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Complex display behaviour during the intraspecific interactions of myrmecomorphic jumping spiders (Araneae, Salticidae)

XIMENA J. NELSON & ROBERT R. JACKSON

School of Biological Sciences, University of Canterbury, Christchurch, New Zealand

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Abstract

Jumping spiders (Salticidae) are known for their elaborate vision-based display behaviour, and a sizeable minority of the species in this large family resemble ants. The display repertoire of two ant-like salticid species from the Philippines is investigated. *Myrmarachne assimilis* is a specialist ant mimic, closely matching the appearance of the weaver ant *Oecophylla smaragdina*. *Myrmarachne bakeri* is a generalist mimic, which, although ant-like, is not a close match to any sympatric ant species. *Myrmarachne* are sexually dimorphic, with males having enlarged chelicerae. The copulatory posture of *Myrmarachne* is unique among salticids, apparently as an adjustment for the male's elongated chelicerae. Details concerning the intraspecific behaviour of *Myrmarachne* appear to be adjustments to living in environments populated by numerous other animals with similar appearance (ants). However, the specialist and the generalist that were investigated have display repertoires that are broadly similar to each other and to those of more typical salticids. Generally, the display behaviour of *Myrmarachne* appears not to have necessitated dramatic deviation from typical salticid display and mating strategies.

Keywords: *Arachnida, Batesian mimicry, communication, conditional mating strategy, jumping spider, mating behaviour, Salticidae, signals*

Introduction

Animal display behaviour (i.e. the use of signals that have been evolutionarily modified in a manner that enhances their capacity to convey information; Smith (1977)) raises questions not only about strategic design, or function, but also about tactical design (Ord et al. 2002; Hebets and Papaj 2005), where “tactical design” refers to ways in which signal structure facilitates information transfer. Tactical design, in turn, raises questions about how “receiver psychology” (Guilford and Dawkins 1991; Fleishman 1992; Hauglund et al. 2006) and prevailing habitat conditions (Endler 1992; Persons et al. 1999; Leal and Fleishman 2004) might affect signal transmission. Here a special habitat condition is considered that might especially matter to a subset of Batesian mimics that

rely on vision-based signals for intraspecific communication. Batesian mimics gain protection from potential predators by resembling unpalatable or dangerous model organisms, misinforming predators by providing signals normally associated with the model (Wickler 1968; Edmunds 1974). For a Batesian mimic that relies on vision for intraspecific communication, part of its habitat is the population of similar-looking model organisms, but little is known about how the mimic's own resemblance to these other organisms might challenge the mimic's discrimination abilities when there is a need to interact with potential mates and conspecific rivals.

The problem of reliable discrimination between conspecific mimics and models might be greater for a specialist than for a generalist Batesian mimic (see Edmunds 2000, 2006), with the terms "specialist" and "generalist" specifying whether or not the mimic closely resembles any one particular model species. The present paper is a step toward investigating this hypothesis by examining a pair of closely related mimic species from a system in which the models are ants and the mimics are ant-like jumping spiders (Salticidae) that rely strongly on vision-based communication.

Most spiders have eyes lacking the structural complexity required for acute vision (Homann 1971; Land 1985), but salticids have a pair of distinctively large forward-facing anterior-medial eyes that support exceptional spatial acuity (Land 1969a, 1969b; Williams and McIntyre 1980; Blest et al. 1990; Harland and Jackson 2004). Not surprisingly, the most elaborate vision-based display behaviour known for spiders (Foelix 1996), and among the most elaborate ever described for any animal group, is found in this family (Jackson 1982a; Jackson and Pollard 1997).

Myrmecomorphic species (i.e. species that are ant-like in appearance) are a sizeable minority in the family Salticidae, with the genus *Myrmarachne* being especially notable (Wanless 1978). With more than 200 described species (Platnick 2007; Proszynski 2007), all of which are myrmecomorphic, *Myrmarachne* is the largest salticid genus and there is extensive evidence that myrmecomorphy in *Myrmarachne* functions as Batesian mimicry (Edmunds 1974; Jackson and Willey 1995). Ants are dangerous and unpalatable prey-size organisms (Blum 1981; Hölldobler and Wilson 1990) and a variety of would-be predators of salticids, including other salticids and mantises, avoid making predatory attacks on, or coming close to, ants (Nelson et al. 2006). Experimental studies have also shown that salticids and mantises that are averse to attacking ants are averse to attacking *Myrmarachne* (Harland and Jackson 2001; Nelson et al. 2004; also see Cutler 1991; Edmunds 1993).

The resemblance of *Myrmarachne* species to ants comes from having slender legs, a narrow, elongated body constricted at the abdomen and cephalothorax to create the illusion of a three-segmented body, and an erratic, ant-like manner of moving (Cushing 1997; Edmunds 2006). The front legs, held raised and waving, or else tapping the substrate, resemble ant antennae. Contrary to its family namesake, *Myrmarachne* rarely jumps, doing so only when severely threatened. All *Myrmarachne* species are sexually dimorphic (Wanless 1978), with males having greatly enlarged chelicerae that increase their total body length by 50–70%. However, oversized chelicerae remain compatible with ant mimicry because predators appear to mistake the *Myrmarachne* males, with their long chelicerae, for ant workers that are carrying objects in their mandibles (Nelson and Jackson 2006).

