

Visual cues used by ant-like jumping spiders to distinguish conspecifics from their models

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Abstract. Despite the conceptual appeal of how morphological mimics visually distinguish between conspecifics and their models, scant attention has been given to this topic. Accurate discrimination between ants and conspecific spiders is likely to be under strong selection because approaching an ant may result in the spider's death, while approaching a different sex conspecific may result in copulation. I addressed this question by examining responses of the ant-like jumping spider *Myrmarachne bakeri* Banks 1930 (Salticidae) toward motionless, odorless lures made from dead conspecifics, ants, or lures using components of non-ant-like salticids, ant-like salticids and ants. I found that chelicerae, legs I and body, but not movement, are important cues used by *M. bakeri* to distinguish conspecifics from ants, but the relative importance of these cues differs depending on a spider's sex.

Keywords: Visual discrimination, mimicry, *Myrmarachne*, recognition

Batesian mimicry is possibly the best-documented example of a deceitful signal, and while the effects of these signals on predators have received considerable attention for over a century (Bates 1862; Wickler 1968; Ruxton et al. 2004) there is scant information on the effects of mimetic signals on conspecifics. This gap in our knowledge is not reflected in the importance of the issue at hand: Batesian mimics resemble an unpalatable or dangerous model, and mimicry has evolved due to its effect on potential predators, which consequently avoid the mimic (Edmunds 1974). However, all animals capable of processing information in the specific sensory modality of the mimetic signal may be fooled by mimics- not just predators. Consequently, if a mimic is a visually guided animal, and it looks like its model, conspecifics themselves may be fooled about its identity. This may be especially pertinent if the model is dangerous to the mimic itself.

Jumping spiders (Salticidae) have acute vision (Land & Nilsson 2002) and complex visually-mediated displays (Richman & Jackson 1992; Nelson & Jackson 2007), that are elicited by optical cues alone (Crane 1949a,b; Jackson & Pollard 1997). Salticids detect and respond appropriately toward conspecifics or prey in the absence of movement cues (Jackson & Tarsitano 1993; Jackson et al. 2005) from distances of 20 body lengths or more (Jackson & Blest 1982; Harland et al. 1999), making them ideal for investigations concerning visual identification.

Myrmarachne is a large genus of ant-like jumping spiders that resemble ants not only morphologically but also behaviorally (Cushing 1997; Ceccarelli 2008). Behavioral similarities include walking rapidly in an erratic manner on six legs and holding the first pair of legs ('legs I') in the air, simulating the ant's antennae. Morphological similarities include the shiny appearance of an ant's exoskeleton rather than the furry appearance of typical salticids, appearing to have three body parts instead of two, and having long, narrow legs instead of the short, stout legs more typical of salticids (Edmunds 1974, 1993; Cushing 1997). Here I investigate whether the ant-like salticid *M. bakeri* is able to discriminate between ants and conspecifics solely on the basis of optical

cues and consider whether movement is a necessary cue for conspecific recognition. I then investigate specifically which morphological traits are necessary for identification of conspecifics.

Ants are well defended against many predators, and evidence strongly suggests that *Myrmarachne* are Batesian mimics that receive protection from predators that are averse to ants (Edmunds 1993; Nelson & Jackson 2006a,b; Nelson et al. 2006). While many species of *Myrmarachne* resemble a specific model very closely, others are less specific- they are 'poor' mimics (Edmunds 2006). *M. bakeri* appears to have no specific model (Nelson 2010) and does not resemble ants as accurately as do better known species of *Myrmarachne* (Nelson & Jackson 2006a; Nelson et al. 2004, 2005). For example, *M. bakeri* does not have a pronounced constriction in its cephalothorax, simulating the division between an ant's head and thorax. However, as with other species in this genus, *M. bakeri* has an elongated body and thin, elongated legs. Despite the relative imprecision of *M. bakeri*'s mimicry, previous studies suggest that *M. bakeri* resemble ants to other salticid species (Nelson & Jackson 2006a) and to mantids (Nelson et al. 2006).

Like all species in this genus, *M. bakeri* is sexually dimorphic, with adult males having greatly enlarged chelicerae (Pollard 1994; Nelson 2010). Although enlarged chelicerae alter the appearance of males substantially, they appear not to compromise mimicry because the chelicerae resemble an object being carried in the jaws of an ant (Nelson & Jackson 2006b).

Myrmarachne bakeri is also polymorphic (Nelson 2010). Polymorphism in *Myrmarachne* is not uncommon, but the typical pattern is for each morph to be confined to particular instars and for each morph to correspond to a distinct ant model, a phenomenon known as 'transformational mimicry' (Cushing 1997; Ceccarelli & Crozier 2007). As young juveniles, *M. bakeri* may be transformational mimics (Nelson 2010). Distinct from other species of *Myrmarachne*, *M. bakeri* adults have two color morphs: either black or similar tones or reddish/brownish tones. Many ant species sympatric with *M. bakeri* are black or reddish (X.J. Nelson: personal observation). In the present study, I used two species that are especially common, often found in the vicinity of *M. bakeri*,

