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Courtship and male-male interaction behaviour of *Orsima ichneumon* (Simon, 1901), an ant-mimicking jumper spider (Arachnida: Salticidae)

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Abstract. This is the first description of male-female courtship and male-male agonistic interactions of *Orsima ichneumon* (Simon, 1901) jumping spiders. *Orsima ichneumon* inhabit low shrubs and grasses along sunny forest edges across South East Asia, including Malaysia and Singapore. They are small-medium sized jumping spiders ranging from 5–8 mm in body length, with no obvious sexual size dimorphism. However, there is sexual dimorphism in body shape, most obviously due to a distinct constriction in the male's abdomen that is less defined in females, and different colouration of the pedipalps. Twenty-eight major behavioural elements were described during intraspecific interactions. Courtship interactions were significantly longer in duration than agonistic interactions, but agonistic interactions were made up of a higher number of behavioural elements. Like most jumping spiders, male *O. ichneumon* had a more complex behavioural repertoire than females, and displayed their colourful body appendages during courtship and contests. This suggests that females are the choosier sex and there is selection on male ornamentation and signalling behaviour. Our behavioural study will form a useful framework from which to base future work on this colourful species.

Key words. intraspecific interactions, contest behaviour, copulation, sexual selection

INTRODUCTION

Jumping spiders (Salticidae) are a hyper-diverse family of spiders with over 5000 species described (World Spider Catalog, 2016). Despite their small size, salticids have exceptional vision when compared to other spiders. They have well-developed spatial acuity and can perceive colour, including ultraviolet, through their large forward-facing principal eyes (Land, 1969; De Voe, 1975; Yamashita & Tateda, 1976; Blest et al., 1981; Land, 1985; Zurek et al., 2015).

Given how highly visual jumping spiders are, it is not surprising that many species incorporate complex dance manoeuvres into agonistic and courtship displays, where they may show off a brilliant array of colours to foes or potential mates (Crane, 1949; Li et al., 2008; Lim et al., 2008; Girard et al., 2011; Lim & Li, 2013; Taylor & McGraw, 2013). During these displays, spiders bring their legs, pedipalps, chelicerae and abdomen into the other spider's field of view, typically in a set of distinct behavioural elements that make up the courtship or contest routine (Jackson & Hallas, 1986). Recently, the tiny peacock spiders (genus *Maratus*) endemic to Australia have risen to fame because of the way the males of these salticids use extraordinarily elaborate visual and vibratory courtship displays to attract females, which in some species includes the flashing of iridescent abdominal flaps that resemble colourful fans (Girard et al., 2011; Girard & Endler, 2014).

Orsima ichneumon (Simon, 1901) is another remarkable jumping spider. It is found across South East Asia, including Borneo, Peninsular Malaysia, Singapore and Sumatra (Peckham & Peckham, 1907; Zabka, 1992). Several characteristics of the spider have led observers to suggest that this spider is an ant-mimic in reverse (Peckham & Peckham, 1907). Elongated spinnerets (silk-laying structures) extend from the abdomen tip: one pair faces upwards and looks like antennae, and the other two pairs face downwards and appear like mouthparts (Reiskind, 1976). Their similarity to ants is further supported by their strong abdominal constriction, which gives the appearance of an ant's head and thorax, while the spider's cephalothorax ('head' end) looks like an ant's abdomen. However, unlike most ant mimics, *O. ichneumon* display an array of striking colours on their cephalothorax and abdomen (Fig. 1a–c). Although not as brilliantly coloured to the human eye, several close relatives of *O. ichneumon*, including *Cosmophasis umbratica* and *Phintella vittata*, have been demonstrated to use ultraviolet ornamentation as a signal during mate choice and agonistic interactions (Lim et al., 2007; Li et al., 2008; Lim et al., 2008; Lim & Li, 2013). An important prerequisite to understanding the evolution of colour ornamentation in spiders is to describe the way individuals interact and use colour as signals during

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Fig. 1. (a) An adult male *Orsima ichneumon*; (b) an adult female *O. ichneumon*; (c) a juvenile *O. ichneumon.*

Fig. 2. (a) Typical forest edge habitat for *Orsima ichneumon*; (b) *Orsima ichneumon* are also found on *Clerodendrum villosum*, a roadside and forest-edge shrub covered in extra-floral nectaries.

courtship and male-male agonistic displays. Here we take a first step toward understanding the role colouration plays for *O. ichneumon* in the context of courtship and male-male contests.

MATERIAL AND METHODS

Collection and maintenance of spiders. Juvenile *Orsima ichneumon* were collected by beating bushes and searching by eye along roadside vegetation in Gombak, Selangor, Malaysia (3°19′27.9″N, 101°45′09.3″E) in June and November 2015. Spiders were brought back to the laboratory at the National University of Singapore where they were kept individually in cylindrical 50-ml plastic containers (diameter × height: 50 × 50 mm) with a mesh cover for ventilation and provided with water via a cotton roll. They were kept in controlled environmental conditions (25 ± 1°C; 70–80% relative humidity; light regime: 10 h light: 14 h dark; lights on at 0800 hrs). Opaque paper cards were inserted between containers to ensure no visual contact between individuals. Each spider was fed five to six laboratory-cultured fruit flies (*Drosophila melanogaster*) twice a week. Juveniles were reared until they reached adulthood and the date of their final moult recorded to know their post-maturation date.

Body size measurements. Upon maturation of the spiders, we took dorsal photographs of 25 females and 37 males to measure body length (total length from anterior tip of cephalothorax to the posterior tip of the abdomen) and carapace width (across maximum points) to the nearest 0.01 mm using ImageJ software (Schneider et al., 2012). The spiders were anesthetised by exposing them to CO_2 for 1 min before photos were taken to allow for easy positioning.

Intraspecific interactions. All trials were conducted from 0900 to 1800 hrs under four full spectrum light tubes (VoltarcUltra Light tubes, 110 W each, powered by a 120 V50/60 Hz electronic ballast; SUPER-TEK, Houston, TX), which were suspended approximately 1.5 m above the experimental setup. Trials were video recorded in full high definition using a digital camera (Casio EXLIM, EX-100).

For ascertaining details about intraspecific interactions, we staged 11 male-male and 11 male-female interactions using randomly chosen virgin males and females. Our testing procedure and terminology were similar to those in earlier studies of salticids (Jackson & Hallas, 1986; Lim & Li, 2004; Tay & Li, 2010; McGinley et al., 2016). For example, we used the conventional expressions such as “usually” or “generally”, “sometimes” or “occasionally”, and “infrequently” or “rarely” to indicate the frequencies of occurrence of >80%, 20–80%, or <20%, respectively. For each interaction staged, we used a fresh Simpoh Air (*Dillenia suffructicosa*) leaf (length: 15–20 cm; width: 10–15

Table 1. The mean (± standard error [SE]) and coefficient of variation (CV %) for body length and carapace width of female and male *Orsima ichnuemon*. Welch *t* tests were used to test for a significant difference in mean size between the sexes for each trait, and *Z* values were calculated to test for a significant difference in the CV % between males and females for each trait.

	Females		**Male**			
	Mean (± SE)	**CV %**	**Mean (± SE)**	**CV %**	***t***	***Z***
Body length (mm)	6.69 (0.10	7.33	6.47 (0.09)	8.71	1.61	0.72
Carapace width (mm)	1.70 (0.01)	3.26	1.71 (0.03)	9.19	0.53	3.94*

*p = 0.0001.

cm) clamped to a stand at 90°–120°, 35 cm above a table top. We introduced two individuals (a pair of males, or a male and a female) to the leaf separately. When pairing a male and female, we introduced the female onto the leaf first from one end and allowed her to acclimate for 3 min before introducing the male onto the underside of the leaf at the opposite end. When pairing two males, the males were introduced at the same time onto the leaf. Courtship displays were observed from the time that males started displaying to females and ended when they successfully copulated. Male-male interactions were categorised from the time males started a display until a winner and loser (first to retreat) were established.

