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COURTSHIP AND MALE-MALE AGONISTIC BEHAVIOUR OF *COSMOPHASIS UMBRATICA* SIMON, AN ORNATE JUMPING SPIDER (ARANEAE: SALTICIDAE) FROM SINGAPORE

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ABSTRACT. **–** The courtship and male-male agonistic behaviour of *Cosmophasis umbratica* Simon, an iridescent jumping spider from Singapore, was studied for the first time. Exhibiting sexual colour and size dimorphism, *C. umbratica* is frequently found on leaves and flowers of tropical plants in open areas. Males are generally larger than females and dominantly green and black with silvery white markings; females are generally a mixture of green, brown, white and black. Sixteen major displays are described for *C. umbratica*. Skittering, vibrating of palps, arching of legs and flexed up abdomens are dominant male behaviours during courtship. Females almost always decamp on first sight of males, although males are very persistent in their courtship. A large repertoire of male-male agonistic displays is observed, with males either decamping after a clash, being lifted up and thrown down, or while embracing are chased away after being pushed back. Drumming is also displayed in both male-female and male-male interactions. This vibratory communication channel during inter- (male-female) and intra-sexual (male-male) interactions away from nests is discussed in regards to the evolution of salticids.

KEY WORDS. **–** Spiders, Salticidae, *Cosmophasis umbratica*, sexual dimorphism, agonistic, courtship, vibratory communication.

INTRODUCTION

Among spiders, jumping spiders (Salticidae) are the most diverse family with approximately 5000 named species from 538 genera (Platnick, 2003). They are distinguished from all other spiders by their unique, complex visual system and acute vision (Land 1969a, 1985; Blest et al., 1990), including colour vision (DeVoe, 1975; Forster, 1985; Nakamura & Yamashita, 2000) with an extensive spectral sensitivity (Peaslee & Wilson, 1989). Though the visual ability has not precluded communication involving other sensory modalities (Jackson, 1982), much of the inter- and intra-specific communication of salticids is highly reliant on vision (Crane, 1949b; Forster, 1982a, b; Clark & Uetz, 1994; Jackson & Pollard, 1996, 1997; Li et al., 1997). Selection pressures from the mate-choice preferences of females have probably driven the evolution of striking colour patterns and active visual courtship displays in salticid males. The elaborate leg waving and stereotypic dance displays may also facilitate species recognition (Peckham & Peckham, 1889, 1890; Crane, 1949a; Forster, 1982a, 1985).

The anterior eyes (also called ‘principal eyes’) enable salticids to recognize objects from 20-30 body lengths away (Jackson & Blest, 1982; Harland et al., 1999), with secondary (lateral and posterior) eyes being involved primarily in detection of long range movement (Land, 1971). Together, the salticid’s eight eyes support vision-mediated courtship, prey capture and escaping from predators (Crane, 1949a, b, Land, 1969a, b, 1985; Forster, 1982a, b). When encountering a potential prey, most salticids adopt a typical stalk-and-leap sequence (Forster, 1982a, b). If the object is a conspecific spider, however, salticids behave differently. In typical male-male agonistic encounters away from nests, salticids threaten each other in leg-wave-and-grappling sequences (Wells, 1988; Faber & Baylis, 1993; Taylor et al., 2001; Taylor & Jackson, 2003). In male-female encounters away from nests, salticids use vision-dependent displays: a common pattern is for the female to remain stationary while the male approaches in a zig-zag courtship display, integrating various postures and patterns of waving the forelegs (Crane, 1949b; Jackson, 1982).

Male-male agonistic and male-female courtship displays during intraspecific interactions have been described in detail for numerous species of salticids (e.g. Jackson 1986a, 1986b; Jackson & Macnab, 1989; Richman & Jackson, 1992). Intersexual displays tend to be especially elaborate and complex (Peckham & Peckham, 1889, 1890; Crane, 1949a, b; Forster, 1982a; Richman & Jackson, 1992; Jackson & Pollard, 1997). Male-male interactions include more behaviour that can be called aggressive (e.g. Crane, 1949a, b; Richmond & Jackson, 1992; Faber & Baylis, 1993; Taylor et al., 2001; Li et al., 2002). However, the number of salticid species studied so far cover only a small fraction of the salticid 538 known genera.