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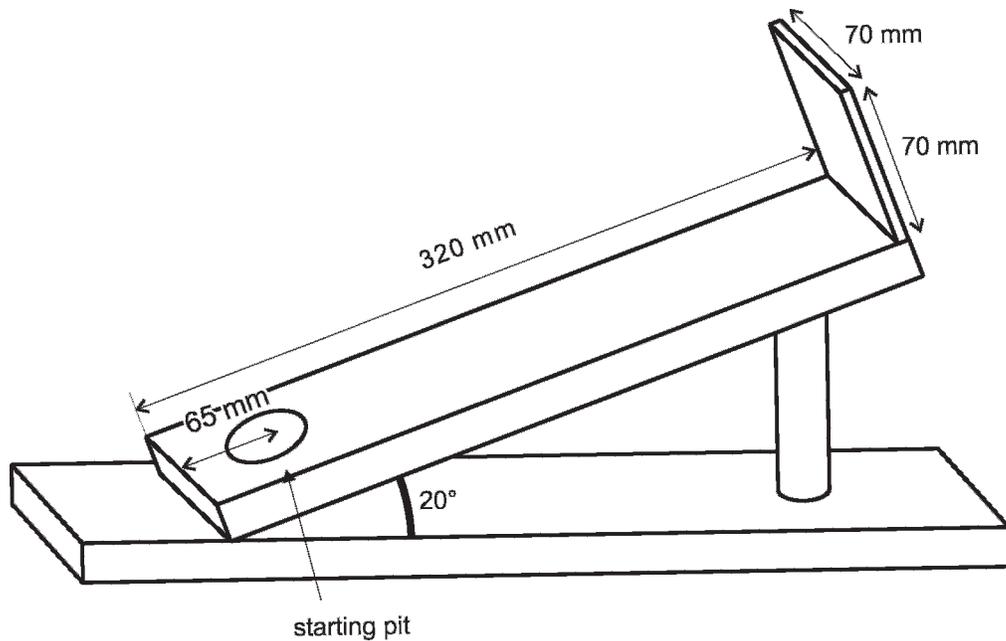


Figure 1.—Ramp used for testing *Myrmarachne bakeri* with altered and unaltered lures of conspecifics and ants.

and towards which *M. bakeri*'s responses are identical (X.J. Nelson personal observation; Nelson & Jackson 2007): *Polyrachis dives* (F. Smith 1857) and *Oecophylla smaragdina* (Fabricius 1775). *P. dives* is a black ant similar in size to *M. bakeri* and similar to the 'black' morphs of *M. bakeri*, while *O. smaragdina* is orange-brown and bears a resemblance to the 'red' morph of *M. bakeri*.

Ants are often predators of salticids and will readily attack *Myrmarachne* (Nelson et al. 2004, 2005). Consequently, *M. bakeri* is potentially at mortal risk if it does not discriminate correctly between an ant and a conspecific, yet *M. bakeri* must approach conspecifics in order to reproduce. Selection for the appropriate response to these situations, specifically to approach a conspecific of the opposite sex and to avoid a similar-looking ant, is clearly strong. In this study, I show that *M. bakeri* does discriminate correctly and elucidate some of the cues whereby this is achieved. The potential cues investigated are features that seem to be either especially conspicuous or characteristically non-ant-like attributes (e.g., presence of palps and, for males, elongated chelicerae). My approach was to make life-like lures from dead salticids and from ants that could be altered by adding or removing anatomical parts of dead arthropods.

METHODS

General.—I collected *Myrmarachne bakeri*, *Polyrachis dives* and *Oecophylla smaragdina* in the vicinity of the International Rice Research Institute (IRRI), Los Baños, Philippines (14°10'N, 121°14'E), and conducted laboratory work at IRRI and at the University of Canterbury (Christchurch, New Zealand). Spiders were tested with lures made of dead *M. bakeri*, dead ants (*O. smaragdina* and *P. dives*) and dead salticids reared in the laboratory (*Portia labiata* (Thorell 1882) and *Aelurillus cognatus* (O.Pickard-Cambirdge 1872)). Ants were collected as required for making lures (see below). Spiders were maintained in individual plastic cages, cleaned

weekly, with a cotton roll through the bottom that dangled in a small cup of water, providing humidity. All spiders were fed twice a week with cultured *Drosophila* and small cultured house flies (*Musca domestica*). Testing was done between 0800 h and 1700 h using sexually mature male and female spiders. Using standard protocol for experiments on predatory behavior, spiders were fasted between 3 to 5 days prior to testing. No individual spider was tested more than once with a given lure.

Experimental methods.—A wooden ramp (see Fig. 1 for dimensions) raised at a 20° angle and supported by a wooden pole glued to a wooden base was used for testing. A thin piece of wood glued to the top end of the ramp served as a background against which the salticid saw the lure. The lure was placed 40 mm from the top end of the ramp, equidistant from both edges. The entire apparatus was painted with two coats of polyurethane.

A 200 W incandescent lamp, positioned ca 600 mm overhead lit the apparatus; fluorescent ceiling lamps provided additional ambient lighting. A white paper screen along three sides surrounded the apparatus, leaving one side open for observations. The ramp was positioned so that during tests the salticid moved away from the open side and the observer. Before each test, a *M. bakeri* was placed in a pit drilled halfway through the thickness of the ramp 200 mm from the lure. The pit was 32 mm in diameter and centered 65 mm from the bottom end of the ramp. The salticid was left in the pit to acclimate for 60 s before a piece of cardboard, which was placed over the pit, was removed, allowing the salticid to exit from the pit.