A total of 13 males and 11 females were used for these staged encounters with 8 individuals used more than once on the same day but given at least 1 h of rest before the next trial. Reusing spiders did not appear to affect the displays used as the spiders actively displayed to their conspecifics during a second trial. We played back videos to enable behavioural elements to be described, and to measure the duration of interactions, including copulation duration. During copulation, palp insertion and the duration of insertion was not discerned in all trials as insertion was not always visible to the camera due to the angle that copulation occurred.

RESULTS

Habitat. *Orsima ichneumon* were most commonly found on shrubs, long grass, ferns and overhanging trees along forest edges, where the plants were often in full or partial sun (Fig. 2a). They were mostly observed actively foraging in the morning and we had less success locating them in the afternoons and evenings. We observed individuals stalking and capturing small arthropods and adult spiders also fed from extra-floral nectaries on *Clerodendrum villosum* plants, where they were found in close association with numerous ant species (Fig. 2b) (Painting et al., in press).

Morphology. Adult *O. ichneumon* are small-medium sized jumping spiders; their body length ranged from 5.38–7.69 mm in males (N = 37) and 5.94–7.52 mm in females (N = 25). There was no significant difference in body length or carapace width between males and females, although male carapace width was more variable than female carapace width (Table 1). Both sexes were brightly coloured and covered in complex patterns of iridescent markings on their carapace, abdomen, legs and palps (Fig. 1a, b). In both sexes the dorsal carapace was emerald green, while the lateral carapace was iridescent pink/purple/black with a narrow white band running along the lateral margin. The dorsal side of the abdomen was covered in orange/red scales with smaller iridescent blue markings, distinct orange/red and black stripes towards the posterior end, while the posterior tip itself is rounded and iridescent black. Males had narrower abdomens with a distinct constriction that was less pronounced in females, and males had relatively longer legs I than females. The male palps were iridescent black while the female palps were yellowish on the dorsal side and black on the lateral and ventral sides. Both sexes had elongated, black spinnerets. Juveniles were distinguished from adults by orange markings around the margins of their eyes and a lack of iridescent markings on their legs (Fig. 1c). Further description on the differences in male and female colouration can be found in Peckham & Peckham (1907).

General locomotion. *Orsima ichneumon* usually moved in a stop-and-go gait (stepped forward for 0.5–1.0 s; paused for 0.3–0.6 s, and stepped forward again). The spider stepped forward in a straight line while bobbing its abdomen. When bobbing, the abdomen was slightly raised such that the posterior end of the abdomen rose ca. 1 mm up from the horizontal plane of its body during a pause in between stepping. The abdomen was then held stationary (< ca. 0.1 s) at a maximum height before being lowered to the lowest position (posterior abdomen lowered ca. 1 mm down from the horizontal plane of the spider) and ended the bob. Abdomen bobbing varied from posterior abdomen rising ca. 1–3 mm above and below the horizontal plane. The abdomen ascended and descended in either a smooth or jerky motion. When smooth, the abdomen moved up and down in one swift motion, often without the abdomen being held stationary, taking less than 0.2 s to complete one bob. When jerky, the posterior abdomen moved up slightly, before moving down a greater distance than the upward movement but did not reach the lowest angle when abdomen was held parallel to the ground at rest. The posterior abdomen then moved slightly upward again but did not reach the previous height, before moving downward a larger distance than the upward motion. This sequence was repeated until the abdomen reached the lowest angle. This gave the impression that the abdomen was 'rattling' while travelling from the lowest position to the highest position. Rattling occurred within the sagittal plane of the spider or veered slightly (ca.

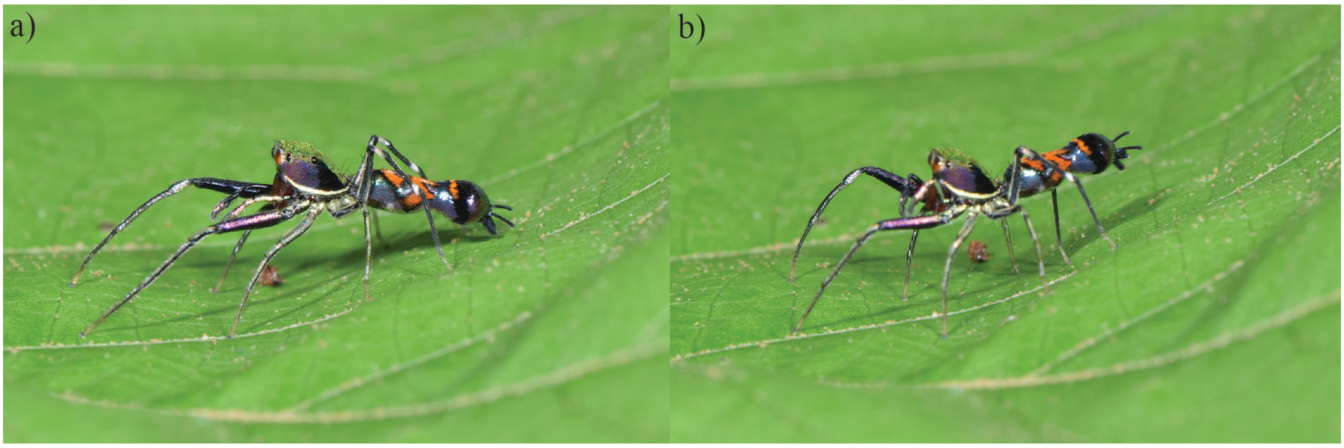

Fig. 3. Male *Orsima ichneumon* in resting position: (a) with legs I stretched out, abdomen lowered to substrate and palps slightly extended in position 2; (b) with hunched legs I, palps held in front of the cephalothorax.