Many species of salticids use distinctly different mating tactics, involving both visual and non-visual communication (e.g., Jackson, 1982; Jackson & Pollard, 1997). Appreciating the varied sensory modalities used by salticids has led to speculation about the evolution of salticids (Jackson & Blest, 1982). However, comparative data from a wide range of species of saltcids combined additional comprehensive studies of individual species are needed for evaluating evolutionary hypotheses. Salticids are most diverse in the tropics. Tropical salticids are of special interest also because they are often especially ornate.

Despite being a small state, Singapore provides exceptional opportunities for research on salticids. Being close to the sea level and nearly on the equator in the wet tropics, Singapore is a centre of extraordinarily rich biodiversity (Turner, 1994), and this includes a very diverse spider fauna (Song et al., 2002). There are 77 described salticid species in Singapore (Song et al., 2002; Zhang et al., 2003), but there have been studies of the displays of only four of these: *Phaeacius malayensis* Wanless (Jackson & Hallas, 1986a), *Epeus flavobilineatus* (Doleschall) (Jackson, 1988), *Thorellia ensifera* (Thorell) (Jackson & Whitehouse, 1989), and *Thiania bhamoensis* (Li et al., 2002). As a step toward our understanding of Singapore salticids, we investigated the courtship and male-male agonistic behaviour of *Cosmophasis umbratica*, an especially active and colourful salticid.

MATERIALS AND METHODS

Individuals of *Cosmophasis umbratica* were collected in the morning (0830-1100 h) from several parks in Singapore, but especially from Kent Ridge Park and Clementi Park Connector. Because observing the interactions of salticids in the field is very difficult, we took adult spiders (12 males and 19 females) from the field back to the laboratory for detailed observations. Spiders were maintained individually in cylindrical cages (diameter: 6.5 cm; height: 8.5 cm) in a controlled-environment laboratory (relative humidity: 80-85%; temperature: 25 ± 1ºC; light regime: 12 h: 12 h; lights on at 0800 h). Additional lights (Arcadia Natural Sunlight Lamp) were used to illuminate cages 4 h daily (0900-1100 h; 1600-1800 h) as these light tubes provided light spectrum that simulated natural sunlight. In addition, these spiders were most frequently spotted on plants exposed to sunlight during late morning and early evenings (personal observations). Water and sugar water were provided *ad libium* via dental rolls. Spiders were maintained on a diet of houseflies (*Musca domestica*), fruit flies (*Drosophila melanogaster*) and small instars of crickets (*Gryllidae* sp.) twice a week. Testing procedures, cage design and terminology were the same as in earlier studies of salticids (Jackson & Hallas, 1986b). This included convention that expressions such as ‘usually’ or ‘generally’, ‘sometimes’ or ‘occasionally’, and ‘rarely’ that were used to indicate frequencies of occurrence of c. >80%, 20-80%, and <20%, respectively.

To observe male-male and male-female interactions, two individuals of *C. umbratica* were used two at a time. A young Simpor Air leaf (*Dillenia suffructicosa*) (length: 15-20 cm; breath: 10-15 cm) was clamped to a stand that was held 20 cm above and parallel to test table. Both spiders (two males, or a male and a female) were introduced onto the leaf at the same time, but at opposing ends. An arrangement of 10 equi-spaced Voltarc Ultra Light tubes (110W each), held 130 cm above table was used to provide full-spectrum illumination during the observations. A total of 12 adult males and 19 adult females were used. No individual was used more than once on any given day for the same test, but might be used on other days in the similar or different tests. The inter- and intrasexual interactions were video recorded.

OBSERVATIONS

Habitat

Cosmophasis umbratica was often found on leaves and flowers of ‘sun-loving’ flowering shrubs or plants that were fully exposed to sunlight. One of these plants, *Ixora javanica* (Fig. 1) (commonly known as ‘Ixora’ or ‘Javanese Ixora’) is native to Southeast Asia and commonly planted in parks for aesthetic purposes as it flowers all year round (Fig. 2). Like many salticids (Jackson et al., 2001), *C. umbratica* is nectivorous and we often found it on or near the inflorescences of Javanese Ixora (Fig. 3).