Tests began when the *M. bakeri* walked out of the pit and on to the ramp and ended when it either was within 1 mm of the lure (preventing the spider from touching the lure so as to avoid chemical contamination of the lure) or walked off the top of the ramp. If the salticid jumped off the ramp at a point below the lure or if it stayed in the pit for more than 30 min

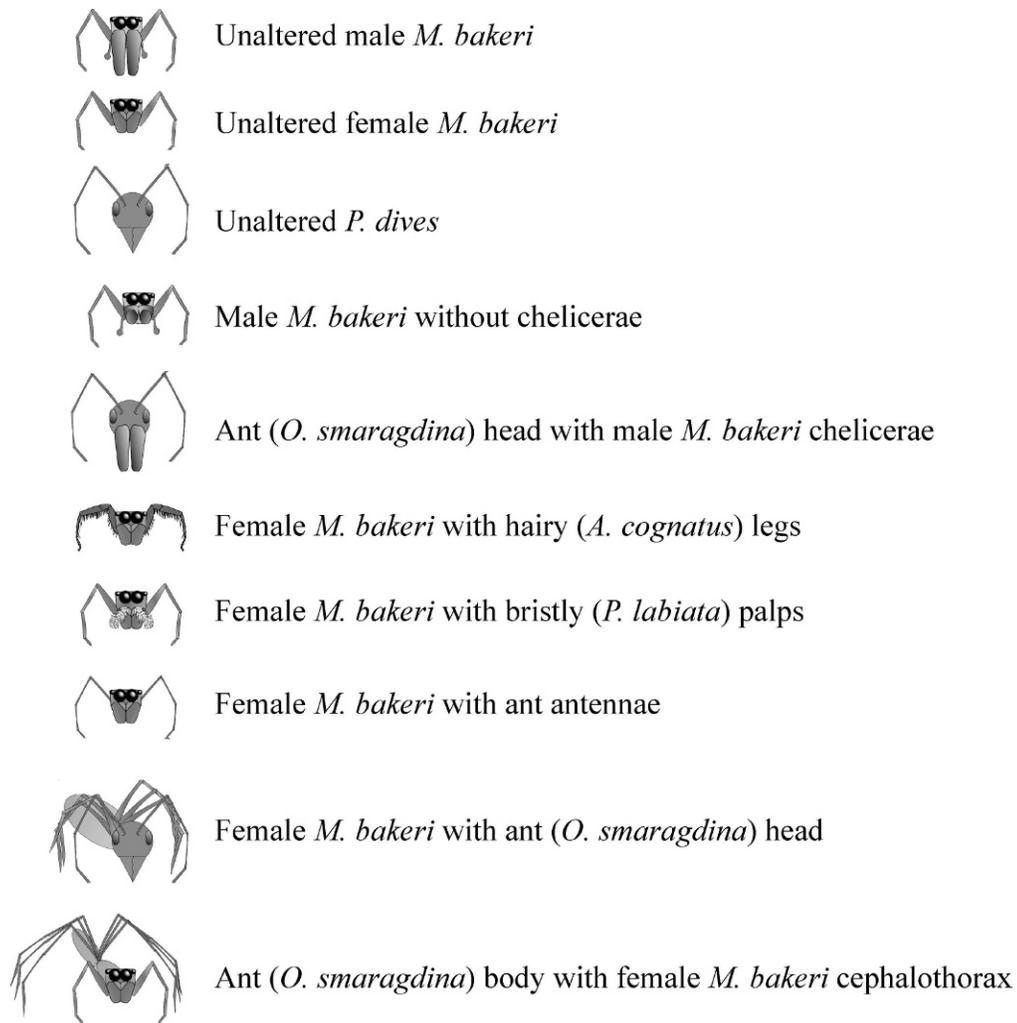


Figure 2.—Lures used for testing cues by which *Myrmarachne bakeri* distinguishes conspecifics from ants.

(no spiders walked under the ramp), tests were aborted (< 5%). Spiders that did not display were excluded from the analysis. The ramp was wiped with 80% ethanol and allowed to dry for 30 min between each test to eliminate possible chemical traces from the spiders.

Lures.—Ten lure types were made (Fig. 2), using whole arthropods ('unaltered lures') or anatomical portions ('altered lures') of three species of salticids (*M. bakeri*, *P. labiata*, *A. cognatus*), and two species of ants (*O. smaragdina* and *P. dives*), which were combined in various ways. The questions addressed for each lure type are described below.

Lures were made by immobilizing an arthropod with CO₂ and placing it in 80% ethanol. One day later, I mounted the arthropod in a life-like posture on the centre of one side of a disc-shaped piece of cork (diameter ca 1.25 × body length of the arthropod; thickness ca 2 mm) using forceps to position it. The lure was then sprayed with a transparent aerosol plastic adhesive for preservation (see Jackson & Tarsitano 1993). I altered lures by removing body parts from a dead arthropod with a scalpel prior to mounting on the cork disc, in some instances replacing them with body parts from another dead arthropod by gluing them with adhesive spray in the relevant location (see Fig. 2). Of the ten lure types, seven were altered

to test for specific cues used for conspecific recognition and for discrimination between conspecifics and ants.

In prior studies (Nelson & Jackson 2007, summarized in Table 1), Jackson and I described the characteristics of typical responses by *M. bakeri* to live conspecific males and females or live ants. I here use these prior observations to assess the responses of *M. bakeri* toward altered and unaltered lures. I posed the question such that comparisons were made between displays to a certain stimulus and 'other' displays (all other displays). I analyzed the data using Fisher exact tests. For example, to address the question whether test spiders displayed in the same way as to a male *Myrmarachne* I compared the number of spiders that used typical display behavior exhibited toward males (as described in Nelson & Jackson 2007) versus the number of spiders that exhibited other displays. Results are reported with Bonferroni adjustments for multiple comparisons. Distances at which displays were initiated and display duration were analyzed using ANOVA in Stat View Version 5 (SAS Institute Inc.).

