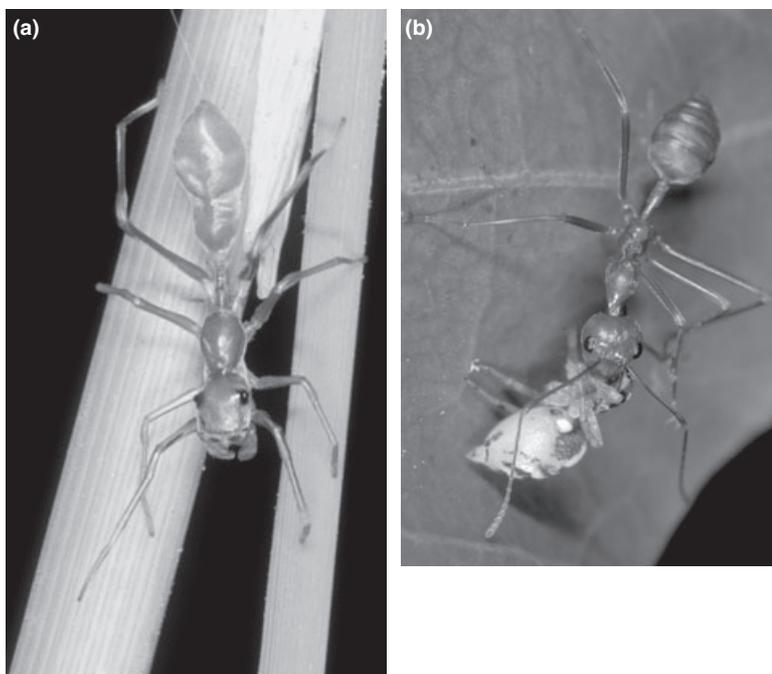


Fig. 1: Ant and salticids from the Philippines: (a) *Myrmarachne assimilis*, a myrmecomorphic salticid, and (b) *Oecophylla smaragdina*. Ant has a non-myrmecomorphic salticid, *Phintella piatensis*, in its mandibles

canosa, USA; *Habrocestum pulex*, USA; *Natta rufopicta*, Kenya; *Siler semiglaucus*, the Philippines and Sri Lanka; *Xenocytaea* sp., the Philippines; *Zenodorus orbiculatus*, Australia) as test spiders (predators). Adult males, being known to be less responsive to prey (Jackson 1982; Li & Jackson 1996; Jackson & Pollard 1997), were not used.

Animal Care and Husbandry

All test spiders came from laboratory culture (F2 generation), and standard spider-laboratory procedures were adopted (see Jackson & Hallas 1986; Li & Jackson 1996). Only modifications and critical details concerning these procedures are given here. Salticid maintenance procedures, which were the same as in earlier spider studies (see Jackson & Hallas 1986; 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 09:00 and 11:00 h (laboratory photoperiod 12L:12D, lights on at 08:00 h) at the University of Canterbury, New Zealand. Predators had no prior contact with any other salticids (except for conspecific individuals in the eggsac before dispersal) or with ants. Salticids were fed house flies (*Musca domestica*) and vinegar flies (*Drosophila melanogaster*) (from laboratory culture) three times per week. Hunger state was standardized by keeping each predator without prey for 5 d before testing.

Experimental Design and Statistical Analysis

We used simultaneous-presentation testing and all testing was with lures (i.e. each individual predator was given access to two lures at the same time, each lure being made from a different prey type). In earlier studies of salticid prey-choice behaviour (Li & Jackson 1996), three types of testing (alternate-day, simultaneous-presentation and alternative-prey) were adopted, and testing was carried out using both living prey and lures. On the whole, findings have been comparable across testing methods, but simultaneous presentation testing using lures was advantageous because it ruled out prey behaviour as an influence on test outcome and forced the predator to rely on static cues from appearance alone.

Each lure was made by asphyxiating an insect or a salticid with CO₂ and then placing it in 80% EtOH. One day later, the insect or salticid was mounted in a lifelike posture on the centre of one side of a disc-shaped piece of cork (diameter *c.* 1.25× the body

length of the spider or insect). The lure and the cork were next sprayed with an aerosol plastic adhesive for preservation (see Jackson & Tarsitano 1993). Arthropods used for making lures were collected from the field, except for house flies and vinegar flies, which came from laboratory cultures (Table 1). All ants were workers. All myrmecomorphic salticids were either adult females or juveniles of species from the genus *Myrmarachne*.