Morphology

Cosmophasis umbratica is a small jumping spider (body length: adult male 5 – 7 mm; adult female c. 5 mm) showing sexually dimorphism in colour and size. The males have complex iridescent markings on several body regions, but especially on the dorsal and sides of cephalothorax, and on the sides of the femora of all of the legs. The abdomen is mostly black with silvery white lines (Fig. 4). The female is generally green (dorsal and side cephalothorax) with a mixture of brown, white and black coloration on the abdomen (Fig. 5). Morphologically, males have slimmer abdomen and longer legs than females. Sexually mature males are readily identifiable from sub-adult males by the presence of a black tip on the tarsi of the palps, and the presence of white hairs on the face (Fig. 6).

Nest structure

Males and females of *Cosmophasis umbratica* built similar nests: a silken sheet and a tube with entrances on both ends. The sheet was wide at the ends, and narrowed as it approached the doors of the tube. The sheet covered over the silken tube (Fig. 7). Prior to oviposition, the gravid female sealed the doors and remained inside the nest. The nests of *C. umbratica* were commonly found in-between leaves of Ixora, or at times on the base of the inflorescences.

Figs. 1-3. (1) Javanese Ixora, *Ixora javanica*, a common garden flowering plant on which *Cosmophasis umbratica* and many salticids were frequently found; (2) Ixora commonly planted along roads and paths in parks; (3) *C. umbratica* on a red inflorescences of Ixora.

Normal locomotion

The normal locomotion of *C. umbratica* was characterized by rapid stop-and-go gaits (stepped forward for 0.3-0.8 s; paused for 0.3-0.6 s). Stepping forward mirrored either a straight line or an arc. A single bob started when the spider paused during stepping and raised its abdomen to a maximum height, and ended when the abdomen was lowered. Ascent and descent of the abdomen was normally smooth and seldom jerky. The abdomen was usually parallel to substrate when the spider transverse between pauses, though posterior of the abdomen was sometimes nearer to the ground than the anterior of the abdomen during a pause after bobbing.

Bobbing of abdomen during normal locomotion involved the quick and jerky flexing up and down (30-70°) of abdomen within the sagittal plane. Two types of abdominal bobbing were observed: low (duration 0.3-0.4 s, abdominal flexed at.30-50°) and high (0.4-0.6 s, abdominal flexed at *c.*50-70°) bobbing, the latter being more common. Stepping faster usually meant faster bobbing, though the spider never steps while raising its abdomen. However, the spider usually had already started to step when the abdomen had lowered to about 30˚ during abdominal descent. In the event of low abdominal bobbing, the spider had already begun to step after onset of abdominal descent. Though single bobbing was common during normal locomotion, double and triple bobbing were also observed but rare. Double and triple bobbing are events where a single bobbing is repeated once and twice, respectively, without the spider stepping off. Most double-bobbing events lasted only 1 s, and double-bobbings ending with low abdominal bobbing resulted in similar stepping pattern as a low abdominal bob: the subject stepped off after onset of abdominal descent

Although the angles of femur-patella and tibia-metatarsus joints were variable, generally all legs were slightly flexed, with legs I and II generally pointing forward, legs III to the side, and legs IV pointing backwards. Legs were well spaced out, with legs I and II normally held at about 70-90° and 150-170° apart respectively, and with femur of both legs facing the front (angled about 30-45° to the axis). Legs III generally pointing sideways (150-170° apart) with tarsi directed forward, and legs IV were held close to the abdomen at about 30-45° apart, with tarsi pointed backwards and diverged. Legs were never observed to be close to each other in any instances during normal locomotion.

Palps were held in front of the face, and hid either part or most of the chelicerae from view (Fig. 8). The angle of the palpal femur-patella joint varied from 30˚ to 90˚, with the femur held near to face with tarsi pointing down or pointing forward (tarsi at c. 70˚ to femora), or a 'raised palp'. Palps were never observed to be fully extended or erect during normal locomotion. While at rest, palps were usually positioned or waved (about 5/s) at close proximity of each other, but palps rarely touched the substrate. Waving of both palps were often in matching phase with each other, and often occurred with bobbing of abdomen, but the matching phase of abdomen bobbing and palps waving was not evident.