- 1) *Is movement a necessary cue for recognition of ants and conspecifics?* Lures made from unaltered males and females of *M. bakeri* and an unaltered ant (*Polyrachis*

Table 1.—Outline of behavioral characteristics of the displays of male and female *Myrmarachne bakeri* toward conspecific males and females and toward ants (based on Nelson & Jackson 2007).

	Male	Female	Ant
Male	Abdomen raised and twitching Body sometimes held high Palps stationary Legs tight in on the body	Abdomen lowered and twitching Body held low Palps moving Legs spread wide away from body	Abdomen raised but not twitching Body sometimes held high Palps stationary Legs in normal posture
Female	Abdomen raised and twitching Body held 'normal' or low Palps stationary Legs tight in on the body	Abdomen raised but not twitching Body sometimes held high Palps stationary Legs tight in on the body	Abdomen raised but not twitching Body held high or low Palps sometimes moving Legs in normal posture

dives) were used. Lures faced 45° away from the starting pit on the ramp and were tested with both male and female *M. bakeri* ('standard methods'). This ensured that potential cues from both the abdomen and cephalothorax were visible to the test spider. Responses toward these stationary lures were assessed based on responses toward live animals of the same sex and species (see Table 1).

- 2) *Are palps an important optical cue by which M. bakeri recognizes conspecific females?* The hairless palps from a dead *M. bakeri* female were removed and replaced with the bristly palps of a non-ant-like salticid, *Portia labiata*. Standard methods were used for testing.
- 3) *Are chelicerae an important optical cue by which M. bakeri recognizes conspecific males and distinguish them from ants?* Two lure types were made, one by cutting the chelicerae off a *M. bakeri* male and the other by gluing the chelicerae of a *M. bakeri* onto the 'face' (anterior part of the ant's head or spider's cephalothorax) of an ant (*Oecophylla smaragdina*). To human observers the former lure resembled a female *M. bakeri*. The second lure, to human observers, resembled a male *M. bakeri*. Standard methods were used for testing.
- 4) *Are legs I an important optical cue by which M. bakeri recognizes conspecific females and distinguish them from ants?* Two lure types were made. In the first type, the hairless legs I of a female *M. bakeri* were exchanged with the antennae of an ant. The second type was made by exchanging a *M. bakeri* female's legs I for the hairy and robust legs I of a non-ant-like salticid, *Aelurillus cognatus*. Standard methods were used for testing.
- 5) *Relative importance of the body and of the face in male recognition of females and ants.* The head of an ant (*Oecophylla smaragdina*) was exchanged for the cephalothorax of a female *M. bakeri*. This provided two lure types, one with the 'body' (thorax and abdomen) of an ant and the cephalothorax of *M. bakeri* and the other with the abdomen of *M. bakeri* and head of *O. smaragdina*. These lures were tested only with male *M. bakeri*. Lures were placed so they

faced directly toward the starting pit (0°), thereby providing cues from the 'face' only.

Voucher specimens of all species have been deposited in the IRRITaxonomy Laboratory in Los Baños, the Philippines, and in the Florida State Collection of Arthropods, Gainesville, Florida, USA.

RESULTS

Is movement a necessary cue for recognition of ants and conspecifics?—Movement is not a necessary cue for eliciting *M. bakeri*'s typical displays toward conspecifics and ants. *M. bakeri* responded to dead, odorless, unaltered lures from conspecific males and females and from ants in the same way as they responded to living conspecific females and males and living ants (Table 1) between 79 and 100% of the time (Tables 2 & 3).

Are palps an important optical cue by which *M. bakeri* recognizes conspecific females?—Females ($P = 0.10$, $df = 1$, $n = 17$; Table 2, comparison 8 vs 2) and especially males ($P = 1.00$, $df = 1$; $n = 13$; Table 3, comparison 8 vs 2) displayed toward altered lures of conspecific females with bristly palps (from *Portia labiata*) in much the same way as toward lures made from unaltered females (Fisher exact tests).

Are chelicerae an important optical cue by which *M. bakeri* recognizes conspecific males and distinguishes them from ants?—Both females ($P < 0.01$, $df = 1$, $n = 25$; Table 2, comparison 5 vs 3) and males ($P < 0.001$, $df = 1$, $n = 22$; Table 3, comparison 5 vs 3) displayed toward the altered lure of an ant with *M. bakeri* male chelicerae differently from how they displayed to a lure made from an unaltered ant (Fisher exact tests). Instead, ants with chelicerae were treated as conspecific males by both males ($P = 1.00$, $df = 1$, $n = 24$; Table 3, comparison 5 vs 1) and females (Fisher exact test, $P = 0.199$, $df = 1$, $n = 24$; Table 2, comparison 5 vs 1) (Fisher exact tests). Females ($P < 0.001$, $df = 1$, $n = 28$; Table 2, comparison 4 vs 1) and males ($P < 0.001$, $df = 1$, $n = 34$; Table 3, comparison 4 vs 1) responded differently toward lures made from an unaltered male and from a male without chelicerae (Fisher exact tests). Neither males ($P = 0.26$, $df = 1$, $n = 25$; Table 3, comparison 4 vs 2) nor females ($P = 0.011$, $df = 1$, $n = 25$; Table 2, comparison 4 vs 2) displayed toward males without chelicerae similarly as toward a conspecific female (Fisher exact tests). However, females ($P = 0.427$, $df = 1$, $n = 29$; Table 2, comparison 4 vs 3), but not males ($P < 0.001$, $df = 1$, $n = 32$; Table 3, comparison 4 vs 3), displayed

Table 2.—Response toward lures used to determine the cues used by female *Myrmarachne bakeri* to distinguish ants (*Polyrachis dives* and *Oecophylla smaragdina*) from conspecifics. Missing percentages due to inability to interpret displays. * Displays were not typical of female-female displays.