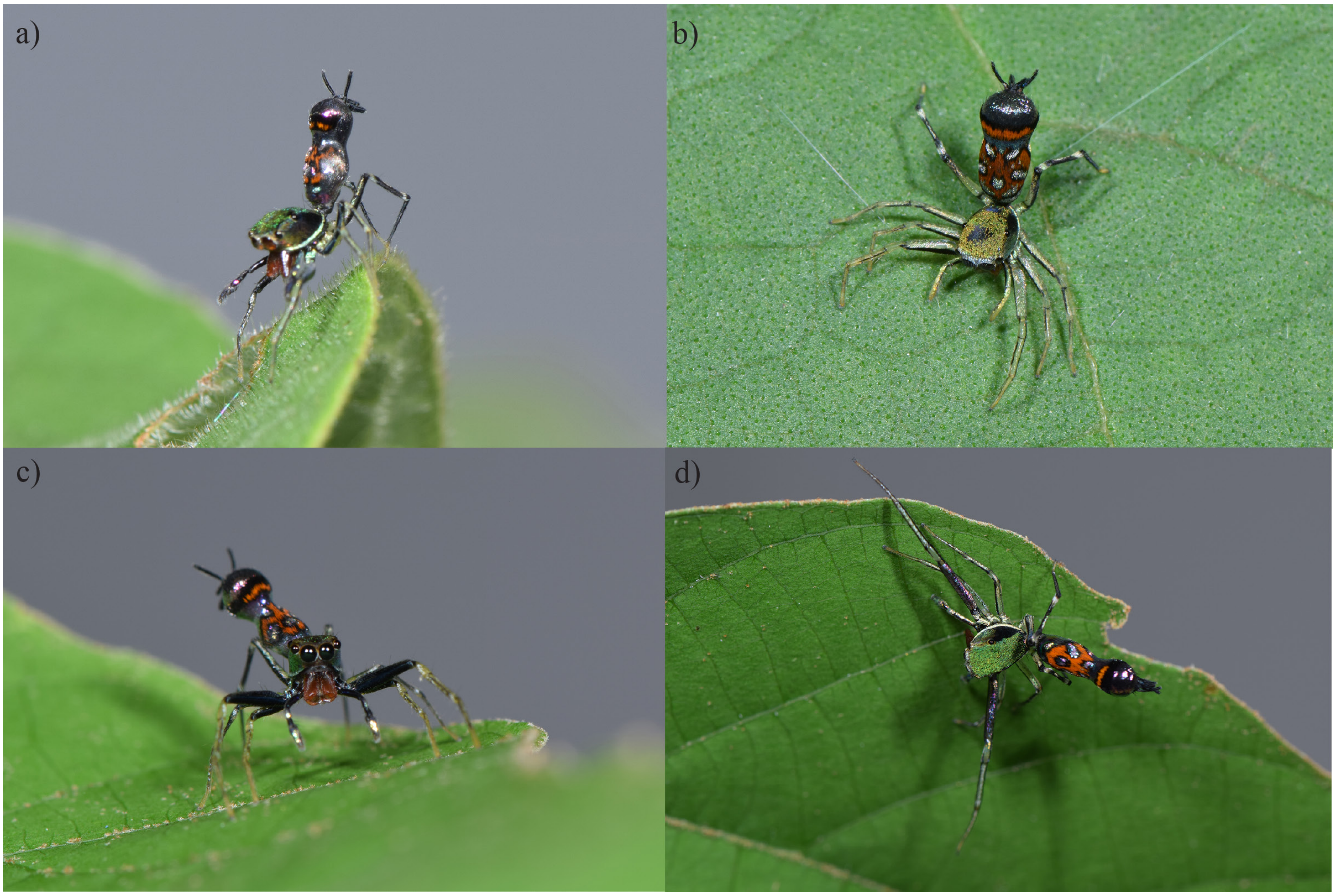

Fig. 4 Abdomen positions (a) Male *O. ichneumon* with extended palps (position 2); opened chelicerae (position 1) and flexed up abdomen (ca. 60°) on edge of leaf in response to a female nearby; (b) Female *O. ichneumon* with arched legs and flexed abdomen; (c) Male *O. ichneumon* with abdomen bent right of the sagittal plane, palps (position 1) and chelicerae held closed; (d) Male *O. ichneumon* displaying during male-male interaction, legs I elevated (position 2) with abdomen flexed up and bent to the left of the sagittal plane.

30°) to the left and right of the sagittal plane during ascent and descent. Rattling was also observed along the horizontal plane of the spider with minimal distance travelled by the posterior abdomen, giving the impression that the abdomen was rattling without travelling upward or downward. Smooth ascent and descent usually occurred in between a stepping motion. Jerky ascent and descent occurred when the spider was stationary and looking around. Stepping faster often coincided with faster bobbing or rattling. However, the spider never stepped while the abdomen was in ascent or descent. Rattling also occurred in the pauses between and during stepping. Posterior spinnerets were held stationary most of the time unless involved in laying down silk. When laying down silk, the spinnerets moved laterally (0°–100° apart) but not up and down. The first pair of spinnerets were held the furthest apart from each other (ca. 140° apart) and approximately 40° above the horizontal plane when not engaged in any activity. The second and third pair were

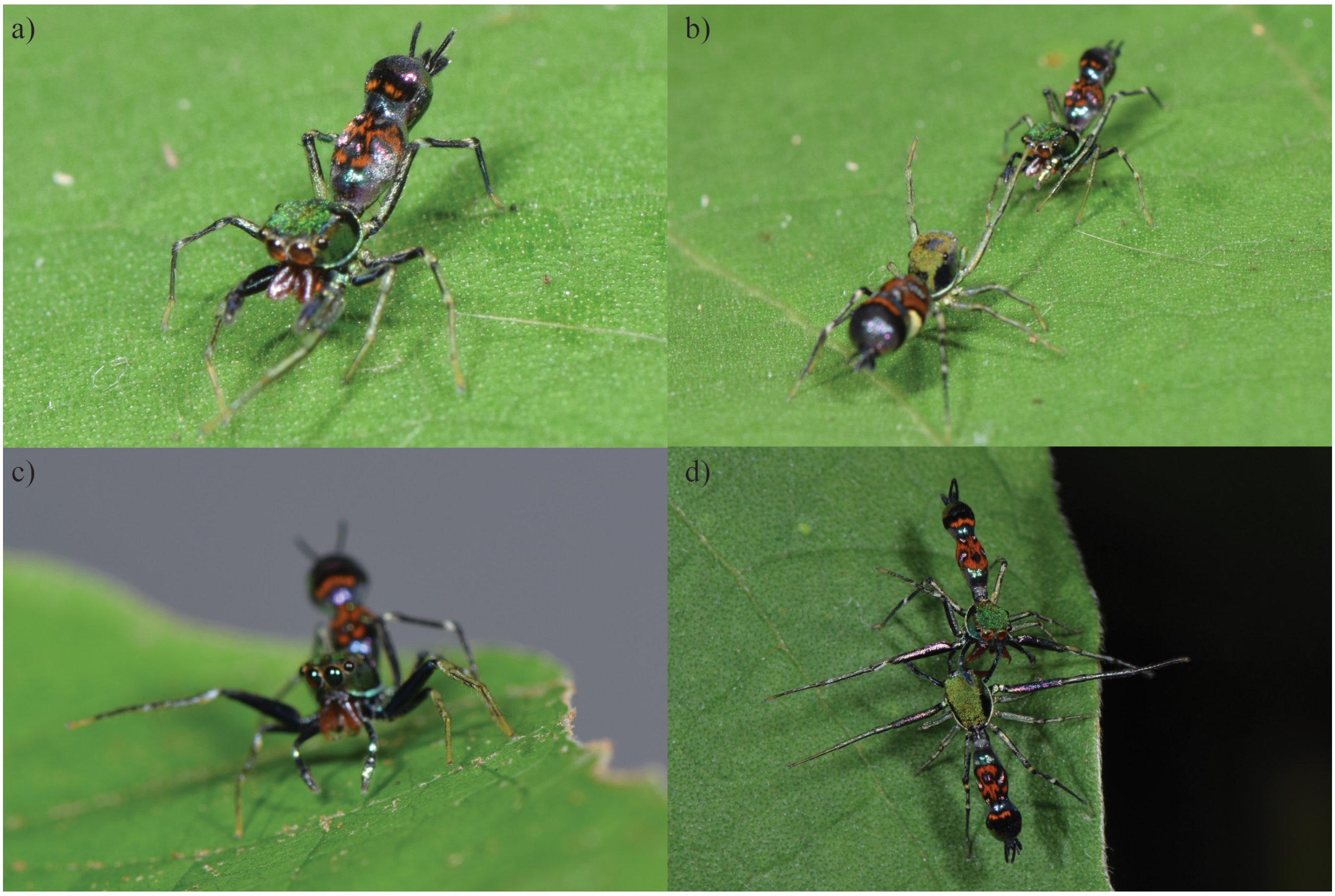

Fig. 5. Chelicerae positions. (a) A female showing chelicerae in position 1; (b) Female (foreground) *O. ichneumon* rejecting male's advances (background) by rapidly raising legs I into elevated legs (position 3) when male creeps with extended legs I and opened chelicerae (position 1) to approach female; (c) Male *O. ichneumon* displaying to another male. Legs I elevated in position 1 and waving in up and down motion, abdomen bent to the right of the sagittal plane with chelicerae slightly open (position 2) and palps held in position 2; (d) Two male *O. ichneumon* lunging with elevated legs I (position 2) and about to embrace. (Top male) Chelicerae are open to 90° and fangs pointing downward (position 2). Palps are held in position 2 before transitioning to position 3 during embrace

held at ca. 70° apart, pointing 80–90° downward from the horizontal plane of the spider. The laying down of silk (draglines), which engaged the lateral movements of the spinnerets during motion forward, was common.