Elements of behaviour occurring during intraspecific interactions

Some behaviour elements were based on movement patterns. Others were static, with the spider holding body parts in particular stances for sustained periods. A total of 29 elements of behaviour are described. These are listed below with each element of behaviour being given an index number: arched legs (6), bent abdomen (5), block (19), clash (29), copulation (22), creep (3), decamp (18), drumming palps (14), elevated legs (9), embrace (24), extended legs (7), extended palps (12), flexed up abdomen (4), grapple and push (25), hook and push down legs (23), hunched legs (8), lift up and throw (26), lowered body (2), lunge (28), mounting and postmount behaviour (21), opened chelicerae (11), posturing (10), prod (20), raised body (1), rapid extend and retract legs (27), scraping palps (15), short skitter (17), skitter (16), vibrate palps (13). The contexts in which behaviours considered to be displays occurred are indicated in Table 1.

1. Raised body. **–** When raised, bodies were held higher than normal above the substrate (Fig. 9). The abdomen was normally elevated, but the anterior cephalothorax was usually held higher than the posterior.

2. Lowered body. **–** When lowered, the bodies were positioned close to substrate, with the abdomens almost parallel to the substrate (Fig. 10).

3. Creep. **–** When crept, bodies were lowered with legs I fully extended and often parallel to the substrate and to each other, with tibia dipping down a little. Palps were also extended (see Element 11, Position 2) (Fig. 11) and usually parallel to substrate.

4. Flexed up abdomen. **–** When flexed up, the abdomen was normally held c. 70° from the cephalothorax, with the anterior cephalothorax often held lower than the posterior (Fig. 12).

Figs. 4-6. (4) Male *C. umbratica* (front dorsal view), with blue-green (dorsal) and violet iridescence on the sides of femurs of legs I to IV, a line of iridescence on the dorsal abdomen from anterior to posterior, and a white line along each side of abdomen, which were joined at the anterior abdomen but discontinued at the posterior; (5) Female *C. umbratica* (front dorsal view). Females are generally less iridescent and have a shorter yet plump abdomen as compared to the slim and elongated abdomen of males; (6) The face of a juvenile *C. umbratica* (6a) lacks white hairs indicating a sexually matured male *C. umbratica* (6b), and black coloration on the tarsus of a palp (6c), a coloration prominent on an adult male's palps (see Fig. 4).

Table 1. Major elements of intraspecific behaviour (list alphabetically) of *Cosmophasis umbratica* and the types of interactions during which they usually occur. Male-female: behaviour performed by males during male-female interactions. Female-male: behaviour performed by females during male-female interactions. All interactions occur away from nests. + = occurred; × = did not occur.

	Male-female	Female-male	Male-male
Arched posturing	+	×	×
Bent posturing	×	+	+
Elevated posturing			
Position 1	×	×	×
Position 2	×	×	×
Extended posturing	+	×	×
Hunched posturing	×	+	+
Rapid extended and retracted posturing	×	×	+
Clash	×	×	+
Creep	+	×	×
Embrace	×	×	+
Grapple and push	×	×	+
Lift up and throw	×	×	+
Lunge	×	×	+
Short Skitter	×	×	+
Skitter	+	×	×
Drum palps	+	×	×
Scrape palps	+	×	+
Vibrate palps	+	×	+

5. *Bent abdomen.* – When bent, the abdomen was tilted about 30˚ to the right or left of the sagittal plane of the cephalothorax (Fig. 13). Sometimes the abdomen was also flexed up c. 30˚ when bent (Fig. 14).

6. Arched legs. - When legs I and II were arched, the side of the femur that faced the front angled at c. 45˚ to the vertical plane (perpendicular to sagittal plane). The femur of both legs were almost parallel to substrate, and both left and right pairs of legs I and II were at about 120˚ apart, resulting in an almost parallel or close positioning of legs I and II from both sides. With femur-patella and tibia-metatarsus joints slightly flexed on both legs I and II, the tarsi contacted the substrate (see Fig. 12).