Understandably, research on *Myrmarachne* has been dominated by interest in the benefit these salticids gain from deceiving would-be predators. Despite the extensive literature on the intraspecific communication of salticids, little attention has been paid to myrmecomorphic species. The early literature characterized salticid display behaviour as stereotypic

and reflex-like (Crane 1949; Drees 1952), but later work has largely supplanted this portrayal with an emphasis on how salticid intraspecific interactions tend to be highly variable and complex (Jackson 1982a; Jackson and Pollard 1997). The early literature also emphasized the role of vision almost to the exclusion of other sensory modalities, but there are now numerous studies illustrating that salticids make extensive use of acoustic, percussion, silk-borne, tactile and chemical signalling during intraspecific interactions (Edwards 1981; Gwynne and Dadour 1985; Jackson 1987; Pollard et al. 1987; Maddison and Stratton 1988; Noordam 2002; Elias et al. 2003, 2005).

“Courtship” may be defined as intersexual communicatory behaviour that forms the normal preliminaries to mating (Jackson 1982a). Crane’s (1949) conclusion that visual stimuli are both necessary and sufficient for releasing salticid courtship may have been compatible with commonsense expectations about adaptive trade-offs in small animals, yet there is no clear evidence that the exceptional eyesight of salticids has adversely affected the ability of salticids to rely on other sensory modalities, with the prevalence of courtship versatility (Jackson and Pollard 1997) being an especially striking illustration of how exceptional eyesight does not preclude using other sensory modalities in disparate communication routines. First documented in detail (Jackson 1977) for a North American species, *Phidippus johnsoni* (Peckham and Peckham, 1883), courtship versatility is a conditional mating strategy in which males use three distinct tactics conditional on the female’s location and state of maturity. Males use vision-based displays when they encounter mature females outside nests (type 1 courtship), they use silk-borne signals when they encounter adult females inside nests (type 2 courtship), and they make a second chamber fastened to subadult females’ nests where they wait until the subadult female matures (cohabitation: see Jackson 1986a). Vision may be necessary and sufficient for eliciting the type 1 courtship of most, but not all salticids (see Elias et al. 2005). However, salticids readily communicate with type 2 courtship and mate inside their nests in total darkness.

Comments in the early literature might suggest that courtship versatility is also prevalent in myrmecomorphic salticids. For example, there are reports of *Myrmarachne plataleoides* (OP-Cambridge, 1869), *M. foenisex* Simon, 1909, and *M. legon* Wanless, 1978 mating in nests, and of the males of the first two of these species cohabiting with subadult females (Mathew 1940; Collart 1941; Edmunds 1978). However, detailed documentation of the display behaviour of only one *Myrmarachne* species, *M. lupata* (L. Koch, 1879) from Australia (a generalist ant mimic), is available in the literature (Jackson 1982b) and no striking evidence was found to suggest that the display behaviour of this myrmecomorphic species departs from the prevalent salticid pattern. However, a wider range of *Myrmarachne* species should be investigated and more attention should be given to possible ways in which Batesian mimicry has influenced the character of intraspecific interactions. Here we consider two myrmecomorphic salticids from the Philippines. One, *Myrmarachne assimilis* Banks, 1930, is a specialized ant mimic that closely matches the appearance of the Asian weaver ant *Oecophylla smaragdina* (Fabricius, 1775). The other, *Myrmarachne bakeri* Banks, 1930, is a generalist ant mimic that is decidedly ant-like in appearance, but is not a close match to any particular ant type in its habitat.

Material and methods

Laboratory cultures at the International Rice Research Institute (IRRI) in Los Baños (Laguna Province, Luzon, the Philippines) and at the University of Canterbury (New

Zealand) were used for observations. These cultures originated from specimens collected at the field site (agricultural plots in the vicinity of Los Baños). Mature voucher specimens have been lodged at the Florida State Collection of Arthropods (Division of Plant Industry) in Gainesville, Florida, USA and the Taxonomy Laboratory at IRRI.

Maintenance, testing procedures, cage design, terminology, and conventions for describing behaviour were as in earlier spider studies (Jackson 1982b; Jackson and Hallas 1986) and only critical details are provided here. Testing in the laboratory was carried out between 08:00 and 1700 h (12:12 laboratory photoperiod, lights on at 08:00 h). No individual spider was tested more than once. The expressions “usually”, “sometimes” and “rarely” were used to indicate frequencies of occurrence of >80%, 20–80%, and <20%, respectively.

When two appendages are moving dorso-ventrally at the same time, they are referred to as moving in “matching phase” if both are maximally dorsal at the same time and maximally ventral at the same time, but the phase is referred to as “alternating” if one is maximally dorsal when the other is maximally ventral (phase difference 180°). Spider legs are referred to as legs I for the anteriormost pair of legs, legs II for the second most anterior pair, etc. Chelicerae have two segments: thick proximal segments (basal segments) and slender distal segments (fangs).