During resting, all the legs were bent slightly (Fig. 3a, b). Legs I and II usually pointed forward, with legs III to the side and legs IV pointing backwards. The legs were generally evenly spaced apart, with legs I and II usually positioned at ca. 70–90° and 150–170° apart, respectively. Femur-patella joints were bent at 90–120° (Fig. 3a). Joints distal to the femur were usually tilted ca. 30° inward toward each other. Legs III usually pointed sideways (ca. 150–170° apart) with tarsi pointing down or slightly forward. Legs IV were positioned close to the abdomen at about 60° apart, with tarsi pointed backwards and diverged. Legs IV were highly bent (ca. 50–90°) at the femur-tibia joint. The palps generally hid the chelicerae during rest. The angle of the femur-patella joint of the palps varied from 30° to 90°, with the femur held near to face and tarsi pointing down forward (tarsi at ca. 70° to femora) (Fig. 3b). During locomotion, palps were never held fully extended or erect. During resting, palps were usually held stationary or waved in a similar rattling motion as the abdomen (abdomen takes ca. 2s to go from the lowest position to the highest position). Palps were held or waved at close proximity to each other but never touching the substrate. Waving of both palps often occurred with abdomen rattling, during which the palps and abdomen moved in phase with each other. However, the palps were not waved in matching phase with abdomen bobbing.

Description of intraspecific interaction elements. We began recording an intraspecific interaction when one spider started to display. Our criterion for recording male behaviour as being 'courtship interaction' was observing males respond to the presence of a female by flexing-up their abdomen, waving their palps and skittering. All behaviours by males and females after this point were considered part of the courtship display. An 'agonistic interaction' was recorded during male-male interactions when a male flexed-up their abdomen and stepped toward the other spider. All behaviours by both males after this point were considered part of the agonistic interaction. In all observations, an interaction was considered to have ended when one or both spiders decamped.

Courtship interactions lasted considerably longer than male-male agonistic interactions (Wilcoxon rank sum test: $W = 5$, N = 11, $p = 0.0003$). Male-male agonistic interactions lasted from 7 to 66 s (mean ± SE = 28.91 ± 5.77 s), while courtship interactions lasted 40 to 545 s (mean ± SE = 194 ± 48.28,

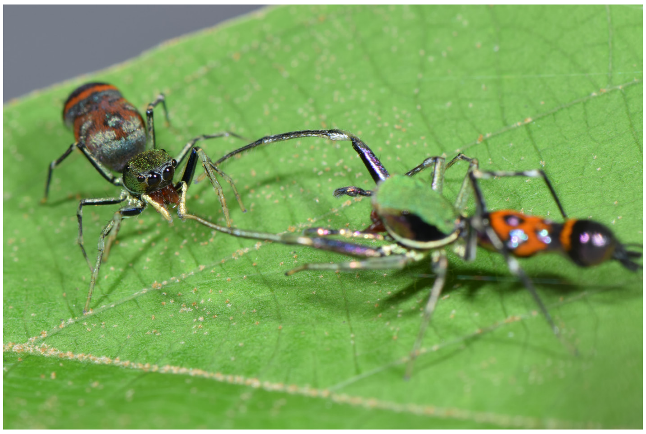

Fig. 6. Male (right) creeps toward female, tapping female's legs I with own legs I, male with extended legs I and extended palps (position 2).

excluding the time spent in copulation). No cannibalism was observed in either courtship or agonistic interactions. The sequence of courtship was highly stereotypical, with all males displaying the same behaviours before copulation. Agonistic displays were also stereotyped, but were more variable in the make-up of display elements.

A total of 28 major elements of display behaviour were observed during inter- and intrasexual interactions in *O. ichneumon* (Table 2). Each behaviour is described below in alphabetical order.

Abdomen movement and position.

Flexed up abdomen: To flex up the abdomen, the spider usually tilted up its abdomen about 70–90° from the transverse plane of the cephalothorax (Fig. 4a, b).

Bent abdomen: A bent abdomen was tilted about 30–60° to the left or right of the sagittal plane of the cephalothorax and flexed up at varying degrees (0–90°) to the transverse plane of the spider with posterior abdomen higher than the anterior abdomen (Fig. 4c, d).

Waving abdomen: Abdomen was held up at ca. 60–90° to the transverse plane of the spider and tilted up 20–40° of the sagittal plane of the cephalothorax. Abdomen was transited from the right to left, and back to the right. Waving tended to coincide with lateral movement of spider. Speed of waving abdomen varied with intensity of display.

Block. The male spider traversed sideways to remain in front of the female and blocked her escape path. Blocking generally resembled arc skittering. The blocking duration of each attempt by the male varied with the direction that the female was escaping in.

Chelicerae opened. The basal articles of the chelicerae were held 0–95° apart with variable fang extension. When maximally extended, the basal articles of the fangs pointed outward at 60° from the body. In position 1, the basal articles were held closed, with the fangs revealed but not pointing downwards (Fig. 5a, b). In position 2, the fangs pointed down with basal articles were held about 0–95° apart (Fig. 5c, d).