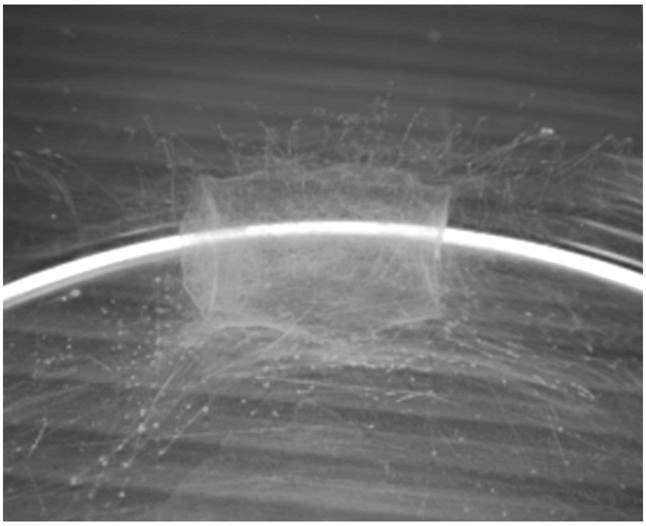


Fig. 7. A silken nest, consisting of a not so dense silken sheet covering a silken tube spun by male *C. umbratica* in a petri dish.

***7. Extended legs.* –** When extended, the femur-patella joints of legs I were slightly flexed and the joints distal to femur-patella were fully stretched and held almost parallel to substratum, with the tarsus angling down slightly at times (Fig. 11).

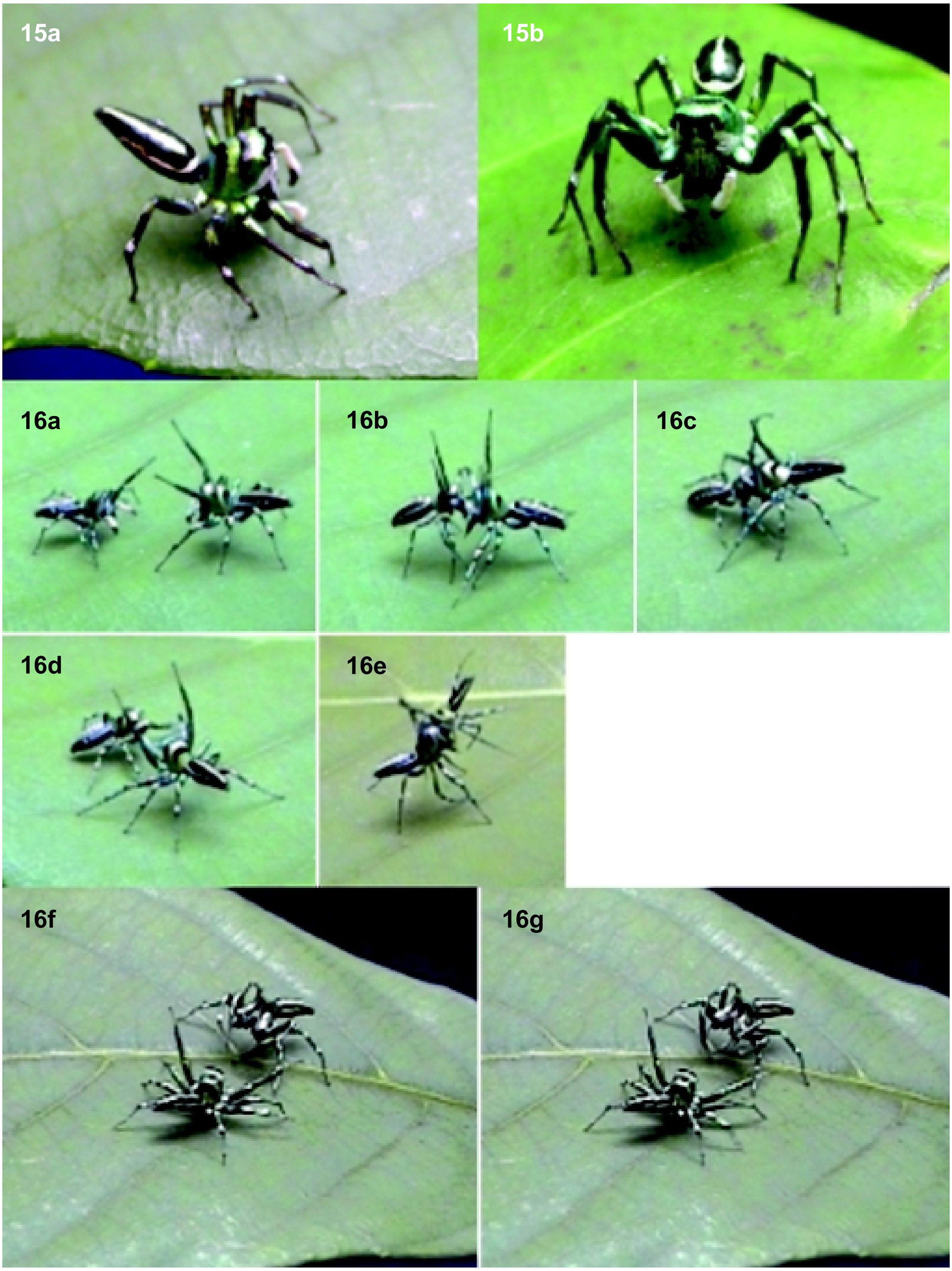
***8. Hunched legs.* –** When hunched, legs I and II were highly flexed at femur-patella and tibia-metatarsus joints, so that tarsi pointed down (leg I) and slightly inwards (leg II) (Fig. 15). Both legs I and II were held almost perpendicular to the sagittal plane of the body. The abdomen was usually bent, and sometimes also slightly raised (c. 30°) from the cephalothorax.