Lure number	Lure	<i>n</i> tested	<i>n</i> displayed	Percent displayed as to a conspecific male (<i>n</i>)	Percent displayed as to a conspecific female (<i>n</i>)	Percent displayed as to an ant (<i>n</i>)
1	Unaltered male <i>M. bakeri</i>	19	13	100 (13)		
2	Unaltered female <i>M. bakeri</i>	19	10		90 (9)	
3	Unaltered <i>P. dives</i>	20	14			78.6 (11)
4	Male <i>M. bakeri</i> without chelicerae	20	15	13.3 (2)	26.7 (4)	60 (9)
5	<i>O. smaragdina</i> with male <i>M. bakeri</i> chelicerae	19	11	81.8 (9)		18.2 (2)
6	Female <i>M. bakeri</i> with hairy (<i>Aelurillus cognatus</i>) legs I	17	3*		0	
7	Female <i>M. bakeri</i> with <i>O. smaragdina</i> antennae as legs I	17	7		100 (7)	
8	Female <i>M. bakeri</i> with bristly (<i>Portia labiata</i>) palps	20	7		42.9 (3)	

toward the male lure without chelicerae in much the same way as toward an ant (Fisher exact tests).

Are legs I an important optical cue by which *M. bakeri* recognizes conspecific females and distinguish them from ants?—Hairless legs are a necessary cue for females ($P = 0.014$, $df = 1$, $n = 13$; Table 2, comparison 6 vs 2) to identify conspecific females, but not necessary for males to identify conspecific females ($P = 1.00$, $df = 1$, $n = 13$; Table 3, comparison 6 vs 2) (Fisher exact tests), as males displayed toward altered lures of females with hairy legs I (*Aelurillus cognatus*) in much the same way as toward lures made from unaltered females.

Ant antennae alone do not elicit the display behavior typical of *M. bakeri* males ($P < 0.001$, $df = 1$, $n = 22$; Table 3, comparison 7 vs 3) and females ($P = 0.002$, $df = 1$, $n = 21$; Table 2, comparison 7 vs 3) to ants (Fisher exact tests). Instead, both males ($P = 1.00$, $df = 1$, $n = 15$; Table 3, comparison 7 vs 2) and females ($P = 1.00$, $df = 1$, $n = 17$; Table 2, comparison 7 vs 2) displayed toward the altered lure

of a conspecific female with ant antennae in the same way as they did toward lures made from an unaltered conspecific female (Fisher exact tests).

Relative importance of the body and of the face in male recognition of females and ants.—Males displayed toward the altered lure made from a conspecific female with an ant's head in much the same way as to a lure made from an unaltered conspecific female ($P = 0.262$, $df = 1$, $n = 16$; Table 3, comparison 9 vs 2), and significantly differently to typical responses in interactions with ants ($P = 0.034$, $df = 1$, $n = 23$; Table 3, comparison 9 vs 3) (Fisher exact tests).

Males responded toward the altered lure of an ant with the cephalothorax of a *M. bakeri* female significantly differently from their response toward an unaltered ant ($P = 0.008$, $df = 1$, $n = 21$; Table 3 comparison 10 vs 3) (Fisher exact test). Instead, males generally responded initially toward the altered lure of an ant with the cephalothorax of a *M. bakeri* female in the same way as they did when courting conspecific females

Table 3.—Response toward lures used to determine the cues used by male *Myrmarachne bakeri* to distinguish ants (*Polyrachis dives* and *Oecophylla smaragdina*) from conspecifics. Missing percentages due to inability to interpret displays. * Lure facing pit (0°). ** All changed display (as toward ants) when they circled the female as part of the courtship dance and then saw the ant's body.

Lure number	Lure	<i>n</i> tested	<i>n</i> displayed	Percent displayed as to a conspecific male (<i>n</i>)	Percent displayed as to a conspecific female (<i>n</i>)	Percent displayed as to an ant (<i>n</i>)
1	Unaltered male <i>M. bakeri</i>	21	18	100 (18)		
2	Unaltered female <i>M. bakeri</i>	17	9		88.9 (8)	
3	Unaltered <i>P. dives</i>	18	16			93.8 (15)
4	Male <i>M. bakeri</i> without chelicerae	20	16	31.2 (5)	50 (8)	18.8 (3)
5	<i>O. smaragdina</i> with male <i>M. bakeri</i> chelicerae	10	6	100 (6)		
6	Female <i>M. bakeri</i> with hairy (<i>Aelurillus cognatus</i>) legs I	10	4		75 (3)	
7	Female <i>M. bakeri</i> with <i>O. smaragdina</i> antennae as legs I	9	6		100 (6)	
8	Female <i>M. bakeri</i> with bristly (<i>Portia labiata</i>) palps	15	4		100 (4)	
9	Female <i>M. bakeri</i> with <i>O. smaragdina</i> head*	8	7		57.1 (4)	42.9 (3)
10	<i>O. smaragdina</i> with female <i>M. bakeri</i> cephalothorax*	8	5		80 (4)**	20 (1)

(their initial view of the lure was face on) ($P = 1.00$, $df = 1$, $n = 14$; Table 3, comparison 10 vs 2) (Fisher exact test). However, during typical courtship with a living conspecific female, males perform dances involving side-to-side stepping (Nelson & Jackson 2007). When test males danced in front of the lure, they got into a position from which the lure was visible from the side, instead of face-on. At this point, the ant's body was visible and in all cases the males immediately switched behavior and briefly displayed as to an ant before fleeing (Table 3).