The testing apparatus was a Y-shaped ramp (two arms) (for details, see Li et al. 1996; Jackson et al. 1998), each arm ending at a perpendicular wooden wall against which the predator viewed a lure. The arm on which each lure was placed was randomized. Before testing started, the test spider was kept in a covered pit near the lower end of the ramp until quiescent. The cover was removed to start a test. The test spider walked up the stem of the ramp and viewed a lure centred 10 mm in front of the wall (facing 45° away from the pit) at the end of each arm. No individual predators and no individual lures were used more than once.

There were two ways in which tests were sometimes unsuccessful: (1) the salticid walked or leapt off the ramp without crossing the threshold (a line, 40 mm from the centre of the pit, at the juncture of the two arms with the stem of the Y-shaped ramp); (2) the salticid remained on the ramp for 30 min, but failed to cross the threshold. Successful tests ended when the predator, after leaving the pit, oriented towards the lure (i.e. aligned its large anterior-medial eyes with the lure) and maintained this orientation while moving past the threshold. 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 walked across the threshold without first orienting towards the lure.

Results

All nine myrmecophagic species chose myrmecomorphic salticids significantly more often than they chose flies (Table 2), and they chose ants (Table 3) and myrmecomorphic salticids (Table 4) significantly more often than they chose ordinary salticids. However, there was no significant difference for any myrmecophagic species in how often myrmecomorphic salticids were chosen and how often ants were chosen (Table 5).

The araneophagic salticid, *P. fimbriata*, always chose the ordinary salticid, *Plexippus paykulli*, instead of the ant (ants used: *Camponotus* sp., *Doleromyrma*

Table 1: Arthropods used in for making lures in simultaneous-presentation tests in the laboratory. In each test, the two lures used were of matching (within 1 mm) body length. Ordinary salticid: species that is not known to associate with ants and are neither ant eaters nor ant mimics. Myrmecomorphic salticids: species that resemble ants. Abbreviation for each species provided

Common name	Species (abbreviation)	Classification	Body length (mm)	Origin
Ants	<i>Camponatus</i> sp. (Cam)	Hymenoptera, Formicidae, subfamily Formicinae	5–6	Philippines
	<i>Doleromyrma</i> (formerly <i>Iridomyrmex darwiniana</i>) (Dol)	Hymenoptera, Formicidae, subfamily Dolichoderinae	2	New Zealand
	<i>Monomorium antarcticum</i> (Mon)	Hymenoptera, Formicidae, subfamily Myrmicinae	3	New Zealand
	<i>Oecophylla smaragdina</i> (Oec)	Hymenoptera, Formicidae, subfamily Formicinae	7–8	Philippines
	<i>Solenopsis geminata</i> (Sol)	Hymenoptera, Formicidae, subfamily Myrmicinae	4	Philippines
House flies	<i>Musca domestica</i> (Mus)	Diptera, Muscidae	7–8	Laboratory culture
Vinegar flies	<i>Drosophila melanogaster</i> (DM)	Diptera, Drosophilidae	2–3	Laboratory culture
	<i>Drosophila immigrans</i> (DI)	Diptera, Drosophilidae	4	Laboratory culture
Fungus gnats	<i>Mycetophila</i> sp. (Myc)	Diptera, Mycetophilidae	5–6	Philippines
Ordinary salticids	<i>Plexippus paykulli</i> (juveniles) (Plex)	Araneae, Salticidae	7	Philippines
Myrmecomorphic salticids (<i>Myrmarachne</i>)	<i>M. assimilis</i> (Ma)	Araneae, Salticidae	7–8	Philippines
	<i>M. kilifi</i> (Mk)	Araneae, Salticidae	2–4	Kenya
	<i>M. lupata</i> (Ml)	Araneae, Salticidae	5	Australia
	<i>M. maxillosa</i> (Mm)	Araneae, Salticidae	6–7	Philippines
	<i>M. naro</i> (Mn)	Araneae, Salticidae	3–4	Kenya
	<i>M. plataleoides</i> (Mp)	Araneae, Salticidae	7–8	Sri Lanka

Table 2: Percentage of myrmecomorphic salticids (*Myrmarachne*) chosen by myrmecophagic salticids. Tests of vision-based prey choice. Used lures made from myrmecomorphic salticids and from flies. N = 30 for each row. Chi-square tests of goodness of fit (null hypothesis: choose each prey type equally often)