***9. Elevated legs.* –** Legs I were elevated, and two modal positions were discerned. In Position 1, the femur was held almost perpendicular to the substrate and close to the cephalothorax, with femur-patella slightly flexed and joints distal to femur-patella fully stretched, such that metatarsi and tarsi were held about 60˚ from substrate and about 30˚ from each other (Figs. 16a and 17). Position 2 differed from Position 1 because all joints were fully extended, and the stiff-looking legs I were almost perpendicular to substrate (pointing upwards vertically) and almost parallel to each other (see Figs. 16b, d).

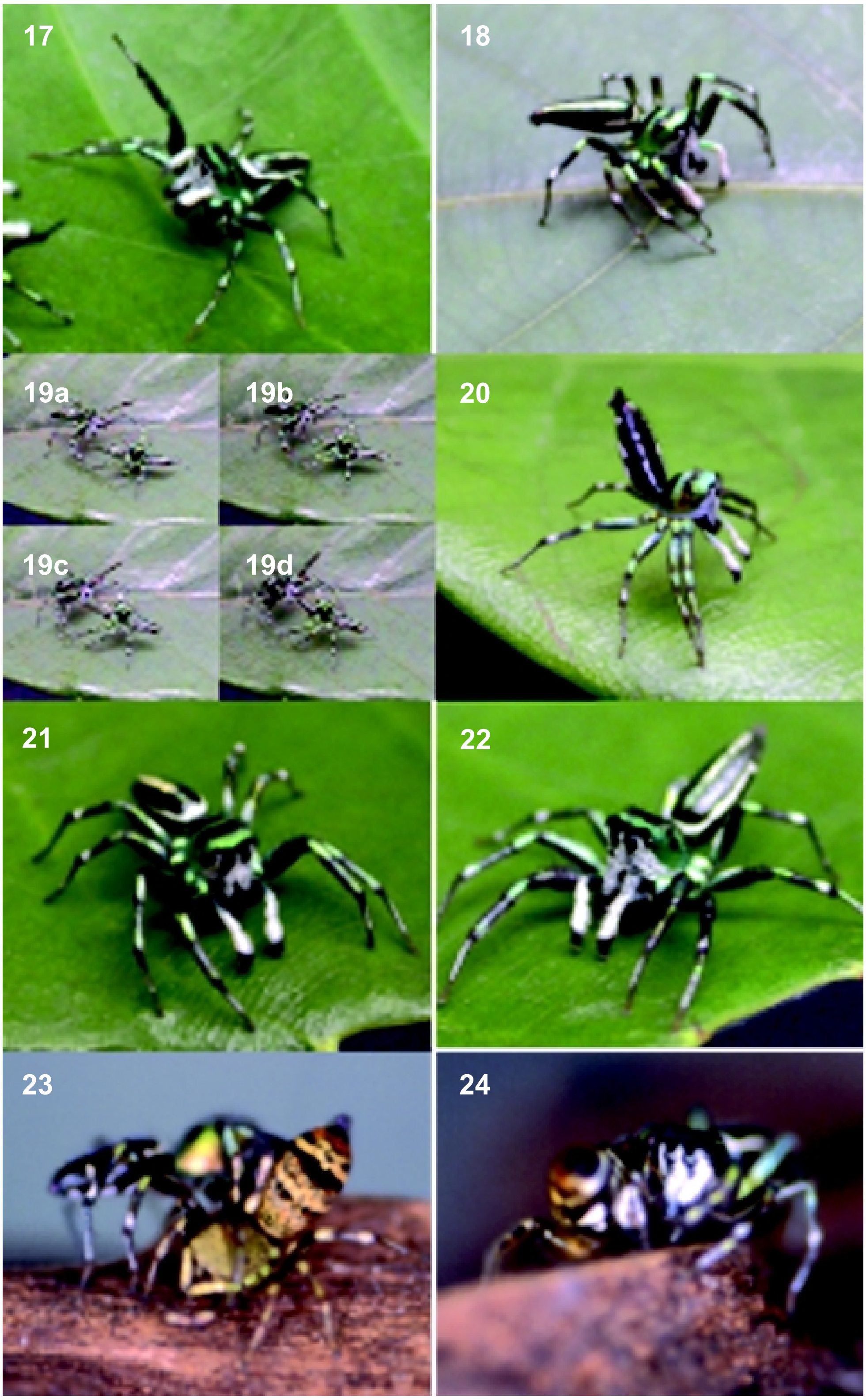
***10. Posturing.* –** The spider postured by standing or stepping as it held its stationary legs arched (arched posturing), bent (bent posturing), elevated (elevated posturing), extended (extended posturing), or hunched (hunched posturing).

***11. Opened chelicerae.* –** When chelicerae were held opened, the basal segments were held 30° - 90° apart. Fang extension was variable. When maximally extended, fangs pointed straight down as the maximum. In Position 1, basal segments

Figs. 8-14. (8) Male *C. umbratica* (facing right). Position its palps in front of its chelicerae during normal locomotion; (Insert) front view of *C. umbratica* using palps to cover its chelicerae; (9) Male *C. umbratica* (facing right). Raising the body with abdomen parallel to substratum; (10) Male *C. umbratica* facing right with body lowered; (11) Male *C. umbratica* (facing