Display distance and duration.—Sex had no main effect on the distance ($F_{(1,167)} = 0.806$, $P = 0.371$) at which displays were initiated toward altered and unaltered lures, nor on their duration ($F_{(1,167)} = 0.773$, $P = 0.381$). However, *M. bakeri* displayed toward unaltered lures from further away than toward altered lures ($F_{(1,167)} = 8.325$, $P = 0.004$), although display duration did not differ ($F_{(1,167)} = 1.887$, $P = 0.171$). There was no interaction effect of distance ($F_{(1,167)} = 1.659$, $P = 0.5839$) or duration ($F_{(1,167)} = 0.091$, $P = 0.763$).

Female display duration was not affected by lure type ($F_{(7,72)} = 0.801$, $P = 0.589$, Fig. 3a). However, lure type did have a significant effect on the distance from which females initiated displays. ($F_{(7,72)} = 3.134$, $P = 0.006$, Fig. 3b). Fisher's PLSD post-hoc tests showed that females displayed toward *Polyrachis dives* from further away than toward conspecific females ($P = 0.002$), females with ant antennae ($P = 0.001$), females with hairy legs ($P = 0.034$), females with bristly palps ($P = 0.001$), males without chelicerae ($P = 0.007$), and males ($P = 0.025$). In other words, females displayed from further away toward ants than to anything that resembled a conspecific, except *Oecophylla smaragdina* with male chelicerae.

Male display duration was not also affected by lure type ($F_{(10,80)} = 1.189$, $P = 0.311$, Fig. 3a). Lure type did have a significant effect on the distance from which males initiated displays ($F_{(9,81)} = 4.214$, $P < 0.001$, Fig. 3b), which followed similar patterns to those of females (see Fig. 3b), with ants being displayed at from the greatest distance, followed by conspecific males, both with and without chelicerae.

DISCUSSION

Myrmarachne bakeri distinguishes conspecifics from ants based on the elongated chelicerae of conspecific males, legs I, as well as body and other facial cues, such as the size and position of the eyes. Taken in combination, results from these display distance and display type data suggest that the enlarged chelicerae of males are fundamental for male recognition - even lures of ants with male chelicerae were displayed at as if they were males. This is intriguing, as non-ant-like salticids respond to male *Myrmarachne* as if they were ants carrying something in their mandibles (Nelson & Jackson 2006b). However, absence of chelicerae is not the sole cue used to distinguish males from females, as neither sex responded to lures of males without chelicerae as if they were females. This is an interesting finding because to the human observer a *M. bakeri* male without chelicerae looks very similar to a *M. bakeri* female. However, both males and females displayed from further away in the presence of ant lures than conspecific lures, implying that they are able to distinguish ants from conspecifics before approaching so close that it may be dangerous (Nelson et al. 2004).

Males did not appear to attend strongly to cues from the palps or legs of females, generally displaying toward these altered lures in the same way as toward conspecific females, and from similar distances. Furthermore, males displayed to lures of females with the head of an ant as if they were females, suggesting that cues from the body are important in recognition of females. Nevertheless, cues from the female's cephalothorax are used, as they also responded to lures made from an ant with the head of a spider in a manner typical of that used toward females - that is, until they saw the ant's body, whereupon they quickly displayed as to an ant and fled. However, females did appear to attend to cues from the legs of females. Unlike males, they responded differently toward unaltered lures of conspecific females than toward lures of females with the legs of other salticids.

A control lure in which body parts were cut and reassembled might have been useful to account for the effects of cutting and gluing. However, responses toward "combination lures" of females and ants, in which males responded to the "face" as to a female, but upon circling the lure and encountering the abdomen of the ant, changed tactics rapidly, suggest that glued 'intact' controls were unnecessary. The actual part that was being responded to in each case was unaltered, but the displays were very clear (one of courtship, the other escape after a brief 'aggressive' display) despite these lures being glued together.

To the human eye, *M. bakeri* legs I and the ants' antennae appear very similar and it seems that they also appear that way to *M. bakeri*. Although neither males nor females were able to distinguish ants on the basis of antennae alone, females appear to be more sensitive than males to the finer distinctions between ants and conspecifics, generally displaying toward lures containing ant parts from further away than toward lures of conspecifics or conspecifics with salticid parts. These findings suggest that *M. bakeri* uses general templates for conspecific recognition. If, on the whole, the cues fit the template, a 'decision' is made regarding the identity of the individual that is the source of the cues. Yet males and females seem to differ in the cues they use for recognizing conspecifics. For example, although males did not discriminate between the combination lure of a conspecific female with hairy legs I and the lure of the unaltered conspecific female, females did discriminate, while the display distance of males, but not females, toward males without chelicerae was more similar to that of males toward males than females. An especially striking example of template matching in jumping spiders occurs with *Maevia inclemens* (Walckenaer 1837). Males of this species are dimorphic, both in morphology and in courtship behavior. Despite these differences females recognize males and will mate with both morphs (Clark & Uetz 1992); however, if the behavior of one morph is superimposed (through the use of computer animation) on the body of the other morph, female receptivity is significantly lowered, suggesting that females match the behavior and morphology of each morph to an existing template (Clark & Uetz 1993).