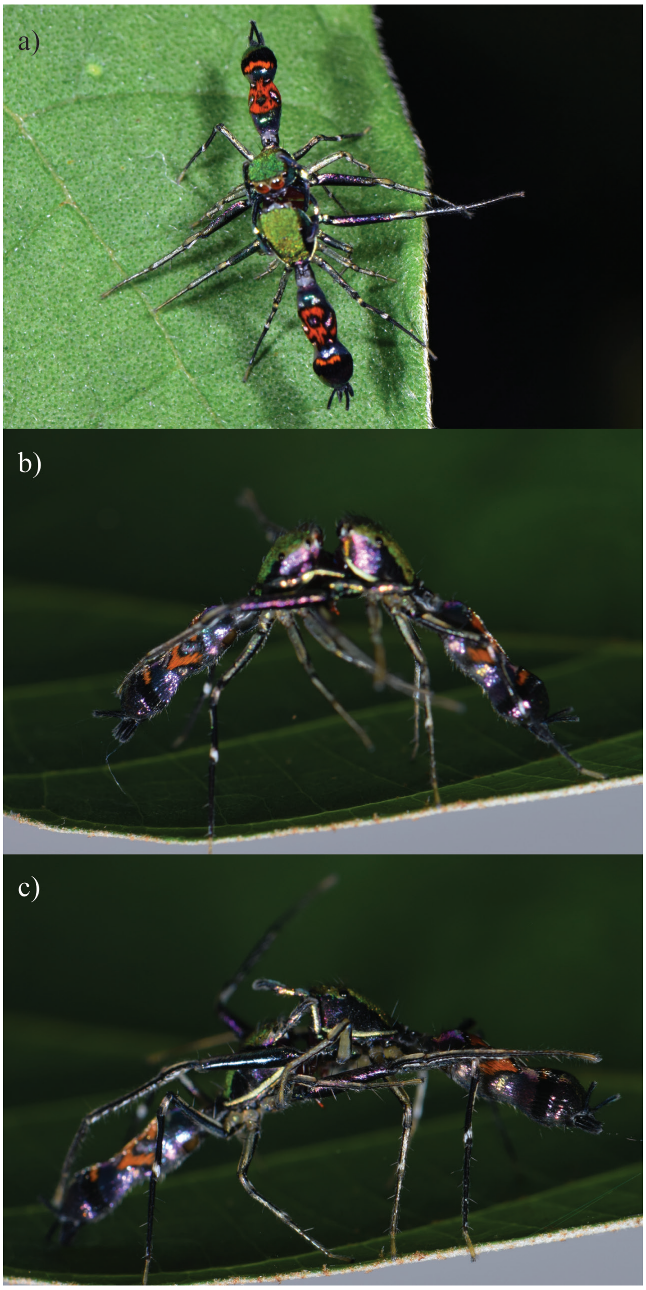

Fig. 7. Fighting positions (a) Two male *O. ichneumon* locked in an embrace (dorsal view), upper male with legs I engaged in hook and push down leg of the lower male. Legs I held in position 2. Bodies are raised off the substrate at maximum height such that leg II is fully extended, close to vertical and perpendicular to the substrate; (b) Two male *O. ichneumon* in an embrace, hook and push with bodies raised such that cephalothorax is higher than abdomen. Anterior cephalothoraxes are pressed together and chelicerae locked together; (c) Two male *O. ichneumon* engaging in grapple and push following an embrace. Legs I hooked and engaging in pushing. Both males have palps in position 3.

Clash. A clash occurred when one or both spiders lunged towards the other. While lunging, the spiders held their forelegs elevated (position 2, see below). Legs I in both the spiders made contact with tarsi touching without any locking

Table 2. Summary of major behavioural elements observed in intraspecific interactions between *Orsima ichneumon* spiders. M-F = Male behaviour during male-female interaction; F-M = Female behaviour during male-female interaction; M-M = Behaviour performed by a male during male-male interactions. X = Behaviour occurred. Behaviours are arranged in alphabetical order. Mount behaviour and copulation were not included here.

Behavioural Element	**M-F**	**F-M**	**M-M**
Abdomen position			
Bent		X	X
Flexed up	X		X
Waving	X		X
Block	X		
Chelicerae (Opened)			
Position 1	X		
Position 2			X
Clash			X
Creep	X		
Decamp	X	X	X
Elevated forelegs			
Position 1			X
Position 2			X
Position 3		X	X
Embrace			X
Grapple & push			X
Hook & push down legs			X
Legs			
Arched		X	
Extended	X		
Hunched		X	X
Lift & throw			X
Lowered body	X	X	
Lunge			X
Palps			
Extended	X	X	X
Scraping			X
Waving extended palps	X		X
Pursuit		X	X
Rapid extend & retract legs			X
Raised body	X		X
Skitter	X		
Stepping			X

of chelicerae. After a clash, the interaction escalated into an embrace, or the spiders resumed displaying.

Creep. The body was lowered with legs I fully extended and often parallel to the substrate and to each other, with tibia dipped down slightly. Palps were also extended (position 2, see below) and usually parallel to the substrate. Slow forward stepping motion (ca. 1–2 mm/s) occurred simultaneously (Figs. 5b, 6).

Decamp. Decamp consisted of one spider either jumping and/or running away.

Elevated forelegs. Elevated legs were observed in legs I. Legs I were held up laterally with tarsi lifted off the ground at varying heights of three positions. In position 1, legs I were bent at femur-patella and tibia-metatarsus joints with femurs held ca. 120–150° apart. Angle of femur-patella and tibia-metatarsus joints varied from 90–180° (Fig. 5c). When upward and downward waving, femurs were held stationary at 120° up from the sagittal plane. Waving occurred by the straightening of the joints from the patella to the tarsi. In position 2, legs I were extended fully forming a straight line and held ca. 80–180° apart from each other (Fig. 5d). Upward and downward waving was also observed. Position 3 occurred when legs I were straightened fully and held almost vertically upward, ca. 40° apart (Fig. 5b). No waving was observed in position 3. Combinations of positions were observed during displays.

Embrace. Both spiders were engaged in an embrace when chelicerae and palps came into contact. Both spiders' legs I were elevated (position 2) (Figs. 7c, 8e). Chelicerae were opened (position 2) and palps were extended (position 3).

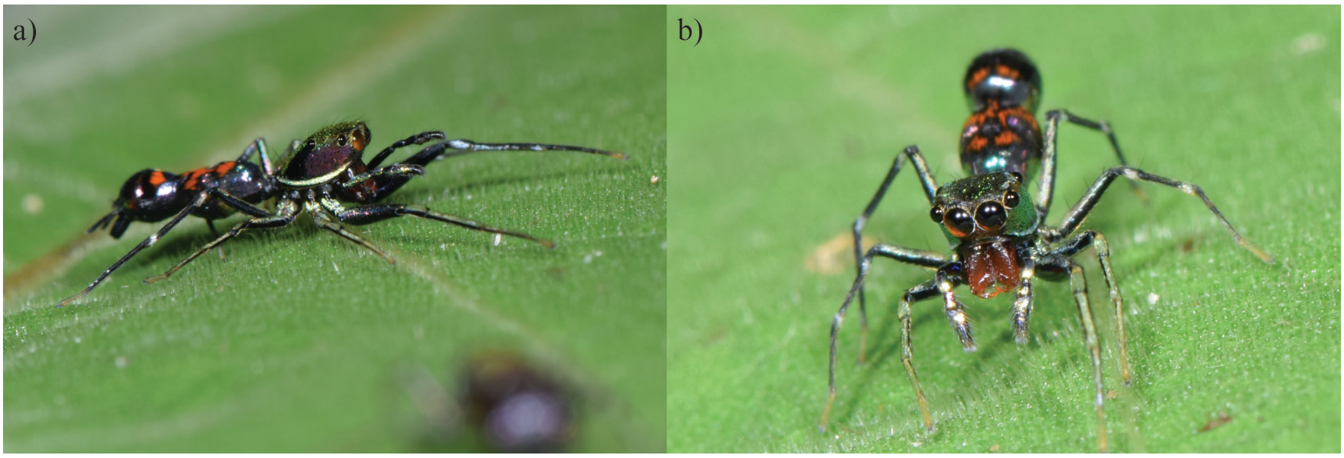

Fig. 8. Leg positions. (a) Male *O. ichneumon* with lowered body to the substrate and extended legs I almost parallel to substrate, palps in position 2; (b) Male *O. ichneumon* with legs hunched and abdomen almost parallel to the substrate.

Their bodies were raised to their maximum height with legs II fully extended, perpendicular to the substrate. The anterior abdomen was held much higher than the posterior. Each embrace lasted 0.5–5.0 s.

Grapple and push. Both spiders' legs I assumed a hooked position while chelicerae were still in contact after an embrace. The palps were extended in position 3 and their anterior cephalothoraxes pressed together (Fig. 8f). Both the spiders' bodies were also raised. The posterior abdomen of the spiders was lower than the anterior abdomen. In legs III and IV, the femur-patella joints of legs III and IV were both bent, but bend in legs IV was more bent than in legs III. During grappling and pushing, one spider was forced back by the other.

Hook and push down legs. The spider used its legs I to hook and push down one or both legs of the opponent spider immediately after an embrace. The legs I used for hooking were held in elevated legs position 2. The femur and tibia of legs I in both spiders experienced maximal contact during attempts to hook each other. When a spider raised their leg I higher than their opponent's, they then pushed down the opponent's legs I, with legs elevated in position 2 (Figs. 7c, 8e).

Legs.