Encounters were staged between conspecific individuals in the laboratory and in the field, with particular attention being given to courtship versatility. Details came especially from testing in the laboratory where interactions could be readily video taped, with testing in the field serving primarily to confirm laboratory–field comparability. Sample sizes in the laboratory were as follows: male–female interactions away from nest, *M. bakeri* $N=19$, *M. assimilis* $N=27$; male–female interactions at nest, *M. bakeri* $N=17$, *M. assimilis* $N=18$; male–male interactions, *M. bakeri* $N=18$, *M. assimilis* $N=23$; female–female interactions, *M. bakeri* $N=14$, *M. assimilis* $N=11$. The nests of *Myrmarachne assimilis*, usually found on the underside of mango leaves close to *Oecophylla smaragdina* colonies, are sparsely woven tubes with slit-like doors at either end. The nests of *M. bakeri* are more densely woven and often have a sparse covering of leaf debris attached to the silk. Although the nests of *M. bakeri* are found on mango, they are more common on cashew leaves. The laboratory encounters were staged with one individual (the “resident”) already on an intact green leaf (about 150 mm long and 100 mm wide), freshly collected from the field (at IRRI, mango leaf; at Canterbury, podocarp leaf) and held ca 150 mm above the surface of a laboratory bench by a crocodile clip on a stand. Before introduction, another individual (the “intruder”) was taken into a plastic tube (plugged with a stopper at each end), kept there until it was quiescent (i.e. until it had stopped running rapidly about inside the tube) and subsequently introduced on to the leaf. Introduction was achieved by removing one stopper and holding the open end so that it touched the leaf petiole. Usually the spider walked out of the tube and on to the leaf shortly after this. If the spider failed to leave the tube within 2 min, the stopper was removed from the opposite end of the tube, a soft brush was inserted and the spider was prodded lightly until it walked out. Either the resident was inside a nest on the leaf or else the leaf contained no nest. For intersexual encounters, the resident was always the female.

Encounters in the field were staged by using methods that were the same as in the laboratory for introducing an adult male on to a leaf (*M. assimilis*, always a mango leaf; *M. bakeri*, mango or cashew leaf) on which an adult female (inside or outside nest) or another adult male (always outside nest) was present, or for introducing a female on to a leaf on which another female (always outside nest) was present. Spiders were then observed until

one or both spiders left the leaf. The individual introduced on to the leaf was either taken from laboratory culture or else collected in the field shortly before being used.

The beginning of interactions away from nests was defined by when one individual oriented its anterior medial eyes towards ("faced") the other and displayed by gesticulating or posturing (see below). Interactions away from nests ended when a spider left the leaf; when the two spiders that had been interacting did not orient toward each other again for 5 min and when, for more than 5 min, the two spiders actively avoided each other (i.e. although they oriented toward each other, they moved about so that they stayed at least 10 mm from each other and they did not display).

Interactions at nests began when one spider walked on to a nest occupied by another and began to display and ended when the occupant left the nest. No interactions occurred between female–female and male–male pairs at nests despite repeated contact of the nest by the second spider. As sequences of behaviour were highly variable, only the general trends for each element of behaviour and each type of interaction are summarized.

Elements of behaviour

Here the elements of behaviour that were seen during intraspecific interactions are defined. For contexts in which each was observed, see Table I.

Table I. Types of interactions of *Myrmarachne* during which different elements of intraspecific behaviour occur.

Elements of behaviour	M→F A	M→F N	F→M A	F→M N	M→M	F→F
Abdomen flutter	Ma, Mb, MI	Ma, Mb, MI			Ma, Mb, MI	
Abdomen twitch	Ma, Mb, MI	Ma, Mb, MI			Ma, Mb, MI	Ma, Mb, MI
Arch palps	Ma, Mb, MI				Ma, Mb, MI	
Arch-up body	Ma					
Bite					Ma, Mb, MI	
Charge			Ma, Mb, MI		Ma	Ma, Mb
Chase	Ma, Mb, MI				Ma, Mb	Ma, Mb, MI
Chew		Ma, Mb, MI				
Embrace	MI	MI	MI	MI	Ma, Mb, MI	Ma, Mb, MI
Gesticulate	Ma, Mb, MI		Ma, Mb, MI		Ma, Mb, MI	Ma, Mb, MI
Lunge			Ma, Mb, MI	Ma, Mb, MI		
Obstruct	Ma, Mb, MI					
Peer over	Ma, Mb					
Postmount tap	Ma, Mb, MI	Ma, Mb, MI				
Premount tap	Ma, Mb, MI	Ma, Mb, MI				
Probe		Ma, Mb, MI				
Pull and hold down silk				Ma, Mb, MI		
Push					Ma, Mb, MI	
Raise legs	Ma, Mb, MI		Ma, Mb, MI		Ma, Mb, MI	Ma, Mb, MI
Scrape	Ma, Mb, MI	Ma, Mb, MI				
Spread-apart chelicerae	Ma, Mb, MI		Ma, Mb, MI		Ma, Mb, MI	Ma, Mb, MI
Spread-apart palps	Ma, Mb, MI		Ma, Mb, MI		Ma, Mb, MI	
Stroke	Ma, Mb, MI	Ma, Mb, MI				
Zigzag dance	Ma, Mb, MI					

A, behaviour observed away from nests; N, behaviour observed at nests; M, male; F, female. Arrow indicates "direction of performed behaviour" (i.e. individual that performed stated behaviour followed by arrow to other individual and whether in or away from nest). Table includes behaviours for Ma, *M. assimilis*; Mb, *M. bakeri*; MI, *M. lupata*.

Routine behaviour: activity and demeanour seen during, but not specific to, intraspecific interactions (i.e. characteristic of spider behaviour in general contexts); in the list below, these are normal body and palp posture; waving abdomen, legs and palps (all other elements of behaviour listed below are specific to intraspecific interactions).

Normal body posture: cephalothorax aligned with abdomen (parallel to, and raised ca 1 mm above, substrate) (Figure 1).

Normal palp posture: femur–patella joints flexed sharply, tarsi about parallel to each other and perpendicular to substrate; female's palps appear to hang loosely in front of her chelicerae (Figure 1), obscuring front-on view of chelicerae. Oversize chelicerae make this posture impossible for the male (male's palps hang down loosely at sides of proximal ends of chelicerae).