Predator-prey interactions necessitate the recognition of the subject as either one or the other. In many cases this may often be achieved simply through size: if it is the bigger one, it is a potential predator, and if it is the smaller one it is a potential prey (Prete 1990; Prete et al. 2002). *Myrmarachne* lives in the

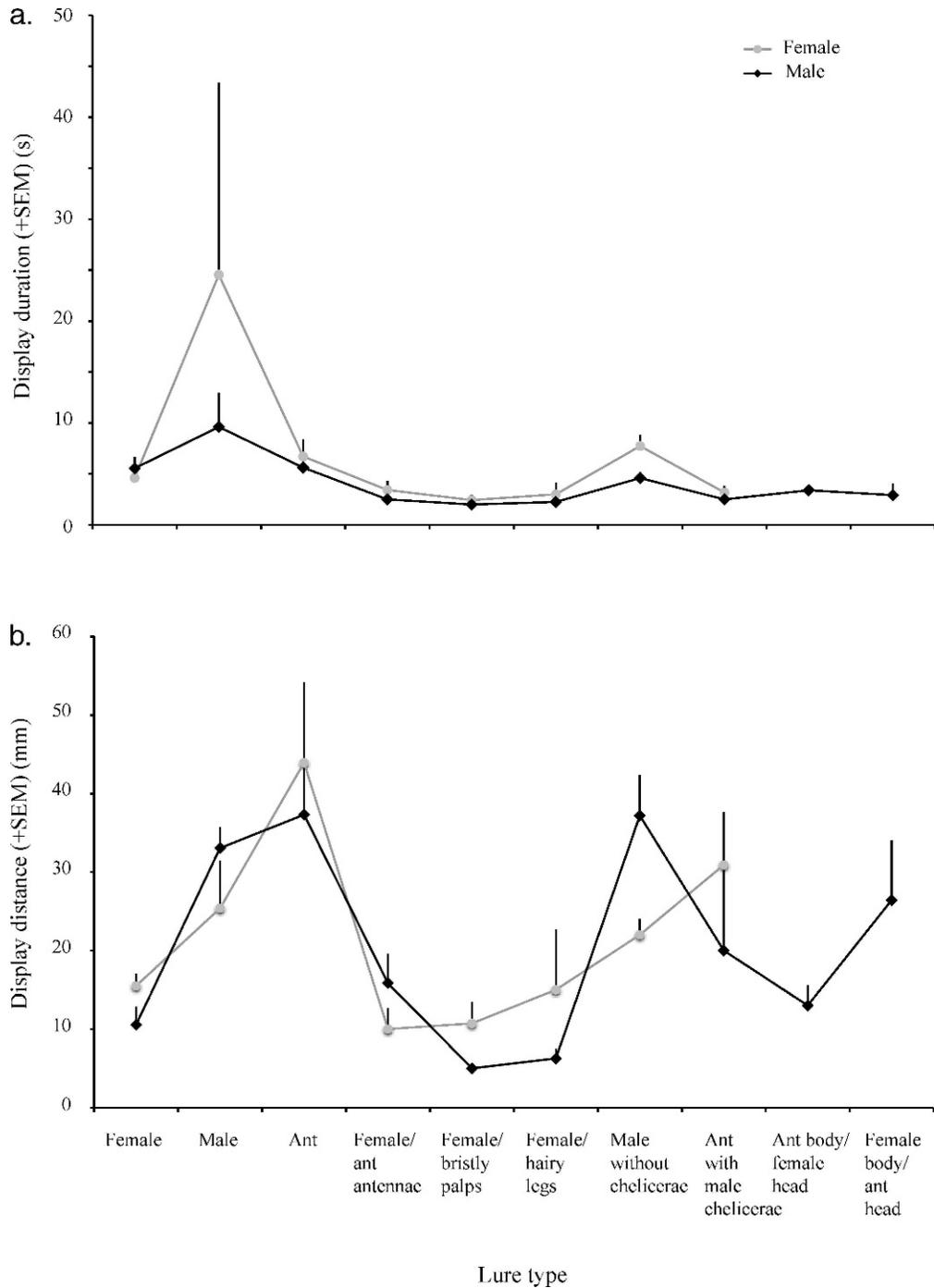


Figure 3.—Mean (+SEM) (a) duration and (b) distance of male and female displays toward lures.

vicinity of ants, and as both model and mimic are active, cursorial predators they often come near each other. In a twist to traditional examples of mimicry, the model itself is a potential predator of the mimic (Nelson et al. 2004, 2005), and this makes the task of distinguishing between the model and its conspecifics critical for *Myrmarachne*.

Other studies have shown that various species of salticids have the ability to recognize prey on the basis of optical cues alone. The most detailed studies of the cues by which salticids make

vision-based discriminations have come from work on prey recognition in araneophagic (spider-eating) salticids in the genus *Portia* (Jackson & Tarsitano 1993; Harland & Jackson 2001, 2002). These studies suggest that the presence of the large, forward-facing anterior medial eyes (AME) are crucial in distinguishing jumping spiders from other spiders. In this study it was not possible to make realistic lures while altering the appearance of the AME. However, these results suggest that this would be a factor well worth further investigation.