Arched legs: The first three pairs of legs were positioned forming an angle of ca. 120° (legs I) and 150° (legs II) between right and left femurs. The right and left femurs of each pair of legs were almost parallel to substrate. Legs I and II on both sides were almost parallel to each other. The femur-patella and tibia-metatarsus joints were bent slightly on both legs I and II (Fig. 4b).

Extended legs: The femur-patella joints of legs I were held slightly bent or fully extended. Legs I were held almost parallel to substrate and to each other, sometimes with the tarsi angling down slightly (Fig. 8a).

Hunched legs: All legs were highly bent at the femur-patella and tibia-metatarsus joints, especially in legs I and II. Femurs of legs I and II were positioned ca. 120° apart, with femur-patella joints bent between c. 90–120°. From the patella to tarsi, joints were mostly straight with slight bend at the metatarsal-tarsal joints. Both legs I and II were almost parallel to each other, and patella to tarsi tilted ca. 45° distal from the femur-patella joints (Fig. 8b).

Lift and throw. With body positioned as when grappling and pushing, one spider ("lifter") raised its body and lifted up the other spider. The lifter had the anterior part of the cephalothorax much higher than the posterior end. When the spider being lifted lost contact with the substrate, the lifter rotated its body suddenly releasing its legs I hook posture and assumed elevated legs position 3, such that the lifted spider was thrown off balance before landing upon contact with the substrate.

Lowered body. Abdomen and cephalothorax was held close to and almost parallel to the substrate (Fig. 8a).

Lunge. A lunge occurred when one or both spiders suddenly raised the anterior end of its cephalothorax and propelled forward by extending legs IV, such that the anterior cephalothorax of the spider was higher than the posterior end of the cephalothorax. Legs 1 were elevated (position 2). The distance between both spiders was about 0.5–1 body lengths (Fig. 5d).

Mounting and Copulation. After creeping and making contact, the male used his extended legs I to tap the female's legs I. Next, it used legs I and II to tap the female's legs I and II and simultaneously moved forward to mount the female. This normally occurred within ca. 1s, and the female responded with taps with extended legs I (Fig. 6). The female either assumed elevated legs I (position 3) to push the male's legs I or immediately turned away but did not decamp (Fig. 5b), or assumed a hunched leg position before lowering her cephalothorax to the substrate while the posterior abdomen was held higher than the anterior abdomen (Fig. 9a). When the female lowered her body, the male's cephalothorax was held over the female's cephalothorax, after which the male positioned himself slightly to the left or right of the female's

Fig. 9. Mount behaviour and copulation (a) Male uses legs I and II to tap female's legs I and II, female assumes hunched legs and lowers cephalothorax to substrate with abdomen tilted higher than cephalothorax, allowing male to walk over her cephalothorax; (b) Male moves to left or right of female's abdomen; (c) Female's abdomen is rotated 30–60° for male to insert palp and copulation occurs.

body (Fig. 9b). The female's abdomen was rotated slightly (ca. 30–60°) either to the left or right to expose her ventral abdomen to the male (Fig. 9c). The male then inserted one of his palps into the female's epigynum to begin copulation. Slight movements of both of the male's palps were observed during and after mounting, but details were not discerned.

Palps.

Extended palps: Three positions were discerned. The joints distal to femur-patella on palps were stretched fully. In position 1, the femora of palps were held parallel to the substrate and each other. The joints distal to femur-patella on palps were held at ca. 45° down from the horizontal plane of the spider. The joints distal to femur-patella on palps sometimes converged 30° inward or diverged outward from the sagittal plane of the body but rarely touched each other (Fig. 4c). In position 2, the whole appendage (femurs to metatarsal joints) were parallel to the substrate and held ca. 90°–120° apart from each other and fully extended (Figs. 3a, 4a, 8a). In position 3, the palps were extended vertically upwards, almost perpendicular to the substrate, with 90° bend at the femur-tibia joint of the palp (Fig. 7c).

Scraping with palps: The palps were bent (ca. 120°) at the femur-tibia. The palp tarsi maintained contact with the substrate and moved ca. 1 mm. This lasted for < 0.5 s. Distance travelled varied with forward stepping.

Waving of extended palps: The palps remained extended (position 1). The joints distal to femur-patella on palps were positioned at ca. 45° down from the horizontal plane of the cephalothorax. They were waved rapidly back and forth away from the spider before moving inward toward the spider while the femurs were held stationary. Waving was often in opposite directions on opposing palps. Rate varied from 0.003 s to 0.02 s per cycle before a short pause. The cycle was repeated again.

Pursuit. The female chased the male when the male decamped during courtship. Occasionally, the female's anterior cephalothorax would make contact or collide with the male's abdomen during decamp when he abruptly ceased his decamp. In male-male interactions, pursuit was also observed when the 'winner' chased the 'loser'.

Rapid extend and retract legs. Legs I and II were hooked (femur-tibia joints at ca. 60°; tibia-metatarsus joint at 60°–120°) and rapidly extended and retracted (Fig. 10a, b). The whole process lasted approximately 4 s from start to end. One complete cycle (one extension and retraction of one side of legs I and II) was approximately 0.01 s. The abdomen was held fixed at ca. 70° and lowered till almost parallel to the substrate. The cephalothorax rose in an upward arc motion from parallel to the substrate to 70° from the horizontal plane. Legs I and II were positioned ca. 45° above the horizontal plane of the body and continued in rapid extension and retraction to 90° overhead from the horizontal plane. This gave the illusion that the spider was rearing upon its legs IV. Upon reaching the maximum upward angle, the spider reversed the upward arc motion while still rapidly extending and retracting its legs to bring its legs down to the original starting position. The process ended when the spider resumed the original posture prior to rapid extension and retraction. In the extension phase, the femur-patella joints were hooked. The femur-patella joints in legs I and II extended away from the body. Tarsi of legs I and II pointed perpendicularly downwards while touching. In the retraction phase, the femur was held close to the body and the femur-patella joints both legs I and II were retracted toward the body. Tarsi were held pointing downwards and further from the substrate, but did not always touch. Legs I and II on each side (left and right) extended and retracted

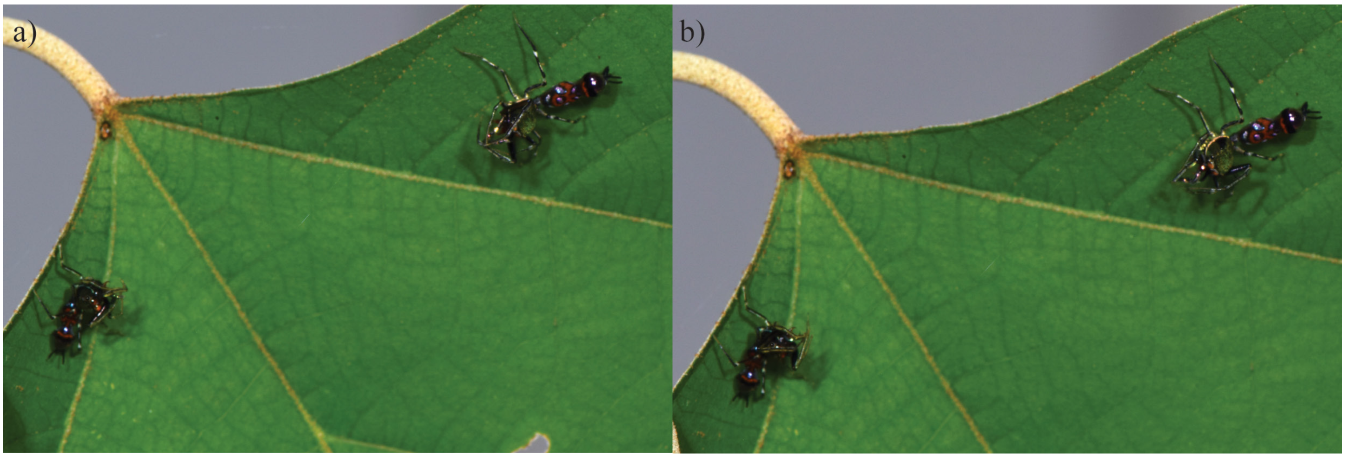

Fig. 10. Two male *O. ichneumon* engaged in rapid extension and retraction of legs I simultaneously. Male (right) is the process of 'rearing' up with legs (a) still held in front of its face (b) above head, at maximum rearing height.

simultaneously in opposite directions. The femur-patella joints of palps were bent at 85–90°. The palps made contact with the tarsi of legs I during extension and retraction.