Normal posture of chelicerae: fangs flexed against basal segments.

Wave palps: move up and down ca 1 mm in continual smooth fashion at $1\text{--}2\text{ s}^{-1}$ in bouts of 1–10 s.

Wave legs: legs I move up and down at ca 5 s^{-1} , with tarsi on or close to the substrate and raised by as much as 45° from the substrate (when reaching highest point in cycle, legs generally in semi-erect Position 2, see below); two legs usually move in matching phase (alternating phase rarely).

Wave abdomen: while walking or during brief pause in walking bout, moves abdomen up and down in smooth pendulum-like fashion (ca 1 mm, $1\text{--}2\text{ s}^{-1}$).

Flex-up abdomen: from pedicel to posterior end, abdomen angled up $10\text{--}90^\circ$ (Figure 2).

Flex-down abdomen: from pedicel to posterior end, abdomen angled down ca 10° .

Flex-to-side abdomen: flexed $10\text{--}80^\circ$ to left or to right of cephalothorax (Figure 2).

Flex abdomen: inclusive term for flex up, down, or to side.

Rotate abdomen: left or right yaw ($20\text{--}75^\circ$) with respect to cephalothorax.

Abdomen twitch: moves up and down from pedicel ($2\text{--}4\text{ s}^{-1}$, 1–3 mm, bouts usually ca 3 s, appears jerky), often with slight side-to-side wobbling superimposed on the up-and-down motion.



Figure 1. *Myrmarachne bakeri* female (facing right and slightly up in photograph) in a normal body posture and with palps and chelicerae also held in a normal posture. Erect legs in Position 3.



Figure 2. *Myrmarachne assimilis* male (facing forward and down in photograph) with his abdomen flexed up and to the side while posturing with erect legs in Position 2.

Abdomen flutter: similar to abdomen twitching, but faster, at lower amplitude and of shorter duration (ca 10 s^{-1} , $<1\text{ mm}$, bouts usually 1–2 s), with no superimposed side-to-side wobble noticeable (smooth in appearance).

Raise cephalothorax: cephalothorax (parallel to substrate) held distinctively higher above the substrate than in the normal posture; abdomen aligned with cephalothorax, or else flexed up or flexed down.

Lower cephalothorax: cephalothorax (parallel to the substrate) held distinctively closer to the substrate (Figure 3) than in the normal posture; abdomen aligned with the cephalothorax or flexed up.

Arch-up body: pedicel elevated higher than normal above the substrate (i.e. middle of spider's body raised), with chelicerae and posterior abdomen (spinnerets) touching or close to touching substrate (Figure 4).



Figure 3. *Myrmarachne assimilis* female (on right) with cephalothorax lowered. Male beginning to mount the female.

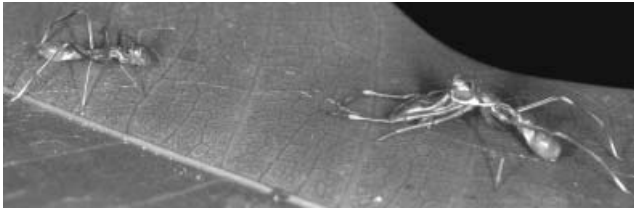


Figure 4. *Myrmarmarchne assimilis* male (on right) with semi-erect legs in Position 1, with his body arched up and while peering over toward conspecific female. Female facing the male while waving palps.

Erect legs I: all joints distal to the patella fully extended but femur–patella joint sometimes flexed (four modal positions: angling of tarsi with respect to body indicated for each position).

Semi-erect legs I: almost, but not fully, extended (only Positions 1, 2, and 3).

Raise legs: inclusive term for erect or semi-erect legs.

Position 1: legs held parallel to substrate, or slightly down, and either extending almost directly forward or angling inward toward each other slightly (Figure 4).

Position 2: legs angled ca 45° to side and ca 45° up (Figure 2).

Position 3: legs held 45–90° to side and about parallel to substrate or angling up by as much as 50°.

Position 4: legs extended almost straight up (i.e. almost perpendicular to substrate).

Peer over: with cephalothorax raised and abdomen flexed down, chelicerae held angling down so that tips of basal segments touching or almost touching substrate (legs I held in Position 1; legs II usually also held parallel, or almost parallel, to chelicerae) (Figure 4).

Posture: maintains one of the erect or semi-erect postures, or the peer-over posture, while standing or while stepping.

Gesticulate: while standing or while walking, with abdomen twitching intermittently, moves legs I repeatedly (usually in alternating phase) from Position 2 to Position 3; on rare occasions, one leg gesticulates while other remains in Position 2 or on substrate.

Arch palps: held ventral to chelicerae with femur–patella joints strongly flexed, tarsi being anywhere on a continuum from parallel to the substrate (angling directly toward each other) to pointing down by 45° (Figure 5).

Spread-apart palps: femora move to side of face, with tibia and tarsi at sides of chelicerae, parallel to each other and perpendicular to substrate (Figure 6).

Zigzag dance: walks alternately 5–20 mm to one side then other side (each cycle, 1–4 s), usually with legs I erect (semi-erect rarely) in Position 1 and with body usually lowered.

Obstruct: male (body lowered and legs I erect or semi-erect in Position 2 or 3) moves about so as to remain directly in front of facing female (when female runs to one side, male promptly sidesteps into her path).