left) creeping towards a female facing right (partially hidden) with extended palps and extended legs that are almost parallel to substrate; (12) Male *C. umbratica* (front view) posturing with flexed up abdomen and extended palps (Position 2); (13) Male *C. umbratica* hunching and bending its abdomen to its left; (14) A side view of the agonistic display of male *C. umbratica* (facing left) hunching, raising and bending his abdomen to his right.



Figs. 15-16. (15a) Male *C. umbratica* (facing right) posturing with hunched legs and bent abdomen; (15b) Male *C. umbratica* (facing on-view) with hunched legs and abdomen not bent; (16a-f) Sequence of main events during agonistic interactions between two males: (16a) two males with elevated legs (Position 1); (16b) two males embracing each other (no pushing was observed) with legs I elevated (Position 2), chelicerae opened with fangs pointed downwards (Position 2), palps extended (Position 3), and body raised; (16c) the larger male (right) hooking and pushing the smaller male, with legs IV flexed at femur-patella-tibia such that body is raised, with posterior (abdomen) higher that the anterior (cephalothorax); (16d) the larger male chasing away the decamping male with elevated legs I (Position 2) and extended palps (Position 3); male (in background) in process of decamping; (16e) the larger male lifting up the smaller male after both were engaged in a hook and grapple; (16f-g) after a clash, males tend to quickly extend and retract legs (male in background).