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LITERATURE CITED

- Bates, H.W. 1862. Contributions to an insect fauna of the Amazon valley. Lepidoptera: Heliconidae. Transactions of the Linnean Society of London 23:495–566.
- Ceccarelli, F.S. 2008. Behavioral mimicry in *Myrmarachne* species (Araneae, Salticidae) from North Queensland, Australia. *Journal of Arachnology* 36:344–351.
- Ceccarelli, F.S. & R.H. Crozier. 2007. Dynamics of the evolution of Batesian mimicry: molecular phylogenetic analysis of ant-mimicking *Myrmarachne* (Araneae: Salticidae) species and their ant models. *Journal of Evolutionary Biology* 20:286–295.
- Clark, D.L. & G.W. Uetz. 1992. Morph-independent mate selection in a dimorphic jumping spider: Demonstration of movement bias in female choice using video-controlled courtship behaviour. *Animal Behaviour* 43:247–254.
- Clark, D.L. & G.W. Uetz. 1993. Signal efficacy and the evolution of male dimorphism in the jumping spider, *Maevia inclemens*. *Proceedings of the National Academy of Science USA* 90:11954–11957.
- Crane, J. 1949a. Comparative biology of salticid spiders at Rancho Grande, Venezuela. Part III. Systematics and behavior in representative new species. *Zoologica* 34:31–52.
- Crane, J. 1949b. Comparative biology of salticid spiders at Rancho Grande, Venezuela. Part IV. Systematics and behavior in representative new species. *Zoologica* 34:159–214.
- Cushing, P.E. 1997. Myrmecomorphy and myrmecophily in spiders: a review. *Florida Entomologist* 80:165–193.
- Edmunds, M.E. 1974. *Defence in Animals*. Longman Group Ltd., New York.
- Edmunds, M.E. 1993. Does mimicry of ants reduce predation by wasps on salticid spiders? *Memoirs of the Queensland Museum* 33:507–512.
- Edmunds, M.E. 2006. Do Malaysian *Myrmarachne* associate with particular species of ant? *Biological Journal of the Linnean Society* 88:645–653.
- Harland, D.P., R.R. Jackson & A.M. Macnab. 1999. Distances at which jumping spiders (Araneae: Salticidae) distinguish between prey and conspecific rivals. *Journal of Zoology* 247:357–364.
- Harland, D.P. & R.R. Jackson. 2001. Prey classification by *Portia fimbriata*, a salticid spider that specializes at preying on other salticids: species that elicit cryptic stalking. *Journal of Zoology* 255:445–460.
- Harland, D.P. & R.R. Jackson. 2002. Influence of cues from the anterior medial eyes of virtual prey on *Portia fimbriata*, an araneophagic jumping spider. *Journal of Experimental Biology* 205:1861–1868.
- Jackson, R.R. & D.A. Blest. 1982. The distances at which a primitive jumping spider, *Portia fimbriata*, makes visual discriminations. *Journal of Experimental Biology* 97:441–445.
- Jackson, R.R. & S.D. Pollard. 1997. Jumping spider mating strategies: sex among cannibals in and out of webs. Pp. 340–351. *In The Evolution of Mating Systems in Insects and Arachnids*. (J.C. Choe & B.J. Crespi, eds.). Cambridge University Press, Cambridge, UK.
- Jackson, R.R. & M.S. Tarsitano. 1993. Responses of jumping spiders to motionless prey. *Bulletin of the British Arachnological Society* 9:105–109.
- Jackson, R.R., X.J. Nelson & G.O. Sune. 2005. A spider that feeds indirectly on vertebrate blood by choosing female mosquitoes as prey. *Proceedings of the National Academy of Science USA* 102:15155–15160.
- Land, M.F. & D.E. Nilsson. 2002. *Animal Eyes*. Oxford University Press, Oxford, UK.
- Nelson, X.J. 2010. Polymorphism in an ant mimic. *Journal of Arachnology* 38:139–141.
- Nelson, X.J. & R.R. Jackson. 2006a. Vision-based innate aversion to ants and ant mimics. *Behavioral Ecology* 17:676–681.
- Nelson, X.J. & R.R. Jackson. 2006b. Compound mimicry and trading predators by the males of sexually dimorphic Batesian mimics. *Proceedings of the Royal Society of London. Series B Biological Sciences* 273:367–372.
- Nelson, X.J. & R.R. Jackson. 2007. Complex display behaviour during the intraspecific interactions of myrmecomorphic jumping spiders (Araneae, Salticidae). *Journal of Natural History* 41:1659–1678.
- Nelson, X.J., R.R. Jackson, S.D. Pollard, G.B. Edwards & A.T. Barrion. 2004. Predation by ants on jumping spiders (Araneae: Salticidae) in the Philippines. *New Zealand Journal of Zoology* 31:45–56.
- Nelson, X.J., R.R. Jackson, G.B. Edwards & A.T. Barrion. 2005. Living with the enemy: jumping spiders that mimic weaver ants. *Journal of Arachnology* 33:813–819.
- Nelson, X.J., R.R. Jackson, D. Li, A.T. Barrion & G.B. Edwards. 2006. Innate aversion to ants (Hymenoptera: Formicidae) and ant mimics: experimental findings from mantises (Mantodea). *Biological Journal of the Linnean Society* 88:23–32.
- Pollard, S.D. 1994. Consequences of sexual selection on feeding in male jumping spiders (Araneae: Salticidae). *Journal of Zoology* 234:203–208.
- Prete, F.R. 1990. Configural prey recognition by the praying mantis, *Sphodromantis lineola* (Burr.); effects of size and direction of movement. *Brain, Behavior and Evolution* 36:300–306.
- Prete, F.R., L.E. Hurd, D. Branstrator & A. Johnson. 2002. Responses to computer-generated visual stimuli by the male praying mantis, *Sphodromantis lineola* (Burmeister). *Animal Behaviour* 63:503–510.
- Richman, D.B. & R.R. Jackson. 1992. A review of the ethology of jumping spiders (Araneae, Salticidae). *Bulletin of the British Arachnological Society* 9:33–37.
- Ruxton, G., T. Sherratt & M. Speed. 2004. *Avoiding Attack: The Evolutionary Ecology of Crypsis, Warning Signals and Mimicry*. Oxford University Press, Oxford, UK.
- Wickler, W. 1968. *Mimicry in Plants and Animals*. Weidenfeld and Nicholson, London.

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