Spread-apart chelicerae: basal segments of chelicerae moved apart, usually with palps spread apart at same time (gap between two chelicerae 10–170°) (Figure 2); often with erect palps (fully extended alongside chelicerae) when chelicerae were spread apart.

Extend fangs: with chelicerae spread apart, one (rarely) or both (usually) fangs positioned away from basal segment (angle between fang and basal segment, 10–170°; when both fangs were extended, both were usually moved away from basal segment to same extent) (Figure 2).

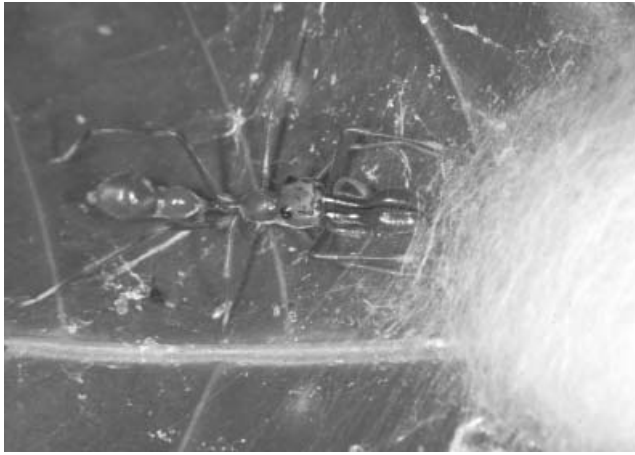


Figure 5. *Myrmarachne assimilis* male (on right) opening door to nest. Palps arched.



Figure 6. *Myrmarachne assimilis* male (upper right) beginning to premount tap female. Male's legs I semi-erect in Position 1. Female: palps spread apart.

Embrace: two spiders stand face to face with chelicerae touching, usually with palps erect and with legs I erect in Position 3 or 4 and sometimes with some combination of palps, legs I and legs II also touching.

Bite: while embracing, one spider places spread-apart chelicerae around one or both chelicerae of other spider (legs typically erect in Position 4) and then closes chelicerae (usually only partially).

Push: attempting to walk forward while embracing (progress usually impaired by other spider pushing back and holding its ground) (normally spiders grapple and push at the same time).

Charge: with legs I usually erect in Position 2 and chelicerae spread, and sometimes with palps erect, spider suddenly runs toward another spider, stopping suddenly within 10 mm of other spider, after which both spiders usually decamp in opposite directions.

Chase: when one spider runs away, other spider rapidly follows, holding legs erect or semi-erect (Position 2 or 3) and chelicerae spread apart.

Lunge: suddenly and rapidly moves body forward several millimetres (propulsion by extending legs III and IV without tarsi leaving substrate; chelicerae often spread apart and palps often erect), returning to original position within a fraction of a second.

Pull and hold down silk: from inside nest, spider moves legs I up so that tarsi contact inner nest layer (usually close to a door) and then moves legs I down, pulling upper nest layer down and holding it against lower silk layer of nest for several seconds.

Probe: from close to door, but outside nest, places legs I and sometimes II on the silk and repeatedly pulls jerkily on the silk for 2–5 s (left and right legs moving in alternating phase).

Chew: with chelicerae in contact with silk, often extended through nest door, male repeatedly opens and closes basal segments of chelicerae (fangs extended only rarely); outward motion of chelicerae sometimes noticeably stretches and tears silk around door, making opening wider.

Open door: after probing from outside, extends legs I, and sometimes legs II, through door and then spreads these legs apart while walking into nest (Figure 5).

Premount tap: with erect or semi-erect legs I in Position 1 (Figure 6), male moves legs I up and down ($1\text{--}3\text{ s}^{-1}$, 45°), contacting the female's carapace or legs I on downstroke (female responds by lowering her cephalothorax; Figure 3).

Mount: after premount tapping, male walks over female, veering to one side and coming to a stop standing at side of female (typically movement over female by intermittent, slow stepping, interspersed with pauses lasting 1–5 s during which male strokes, postmount taps or remains quiescent) (Figures 3, 7).

Postmount tap: male positions his cephalothorax over female's pedicel and then moves legs I and II up and down, contacting sides of female's abdomen and her legs II and III on downstroke (amplitude $<5\text{ mm}$; ca 3 s^{-1} ; bout length usually 1–2 s).

Stroke: while leaning to one side of female's abdomen, the male gently moves leg I and sometimes palps up and down (amplitude of 5–10 mm; ca 1 s^{-1}) so that the tarsus rubs across the ventral surface of the female's abdomen (female's abdomen rotates and flexes up while male strokes).

Stand at side of female: after mounting, male stands with his body to left or right of female's body, legs I, II, and III over her body, but tarsi in contact with substrate on female's other side (usually not touching her) with his closer palp flush with anterior end of female's abdomen (Figure 7).



Figure 7. Male and female of *Myrmarachne assimilis* copulating. Male standing beside female (facing to right) while applying palp. Female: cephalothorax lowered; abdomen flexed and rotated.

Scrape: while standing at side of female, male moves nearer palp back and forth (ca 5 s^{-1} ; 1–2 mm) in the vicinity of the epigynum on female's ventral abdomen.

Apply palp: male's palpal organ stationed on female's epigynum (presumably embolus inserted) and scraping ceases (Figure 7), accompanied by frequent pulsations of haematodocha and intermittent abdomen twitching.

Decamp: moving away from other spider by walking or running (or rarely by jumping) (Figure 8).

Watch: keeping body oriented such that anterior-medial eyes line up with other spider (Figure 8).