Raised body. Body was held above the substrate, higher than when in the resting position (Fig. 11). Cephalothorax was held parallel to the substrate while the abdomen was usually held at varying angles (0–90°) to the horizontal plane of the spider with posterior abdomen higher than the anterior abdomen. Posterior abdomen was sometimes held lower than the anterior abdomen, closer to the substrate.

Skitter. Skittering resembled the stop-and-go gaits seen in general locomotion, except that the duration of steps taken was shorter and faster. The route taken also differed. Arc skittering occurred when the spider traversed in an arc around a female. The spider stepped left or right for ca. 0.2–0.3 s with short pauses of ca. 0.2 s before stepping in the same direction again. The cycle continued for ca. 0.5–0.6 s. The spider halted for a short pause (ca. 0.2 s), then stepped in the opposite direction for 0.5–0.6 s, halted for ca. 0.2 s and the cycle repeated. Side-to-side skittering was similar to arc skittering except the spider traversed left and right on the same plane instead of arcing. Side-to-side skittering was rare and occurred for shorter durations than arc skittering. In the process of a stop-and-go skittering, the spider stepped forward for 0.1–0.3 s, halted for ca. 0.2 s, before stepping forward for 0.1–0.3 s again. This cycle was then repeated. Arc skittering was more common than stop-and-go skittering. The time taken to complete arc skittering was dependent on the distance ranging from 1 to 6 body lengths. During skittering, the male's abdomen was often held at ca. 30° but flexed to (ca. 70° to 90°) during the pause in between skittering. Spiders often bobbed their abdomen while skittering. A bob entailed a fast transition of the abdomen from being held at 30–45° to 90°.

Fig. 11. Male *O. ichneumon* with raised body and slightly flexed up abdomen (ca. 30°), palps in position 1.

Stepping. Hunched legs were assumed in legs II–IV. The spider proceeded to step left or right in a smooth motion unlike that seen in skittering. Abdomen waving usually accompanied stepping. The spider took 3–4 small steps (total distance travelled ca. 2–3 mm) before a short pause (< ca. 0.5 s) and stepped in the opposite direction. During pauses in between stepping, the spider sometimes waved legs I (position 1) and waved palps. The duration of stepping varied (1–4 s) depending on the intensity of the display.

Male-female interactions. During courtship interactions, a female decamped frequently when a courting male first approached. The female decamped to the underside of the leaf before being returning to the topside of the leaf. The male usually made multiple attempts before it was able to mate successfully.

When a male first detected a female, he froze and visually orientated towards her. If he did not decamp, he began courting with raised body, flexed up abdomen, open chelicerae (position 1), extended palps (position 2), and waving the extended palps parallel to the substrate. Forward and arc skittering then occurred regardless of whether the female was oriented toward the male or not. The female then orientated her body to face the male. The distance between the male and the female when courtship occurred was between 6–15 body lengths away. If the spiders first viewed each other with a shorter distance between them, the female usually decamped. During the display by the male, his abdomen was raised up to 90° from the horizontal plane of the body. Waving and smooth bobbing of the abdomen was also observed during uni-directional skittering. When the males paused for a longer period, they rattled their abdomens before skittering in the opposite direction. Spinnerets were not involved in any of the displays. The spinnerets were held in the usual position when they are not being used to lay silk draglines. Females responded to a courting male by orientating toward the male, legs hunched or arched with palps extended (position 1) and occasionally with abdomen bent towards the side. If the female attempted to decamp, the male usually blocked the female by skittering across the path. If the female turned away, the male would similarly skitter directly in front of the female to re-attract her attention. Occasionally the female pursued the courting male after he decamped. The male decamped to 6–10 body lengths or to the underside of the leaf before reattempting the courtship display again. Once the courtship began, most males exhibited continuous focus on the female.

If the female did not decamp after the male's initial display, the male usually skittered close enough to the female to mount. Prior to mounting, the male approached the female by creeping and extending legs I to tap the female's legs I. The female could prevent the male from approaching by rapidly raising legs I into a vertical position (elevated legs, position 3) such that they collided with male's legs I and II and flicked the male's legs away. Alternatively, the female turned away from the creeping male. Prior to mating the female held her forelegs in an extended position and tapped the male's forelegs before lowering her cephalothorax to the substrate with her abdomen tilted such that the posterior abdomen was higher than the anterior end. The male then walked over the cephalothorax of the female while using legs I and II to tap the female's legs I and II. Copulation began when the male moved slightly to the left or right of the female's abdomen (rotated 30–60°) and inserted his palp into the female's epigynum (Fig. 9c). The male's right palp was inserted on the right side of the female's epigynium and vice versa. In rare occasions, the female attempted to pull away during copulation. Sometimes the male used both palps during copulation by inserting the other palp immediately on removal of the first palp without the female decamping. The male and female faced opposite directions during copulations. The right palp was inserted on the right side of the female and vice versa. Copulation duration was highly variable, ranging from 1 to 21 min (N = 11 pairs, Mean ± S.E = 10.8 ± 1.9 min), and always began within 20 s after the male's initial contact with the female. Copulation ended when either spider decamped.

Male-male interactions. Agonistic displays were observed to take place when the males were 10–15 body lengths apart. If there was a shorter distance between them at first sighting, one or both males would decamp. Agonistic display began when one or both spiders sighted the rival and assumed a stance of raised bodies, abdomen bent 30–60° from the sagittal plane. Both males then stepped left or right in the opposite direction from their rival, with elevated legs I transitioning between position 1 and 2. The abdomen was usually held at a 75–90° angle above the substrate during agonistic display. Abdomen waving and rattling accompanied the stepping and foreleg waving. The palps were held extended and transitioned between positions 1 and 2. The chelicerae was held in position 2 and revealed by the extended palps. During the initial display stage, decamps were common among smaller males facing larger rivals.

If no male decamped, agonistic displays escalated by one or both males rapidly advancing forward 1–2 body lengths with abdomen flexed and bent. The palps were fully extended (position 1) and scraping the substrate once with every forward advance, before halting and stepping in opposing direction with legs I waving and abdomen flexed and bent. During pauses in stepping, palps were observed to wave in position 1 before stepping resumed. The process was repeated with stepping forward 1–2 body lengths again. Occasionally one or both spiders rapidly extended and retracted legs I and II when about 5–6 body lengths away from each other. If one male displayed this element, the other male occasionally paused its stepping and watched or copied the other male by extending and retracting legs. Rapid extension and retraction usually occurred only once per spider during an encounter after which the pace quickened in the display of the subsequent elements. Only larger males (>6.9 mm) tended to display this behaviour. Spiders spent more time stepping as the distance closed between them. Stepping occasionally resembled rivals 'circling' each other with the actual distance travelled equivalent to a quarter circle (diameter = distance between spiders). This phase continued until spiders were 1–3 body lengths apart from one another. Decamp occurred at any stage of this phase.