Myrmecophagic salticid	Myrmecomorphic salticid	Fly	Myrmecomorphic salticid (%)	Test of goodness of fit (χ^2 , p)
<i>Aelurillus aeruginosus</i>	Mp	DM	96.67	26.13, <0.001
<i>Chalcotropis gulosa</i>	Ma	DI	86.67	16.13, <0.001
<i>Chalcotropis gulosa</i>	Ma	Mus	83.33	13.33, <0.001
<i>Chalcotropis gulosa</i>	Ma	Myc	100	30.00, <0.001
<i>Chalcotropis gulosa</i>	Mm	DI	83.33	13.33, <0.001
<i>Chrysilla lauta</i>	Mp	DM	100	30.00, <0.001
<i>Corythalia canosa</i>	Mp	DM	80	10.80, <0.01
<i>Habrocestum pulex</i>	Mp	DM	86.67	16.13, <0.001
<i>Natta rufopicta</i>	Mk	DM	93.33	22.53, <0.001
<i>Natta rufopicta</i>	Mn	DM	80	10.80, <0.01
<i>Siler semiglaucus</i>	Ma	DM	100	30.00, <0.001
<i>Siler semiglaucus</i>	Ma	DM	76.67	8.53, <0.01
<i>Xenocytaea</i> sp.	Ma	DM	100	30.00, <0.001
<i>Zenodorus orbicularis</i>	Ml	DM	100	30.00, <0.001

darwiniana, *Monomorium antarcticum*, *Oecophylla smaragdina* and *Solenopsis geminata*) (N = 20, $\chi^2 = 20.00$, $p < 0.001$, for each) and instead of the myrmecomorphic salticid (*M. assimilis*, *M. lupata*, *M. maxillosa*, *M. naro*, *M. plataleoides*) (N = 20, $\chi^2 = 20.00$, $p < 0.001$, for each), and in all but one instance *P. fimbriata* chose *P. paykulli* instead of *M. kilifi* ($\chi^2 = 16.2$, $p < 0.001$, N = 20).

In choice tests in which *P. fimbriata* was presented with a lure made from a fly and another made from an ant, *P. fimbriata* chose flies significantly more

often than they chose ants (Cam-Myc 93%, $\chi^2 = 11.27$, $p < 0.001$; Dol-DM, Mon-DM, Oec-Mus, Sol-DI all 100%, $\chi^2 = 15.00$, $p < 0.001$; N = 15 for each combination) (see Table 1 for abbreviations). Furthermore, in choice tests in which *P. fimbriata* was given a choice between flies and myrmecomorphic salticids, *P. fimbriata* always chose flies (Ma-Mus, Mk-DI, MI-DI, Mm-DI, Mn-DI, Mp-DI all 100%, $\chi^2 = 15.00$, $p < 0.001$; N = 15 for each combination). Lures were matched for body length (within 1 mm) in all tests.

Table 3: Percentage of ants chosen by myrmecophagic salticids. Tests of vision-based prey choice. Used lures made from ants (*Monomorium antarcticum*) and from ordinary salticids (*Plexippus paykulli*). N = 30 for each row. Chi-square tests of goodness of fit (null hypothesis: choose each prey type equally often). Lures matched for body length (within 1 mm)

Myrmecophagic salticid	Ant (%)	Test of goodness of fit (χ^2 , p)
<i>Aelurillus aeruginosus</i>	80	10.80, <0.01
<i>Chalcotropis gulosa</i>	96.67	26.13, <0.001
<i>Chrysilla lauta</i>	93.33	22.53, <0.001
<i>Corythalia canosa</i>	80	10.80, <0.01
<i>Habrocestum pulex</i>	90	19.20, <0.001
<i>Natta rufopicta</i>	83.33	13.33, <0.001
<i>Siler semiglaucus</i>	96.67	26.133, <0.001
<i>Xenocytaea</i> sp.	80	10.80, <0.01
<i>Zenodorus orbiculatus</i>	90	19.20, <0.001

Table 4: Percentage of myrmecomorphic salticids chosen by myrmecophagic salticids. Tests of vision-based prey choice. Used lures made from myrmecomorphic salticids (*Myrmarachne assimilis*) and from ordinary salticids (*Plexippus paykulli*). N = 30 for each row. Chi-square tests of goodness of fit (null hypothesis: choose each prey type equally often). All lures 7 mm in body length

Myrmecophagic salticid	Myrmecomorphic salticid (%)	Test of goodness of fit (χ^2 , p)
<i>Aelurillus aeruginosus</i>	96.67	26.13, <0.001
<i>Chalcotropis gulosa</i>	96.67	26.13, <0.001
<i>Chrysilla lauta</i>	90	19.20, <0.001
<i>Corythalia canosa</i>	80	10.80, <0.01
<i>Habrocestum pulex</i>	76.67	8.53, <0.01
<i>Natta rufopicta</i>	100	30.00, <0.001
<i>Siler semiglaucus</i>	96.67	26.13, <0.001
<i>Xenocytaea</i> sp.	100	30.00, <0.001
<i>Zenodorus orbiculatus</i>	90	19.20, <0.001