Follow: walking or running so as to remain close to a decamping spider (watching and following usually occur together).

Organization of behaviour

Male-female interactions away from nests (Type 1 courtship)

After orienting toward females, males usually moved their palps into the arched posture, twitched their abdomens and postured with semi-erect or erect legs I in Position 3, moving to Position 1 as they got closer. Subsequently, there were highly variable sequences of males alternately standing and walking and also alternating between posturing and gesticulating. Males of *Myrmarachne assimilis*, but not *M. bakeri*, sometimes spread their chelicerae apart, although never by more than ca 10° and only for 2–5 s. Males consistently adopted the peer-over posture (Figure 4), and sometimes flexed, twitched, or fluttered their abdomens, with palps arched or frontal, and often waving ($<1\text{ mm}$, ca 2 s^{-1}). A female's first response was usually to face the male (Figure 4), with her palps waving rapidly, and then to decamp, with the male watching and following her (Figure 8). When the female faced the male again, he resumed posturing and gesticulating. Females often postured briefly while facing males (Figure 9), holding their bodies normal or their cephalothoraces lowered, and they often flexed their abdomens up (sometimes abdomen also slightly rotated and sometimes twitching their abdomens). On the rare occasions when the female remained stationary for 5–10 s, the males usually zigzag danced. Females sometimes lunged or charged while males were dancing.

Females often ran to one side of the male, with the male usually succeeding in obstructing her forward progress. With or without first displaying at the male (semi-erect or erect legs I in Position 2 when more than 20 mm in front of male and Position 3 when closer than 20 mm), the obstructed female turned $90\text{--}180^\circ$ and decamped or, more often, backed away and then tried again to run past the male. However, the female sometimes eventually



Figure 8. *Myrmarachne assimilis* male (on right) watching and following decamping *M. assimilis* female.



Figure 9. *Myrmarachne bakeri* female (facing to left) posturing (erect legs in Position 2).

became quiescent in front of a male and the male approached. When he was within touching distance, he brought erect legs I into Position 1 over the female's legs I or cephalothorax (Figures 3, 6), after which she sometimes decamped (sometimes after first lunging), and sometimes remained quiescent while copulation (Figure 7) ensued. The duration of courtship was usually about 2 min.

Only one instance of cannibalism was observed in this study. This was during a male–female interaction of *M. bakeri*. After the male had been displaying for ca 1 min, the female decamped and the male ran after her, overtook her, and then killed and ate her.

Male–female interactions at nests (Type 2 courtship)

When a male contacted a female's nest, his first response was usually to probe and to twitch his abdomen, with the female reciprocating by twitching her abdomen from inside the nest. Abdomen twitching continued to be the primary activity of the male and of the female throughout most interactions. Interaction duration was highly variable (1–60 min) regardless of whether it ended with the pair mating (usually inside the nest) or with the pair separating without mating. As the interaction progressed, the male, with his body lowered, spent more and more time with his legs I and sometimes II extended through one of the nest doors (Figure 5), intermittently probing and occasionally chewing. With the male at the door, the female lunged intermittently, but her primary activity was to pull and hold down silk. Most interactions ended with the female decamping through the door opposite the male, but the female sometimes remained inside while the male entered and eventually mated.

Copulation

While copulating, typically the male and female stood oriented 180° to each other (bodies parallel; female's abdomen flexed up and rotated; one of male's palps applied; Figure 7),

with at least some of the male's legs passing over the female's body and contacting the substrate on the other side. These legs rarely made contact with the female. There was occasional variation in this copulatory posture because females sometimes shifted their bodies slightly after the male applied his palp and the pair continued copulating, but with the female now facing either as much as 20° away from or as much as 20° toward the male. When the male was facing away from the female, the female's posterior abdomen was closer to the male and sometimes the male's chelicerae rested on the female's abdomen and legs. When the female was facing toward the male, the male's legs sometimes ended up all being on the same side of the female's body.

Copulation usually consisted of the male applying each palp once or twice in alternation (on rare occasions, same palp applied twice before switching sides). More than two applications per palp were rare. Copulation duration (time elapsing from start of first to end of last palp application, discounting intervening time between successive palp applications) was similar for *M. assimilis* (1.84 ± 0.30 min, $N=19$) and *M. bakeri* (1.43 ± 0.20 min, $N=7$) ($t_{24}=0.807$, $P=0.428$).

When the male disengaged his applied palp, he moved over the female (her abdomen no longer raised or rotated), tapped and stroked and then, once positioned again beside the female, the male scraped his palp across her now flexed-up and rotated abdomen and resumed copulation. Before next palp application, while centred over the female, the male sometimes stepped backwards and forwards, stroking and tapping intermittently.

Male–male interactions away from nests

When males encountered each other, they usually first raised their bodies, flexed-up their abdomens, and began abdomen twitching (Figure 2). This was followed by highly variable sequences of posturing (all positions occurred, but Position 2 was the most common), with the interaction usually lasting ca 2 min. Often palps were erect and chelicerae were spread apart. The angle to which chelicerae were spread increased as the two spiders approached each other, but embracing, biting, and pushing were rare. When one male decamped, the other often gave chase, but usually only briefly.

Female–female interactions away from nests

Females usually postured (Figure 9) for, at most, a few seconds (legs I in Positions 1 or 2, abdomens flexed up or bodies raised) and then decamped in opposite directions, with instances of watching and following and renewing display being rare. There were rare occasions when the two females stood posturing at each other for 30 s or longer before eventually decamping.