If no spider decamped, the display progressed to the contact phase where one spider lunged forward and clashed with the rival, often forcing the rival backward. The 'pushed' rival occasionally reciprocated with a lunge and clash. Lunge and push occasionally occurred multiple times. One male usually decamped after being lunged at. Sometimes, the display escalated from a lunge and clash to an embrace when both spiders lunged simultaneously and locked chelicerae in position 2 with legs I elevated in position 2. This was followed by hook and push of legs I that were in position 2. Hook and push lasted for about < 0.5 s. After hook and push, grapple and push followed. This lasted for about 0.5 to 5 s. Grappling and pushing occasionally escalated to a lift and throw. One male lifted the rival's anterior cephalothorax slightly off the substrate while fangs engaged with the rival. The lifting male then twisted his anterior cephalothorax either to the left or right to throw the rival off balance. Lift and throw was not common as most agonistic displays ended with one male decamping at the hook and push stage. The winner pursued the loser (first male to decamp) upon release from contact.

DISCUSSION

We found that *Orsima ichneumon* use a series of complex behavioural elements during intraspecific interactions. In general, the repertoire of behaviours was similar to other jumping spiders both in terms of the number of elements and the types of behaviours observed (Jackson & Macnab, 1989; Alcock, 1991; Jackson & Macnab, 1991; Li et al., 2002; Lim & Li, 2004; Cross et al., 2008; Tay & Li, 2010; Girard et al., 2011; McGinley et al., 2016). In particular, a study of a closely related species, *Cosmophasis umbratica*, identified a very similar number (29 major elements) and repertoire of behavioural elements compared to *O. ichneumon* (28 major elements) (Lim & Li, 2004). Male *O. ichneumon* performed a higher number of behaviours (27 elements) than females (10 elements) and only one behaviour was performed uniquely by females ('arched legs'); it was used in reaction to male courtship advance. Otherwise, during male-female interactions the female would largely alternate between watching the male from a distance and decamping, with the male doing most of the work holding the female's attention and gaining her cooperation before copulation.

While sexual selection on males to attract and compete for mates is thought to drive the evolution of elaborate displays (Jackson & Pollard, 1997), there are multiple hypotheses proposed to explain why intraspecific displays are so complex (Candolin, 2003; Hebets & Papaj, 2004). For example, complex signals made up of multiple elements may maximise information provided to the receiver about both the signaller's identity and quality (i.e. multiple messages hypothesis), or may operate as backups to ensure effective signalling in variable environments (i.e. efficacy based hypothesis). For example, *Rabidosa rabida* wolf spiders use both vibratory and visual courtship signals, which vary in their importance depending on substrate and light conditions and allow males to mate across a dynamic natural environment (Wilgers & Hebets, 2011).

A more complex behavioural repertoire by female *O. ichneumon* may have been identified if we had also observed female-female interactions, because this may have revealed behavioural elements performed only in the context of female-female aggression. For example, some jumping spider females predate on other female's eggs or compete for resources, leading to agonistic interactions between them (Jackson, 1988). However, despite incorporating observations of female-female interactions, other studies have generally identified a more complex behavioural repertoire by male jumping spiders, with females being the choosier sex (Jackson & Pollard, 1997; Tay & Li, 2010; McGinley et al., 2016).

Male *O. ichneumon* used their brightly coloured pedipalps, legs and abdomen in multiple behavioural elements during courtship and agonistic displays, suggesting the importance of these highly conspicuous appendages during intraspecific signalling. The abdomen, for example, played a central role in the repertoire of male displays. During courtship, males first raised their abdomen and extended their palps before skittering, while bobbing the abdomen. During agonistic interactions, males also raised and bent their abdomen to the side. The abdomen was then waved from side to side as the male stepped left and right. In both scenarios, the observer is exposed to the male's abdomen colour, especially because the moving abdomen was often the only conspicuous body motion, which may draw attention to that appendage. The colours may function as a mechanism to attract the attention of a female or rival and communicate quality and strength. *Orsima ichneumon* are found on forest edges in sunny patches, which are typically areas higher in overall irradiance and relatively high in red light compared to shady areas (Endler, 1993; Taylor & McGraw, 2013). Their sunny location may allow the spiders to show off their abdomen colours. Although currently unknown, the array of colours displayed by male *O. ichneumon* may be driven by sexual selection. Among other jumping spiders, including the closely related *C. umbratica*, colourful scales are used as ornaments to signal male quality to females or resource holding potential to rivals (Lim et al., 2007; Li et al., 2008; Lim et al., 2008; Lim & Li, 2013; Taylor & McGraw, 2013). It is interesting that other ant mimicking jumping spiders are not similarly brightly coloured (Nelson & Jackson, 2006; Pekár & Jarab, 2011), suggesting very different evolutionary history and selection pressures between these species. The arrangement of orange/red and black colours on the abdomen may also function as an aposematic warning signal to potential predators, such as has been identified in black widow (*Latrodectus* spp.) spiders (Brandley et al., 2016), but this remains to be tested. Future studies that address the precise role of colouration in this species will be important to tease these hypotheses apart.

Similar to other jumping spiders, male-male agonistic interactions were made up of distinct stereotypical and complex behavioural elements within a series of escalating phases (Jackson & Macnab, 1989; Taylor & Jackson, 1999; Li et al., 2002; Lim & Li, 2004; Elias et al., 2008; McGinley et al., 2015). *Orsima ichneumon* males used a larger repertoire of elements during contests (22 elements) compared to a smaller number of behaviours during courtship interactions (12 elements). Males began agonistic interactions with a pre-contact stage by bending their abdomen to the side, which could be a defensive stance given that males did not do the same behaviour when encountering and courting a female. This was followed by a series of abdomen movements (waving and rattling) and stepping behaviour, with extended legs, chelicerae and palps. These displays would begin at a distance, probably allowing for visual assessment of rivals at a safe distance, but advanced to closer proximity if neither male decamped.

Contests rarely escalated to the contact phase with physical clashes, pushing and grappling, during our observations. Furthermore, while agonistic interactions were made up of more behavioural elements than courtship, agonistic interactions were shorter in duration. Given that agonistic interactions are potentially costly in terms of injury or fatality, there is likely to be strong selection on males to be able to resolve contests as quickly as possible. Reducing the potential costs of male-male interactions may therefore be an important driver of both the duration and structure of contests. During courtship, on the other hand, males would continue to attract the female's attention, despite her repeatedly decamping during the interaction. This suggests that lengthy courtship displays may be necessary for males to convince the female to mate. Although courtship displays may be costly to the male in terms of increased risk of predation and lost foraging opportunities (Hoefler et al., 2008), males cannot avoid these interactions if they are to have a chance of mating.

In addition to visual displays, many jumping spiders use vibratory signals to communicate during courtship (Edwards, 1981; Taylor & Jackson, 1999; Elias et al., 2003; Girard et al., 2011; Elias et al., 2012). Non-visual communication can be particularly important when males court while females are out of view within their silk retreats (Jackson, 1977). A recent study identified multimodal courtship in peacock spiders, and found that vibrations were measured when males oscillated their abdomen (Girard et al., 2011). We did not measure seismic communication in our study and did not include behavioural assays where interactions occurred around the female nest. However, we propose that future work on *O. ichneumon* could address this because several of the behavioural elements observed (e.g., abdomen waving/rattling, palp waving/scraping) may be used as vibratory signals, and it is possible that males also use vibration when courting females within silk retreats.

In conclusion, this study is the first detailed description of the behaviour of *O. ichneumon*. We intend this work to be used as a framework from which to base further studies on the evolution of colouration, ant mimicry and signalling behaviour in this fascinating species.

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