Myrmecophagic salticid	Myrmarachne	Ant	<i>Myrmarachne</i> (%)	Test of goodness of fit (χ^2 , p)
<i>Aelurillus aeruginosus</i>	Mp ^a	Mon ^a	45	0.40, NS
<i>Chalcotropis gulosa</i>	Ma ^a	Cam ^a	57.50	0.90, NS
<i>Chalcotropis gulosa</i>	Ma	Dol	35	3.6, NS
<i>Chalcotropis gulosa</i>	Ma	Mon	45	0.40, NS
<i>Chalcotropis gulosa</i>	Ma ^a	Oec ^a	35	3.6, NS
<i>Chalcotropis gulosa</i>	Ma	Sol	35	3.6, NS
<i>Chalcotropis gulosa</i>	Mm ^a	Cam ^a	50	0.00, NS
<i>Chrysilla lauta</i>	Mp	Dol	57.50	0.9, NS
<i>Corythalia canosa</i>	Mp	Mon	52.50	0.10, NS
<i>Habrocestum pulex</i>	Mp	Mon	50	0.00, NS
<i>Natta rufopicta</i>	Mk ^a	Mon ^a	57.50	0.9, NS
<i>Natta rufopicta</i>	Mn ^a	Mon ^a	50	0.00, NS
<i>Siler semiglaucus</i>	Ma	Mon	40	1.60, NS
<i>Siler semiglaucus</i>	Mm	Mon	45	0.40, NS
<i>Zenodorus orbiculatus</i>	MI	Mon	45	0.40, NS
<i>Xenocytaea</i> sp.	Ma	Dol	60	1.60, NS

^aLures matched for body length (within 1 mm).

Consistently, when *P. fimbriata* chose an ordinary salticid, it adopted cryptic stalking, but *P. fimbriata* never adopted cryptic stalking in conjunction with choosing a fly.

Discussion

By using motionless lures, we tested the responses of salticids specifically to the static appearance of potential prey. Responses of araneophagic and of myrmecophagic salticids to ants and to *Myrmarachne* were comparable. The nine species of myrmecophagic salticids that we tested chose ants and chose myrmecomorphic salticids in preference to ordinary salticids and to flies, but in test series with even larger sample sizes chose ants and myrmecomorphic salticids in similar numbers. These findings suggest that *Myrmarachne*'s ant-like appearance deceived not only araneophagic salticids but also myrmecophagic salticids. Evidently, these predators classify *Myrmarachne* as ants rather than as salticids. Besides corroborating the hypothesis that species in the genus *Myrmarachne* are Batesian mimics of ants, these findings suggest a potential adaptive trade-off to which Batesian mimics may be subject. Adaptations that reduce their attractiveness to ant-averse predators may render Batesian mimics more attractive to predators that specialize on the model. Variation in experience, maternal effects and other indirect genetic effects were minimized (see Moore et al. 1998; Roff 1998; Wade 1998) because all individuals tested were laboratory reared to second generation under standardized conditions and had no prior experience

Table 5: Percentage of myrmecomorphic salticids chosen by myrmecophagic salticids. Tests of vision-based prey choice. Used lures made from myrmecomorphic salticids and from ants. N = 40 for each row. Chi-square tests of goodness of fit (null hypothesis: choose each prey type equally often)

with the arthropods used for making mounts. Despite the widespread tendency in the literature on Batesian mimicry to emphasize the role of learning (Brower 1958; Edmunds 1974; Berenbaum & Miliczky 1984; Ritland 1995, 1998; Uesugi 1996; Mappes & Alatalo 1997), our findings appear to reveal the innate salience of ants and *Myrmarachne* to araneophagic and myrmecophagic salticids.

The Queensland *P. fimbriata* showed an especially pronounced preference, choosing an ant only once and never choosing a myrmecomorphic salticid over a fly. Not choosing ants and not choosing *Myrmarachne* might suggest an alternative to the Batesian-mimicry hypothesis. For *P. fimbriata*, perhaps ants and *Myrmarachne* simply fail to provide prey-capture cues. However, other studies suggest that ants are particularly salient to salticids. Ants sometimes prey on salticids and many salticids appear to be innately predisposed to avoid coming close to these potentially dangerous arthropods (Nelson et al. 2004). This suggests a straightforward Batesian-mimicry explanation for our findings (i.e. that *P. fimbriata* mistakenly identifies salticid species from the genus *Myrmarachne* as being ants).

Batesian mimicry may be particularly risky for prey species that encounter not only predators that are averse to the model but also predators that specialize on the model. For myrmecomorphic salticids, Batesian mimicry may be a successful strategy only so long as deceived ant-eating predators are scarce relative to deceived ant-averse predators.

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