Male–male and female–female interactions at nests

After walking on the nest, the intruder sometimes briefly did some combination of probing, chewing, and twitching of its abdomen, and the resident sometimes pulled and held down the silk. Soon afterwards, the resident or the intruder decamped. These interactions rarely lasted longer than 15 s.

Cohabitation

When an adult male encountered a nest with a subadult female (i.e. a female that was one moult short of maturity) inside, he sometimes spun another nest chamber alongside and

connected to the female's nest. If the female did not decamp, he remained with her in the double-chambered nest until she moulted (matured), whereupon he entered the female's chamber and the pair mated.

Discussion

For *Myrmarachne bakeri* and *M. assimilis*, only a few differences were found in display repertoires, and these differences did not have any obvious links to the generalist–specialist distinction that applied to these two species. On the whole, the intraspecific interactions of *M. assimilis* and *M. bakeri* also appear to be similar to the intraspecific interactions of *M. lupata* (Table I) (Jackson 1982b) and, in broad respects, similar to that of most salticids. The males of these three myrmecomorphic salticids adopt a conditional mating strategy (courtship versatility: three disparate tactics conditional on the female's location and state of maturity). Courtship versatility may be a universal characteristic of salticid spiders, as every detailed published study designed to look for evidence of this conditional strategy has succeeded in documenting its occurrence (for references, see Jackson 1992): vision-based signals when the males encounter females away from nests (or webs, for the minority of salticids that use webs) (type 1 courtship); silk-borne signals when males encounter adult females inside a nest (or web) (type 2 courtship); waiting in double-chambered nests (or in webs) until the females moult and mature (cohabitation; see Jackson 1986a). Post-contact tactile (or chemotactic) courtship, a phase common to type 1 and 2 courtship, is another feature that appears to be universal in salticid courtship. Yet another facet of display complexity appears to be universal in the Salticidae: adoption of a repertoire of distinct display elements during type 1 and during type 2 courtship, with the way elements are combined and sequenced being highly variable.

Sexual selection and cannibalism have been dominant topics in the literature on salticid courtship ever since the 19th century (Peckham and Peckham 1889; Bristowe 1941; Jackson 1981; Richman 1982; Masta and Maddison 2002). Hypotheses concerning sexual selection in salticids most often pertain specifically to intersexual selection, a consequence of mate choice (see Harvey and Bradbury 1991). During male–female interactions, salticid males are typically the more persistent in displaying (Jackson and Pollard 1997), with females tending to alternate between watching the male and moving a short distance away (for exceptions, see Jackson and Hallas 1986; Jackson and Macnab 1989; Clark and Uetz 1992; Jackson and Willey 1995). In most salticid species, the female appears to determine whether mating takes place by either allowing or not allowing the male to approach, mount, and copulate. Female choosiness may make accounting for male behaviour relatively easy (to mate, the male has to convey information regarding his fitness to the female; see Bradbury and Anderson (1987); Alexander et al. (1997)), but why salticid females are choosy is not so clear. Even if variability in the male's display repertoire were demonstrated to be a criterion used by females when choosing, the advantage females might gain by favouring more complex, variable male display behaviour remains uncertain. We are no closer to answering this question with *Myrmarachne* than we are with any other salticids.

Myrmarachne becomes especially interesting when considering the question of how salticid display complexity might be related to cannibalism. The literature on spider courtship has a long tradition of linking identification with an anti-cannibalism function to explain male courtship. Female spiders, according to conventional wisdom, are ravenous predators and males must identify themselves or else run the risk of being perceived as prey (Robinson 1982). Certainly there are spider species for which sexual cannibalism (more

specifically, females eating males) is frequent during courtship and mating (Elgar 1992; Schneider and Lubin 1998; Andrade 2003) and regardless of whether it is frequent or not, the potential of cannibalism seems to be generally applicable for courting spiders, as all spiders are predators of other arthropods, including arthropods similar in size to a potential mate. However, for salticids (Jackson 1982b; Richman and Jackson 1992; Jackson and Pollard 1997), and perhaps for spiders in general (Jackson and Pollard 1982, 1990; Starr 1988), the idea of a link between males identifying themselves and thereby reducing their risk of being eaten does not hold up well to scrutiny.

It is interesting that we only observed one instance of cannibalism in the present study, and this was an instance of a *Myrmarachne bakeri* male killing a female, not the other way around. Yet this is not an unusual finding for salticids, as there are few salticid species for which females appear to prey on males disproportionately more often than males prey on females (Jackson and Pollard 1997). For salticids, cannibalism may be a significant risk during encounters between conspecifics, but this is with males eating females as well as females eating males, along with males eating other males and females eating other females (Jackson 1982a, 1992). For these spiders, with their extraordinarily good eyesight, misidentification seems to have little to do with who eats whom.

Problems with simplistic cannibalism–identification hypotheses for the function of salticid courtship may become especially evident when we consider *Myrmarachne*. Perhaps identification is important for these salticids during male–female encounters, but in the context of being Batesian mimics of ants rather than in the context of being ant-like arthropods that might be mistaken for prey. *Myrmarachne* is a genus of salticids that look like ants, but they do not normally eat ants or anything that looks like an ant (Jackson 1986b; Jackson and Willey 1994). On the contrary, regardless of the need to live in the vicinity of ants for making Batesian mimicry effective, ants are dangerous company for *Myrmarachne* (Nelson et al. 2004, 2005).

Perhaps the details of some of the *Myrmarachne* male's display behaviour helps females discriminate him from an ant and thereby facilitates the male's approach, but this hypothesis would appear to be almost the antithesis of the traditional anti-cannibalism hypothesis (i.e. this hypothesis is that the function of identification is to inhibit the female's behaviour of fleeing from an ant that is getting too close rather than to inhibit the female's behaviour of making a predatory attack on prey). In particular, peering over and arched-up bodies (Figure 4), distinctive display postures adopted by the males of *M. assimilis* and *M. bakeri*, have not been described for other salticids. These display postures are especially interesting because they move the male's large chelicerae out of a facing female's line of sight, giving her an unobstructed view of something ants lack, the male's large anterior-medial eyes. It is also interesting that *Myrmarachne* males dispense with their erratic and ant-like manner of walking when they encounter *Myrmarachne* females, and adopt zig-zag dancing and other display behaviour commonly seen performed by other salticids. Obstructing in *Myrmarachne* courtship behaviour might be related to these spiders being ant mimics, but not necessarily in the context of identification. Like ants, *Myrmarachne* females tend to dash about, with frequent changes in direction, and obstructing appears to be, for the male, an effective countermeasure to female hyperactivity.

Additionally, there is a peculiar bias in the literature on the cannibalism–identification hypothesis that envisages identification as being the female's problem, but not the male's. Salticid males do not normally display indiscriminately, instead using courtship displays specifically for encounters with conspecific females. As it is not the habit of *Myrmarachne* to display toward either prey or ants (Nelson and Jackson 2007), they demonstrate by being

the first to display that they have identified a female without needing to see her display. Given that males can accurately identify females without females necessarily displaying at them, an explanation is needed for why females cannot do the same. In fact, *Myrmarachne* females make frequent brief displays (especially erect posturing, see Figure 9) toward males and they are often the first to display during an encounter. The female, with her chelicerae not enlarged like the male's and her anterior-medial eyes not being obscured from front-on view, may be making sure that the male quickly detects that she is not an ant, as ants do not adopt postures resembling the erect-legs displays of *Myrmarachne*.

Yet, for understanding the ultimate causation of salticid display complexity, simplistic emphasis on identification is probably misleading. It has been suggested elsewhere (Jackson and Pollard 1997) that a more useful perspective might be derived from ideas related to sensory exploitation (e.g. Clark and Uetz 1992, 1993; Proctor 1992; Ryan et al. 2001) and receiver psychology (e.g. Guilford and Dawkins 1991; Rowe 1999), but with a greater emphasis on complexity, flexibility, and dynamic interaction between signaller and receiver. This may seem like a subtle distinction, but it is a departure from the idea that a male's problem is simply to turn off the female's predatory inclinations by revealing to her his true identity (i.e. identifying himself as a potential mate, not just another potential meal). It may be more useful to envisage displaying salticids as orchestrating a careful balance between stimuli that provoke and stimuli that inhibit predatory attacks from each other, as though the male and the female were each playing mind games with a predator (something "similar to a lion trainer and a lion, where each salticid may be analogous to the trainer or the lion, if not both at the same time"; Jackson and Pollard (1997)). Simple identification would be more compatible with highly stereotypical courtship, not the complex, highly variable sequences actually found in salticids.

From this perspective, *Myrmarachne* becomes especially interesting. The general similarity of *Myrmarachne* display behaviour to that of other salticids suggests that *Myrmarachne* may also be attempting to gain dynamic fine control of conspecific individuals' behaviour, but it is not so straightforward to envisage the display behaviour of *Myrmarachne* as tapping into the neural machinery of perceiving and reacting to normal prey. A perspective that links sensory exploitation and receiver psychology to display behaviour may be heuristic when applied to *Myrmarachne*, but the details of how to apply this perspective to *Myrmarachne* may be strongly connected with their mimicry of dangerous models.

The copulatory posture of *Myrmarachne assimilis* and *M. bakeri*, like that of *M. lupata*, is a striking deviation from the copulatory posture of more typical salticids. We predict that this posture may be the norm in the genus *Myrmarachne*, as it appears to be an adjustment made for the greatly elongated chelicerae characteristic of *Myrmarachne* males. As is seen when typical salticids mate, the male's closer palp is in contact with the female's epigynum on the ventral surface of her rotated abdomen, but the male stands beside the female (Figure 7), with his nearer palp extending out to the side. The copulatory posture of typical salticids is with the male standing over (not beside) the female, with his palp being applied when he leans over to one side, facing somewhat downward. This posture would appear to be awkward, if not incompatible, with a *Myrmarachne* male's anatomy. Leaning over and down would probably wedge the female's legs against her body and press the anterior ends of the male's chelicerae into the substrate.

The generalist–specialist distinction (*Myrmarachne bakeri* is a generalist ant mimic and *M. assimilis* is a specialist mimic of weaver ants) appears to be a fine detail that has not brought about conspicuous divergence between display repertoires of these two species.

The small interspecific differences we found between these two species did not relate in any obvious way to the accuracy of their mimicry. On the whole, the display behaviour of these two species is comparable to that of *M. lupata*, and we predict that the general conclusion from the earlier study (Jackson 1982b) applies to this genus as a whole: drastic changes in the character of intraspecific interactions need not accompany the evolution of ant mimicry in salticids. Despite being myrmecomorphic, *Myrmarachne* tends to adopt displays and other behaviour during intraspecific interactions that have broad similarity to the behaviour of non-myrmecomorphic salticids. When these ant mimics encounter each other, it is as though they quickly shift from pretending to be ants to acting like bona fide salticids.

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