Figs. 17-24. (17) Male *C. umbratica* posturing with elevated legs (Position 1) during agonistic interactions with another male (partially hidden); (18) Male *C. umbratica* in a hunched position with chelicerae opened and fangs showing a little (Position 1); (19a-d) Sequences before an embrace of two male *C. umbratica*, with chelicerae opened in Position 3: (19d) extension of palps (Position 3) were only prominent just before contact; (20) Male *C. umbratica* (facing right) posturing with flexed up abdomen and extended palps (Position 1); (21) Male *C. umbratica* with almost fully extended palps contacting the substrate; (22) A slightly flexed palps on contact with the surface during agonistic displays. Here the male has a slightly raised and bent abdomen; (23) Copulating position of *C. umbratica*, with the male's leg II (facing right) going over the female's cephalothorax (facing downwards); (24) Male *C. umbratica* (facing on-view) copulating with a female (facing inside). The female's abdomen was rotated about 30˚ and lifted slightly from its lowered body posture, so that access to the epigynum and engagement of palp will be faster and easier. During copulation the male always faces the opposition direction of the female, though this position may change as copulation proceeds, with the female failing in her attempt to pull away, or with males pushing slightly at the female.

were held about 30-60° apart, with fangs showing but not pointing downwards (Fig. 18). In Position 2, the basal segments were held about 30-60° apart, with fangs pointing down (see Figs. 19, 16b).

12. Extended palps. - When extended, the joints distal to femur-patella on palps were fully stretched, and three positions occurred. In Position 1, extended palps were held at c. 45˚ down from the horizontal plane of the cephalothorax (Fig. 20). When fully extended, palps were about parallel to the dorsal part of the flexed up abdomen. Sometimes both palps were parallel to each other. More often their tarsi converged somewhat, but without contact at both ends of the tarsi. In Position 2, fully extended palps were held parallel to substrate (see Fig. 12). Otherwise, Position 2 was similar to Position 1. In Position 3, the palps extended upwards, almost perpendicular to the substrate, and about 30˚ from each other (see Fig. 16b).

13. Vibrate palps. – When palps vibrated, they moved up and down together in matching phase. While they vibrated, they remained extended or they were slightly flexed (femur-tibia angled about 150˚). When vibrating palps, the highest position was when the femur was raised such that tibia were almost parallel to substrate (Element 12 Position 2). The lowest position was when femur was lowered such that tibia was c. 45˚ to the horizontal plane (Element 12 Position 1). Rate varied from 0.05 s to 0.2 s per cycle, and bout duration was usually about 1s.

14. Drumming with palps. – When palps drummed on the substrate, tarsi made contact (Figs. 21, 22). Palps were held slightly flexed (femur-patella-tibia angle about 120˚). Movement was at low amplitude (c. 10˚), and much variation in rate, duration and phasing was observed.

15. Scraping with palps. – When scraping, palps were held slightly flexed (femur-tibia angled about 120˚). The palp tarsi moved c. 1 mm across the substrate, maintaining contact with substrate, for ≤ 1 s. Phase matching between palps during scraping was not evident.

16. Skitter. – Skittering was somewhat similar to the stop-and-go gaits seen in normal locomotion, except that stepping was of shorter duration and route taken different. The spider spent less time moving (0.3-0.5 s) during zigzag (spider stepepd left or right for 0.3-0.5 s, halted for <0.3 s, then stepped in opposite direction for 0.3-0.5 s, halted for <0.3 s, and cycle repeated) and stop-and-go (spider stepped forward for 0.3-0.5 s, halted for <0.3 s, then stepped forward for 0.3-0.5 s, and cycle repeated) skittering as compared to normal locomotion. Arc skittering was less common compared to zigzag and stop-and-go skittering, and time taken to complete arc skittering was dependent on distance, which occurred in bouts lasting 0.4-1.4 s and covering distances ranging from 1 to 4 body lengths. During skittering, the male's abdomen often remained flexed up (c. 70˚). Spiders seldom bobbed their abdomens while skittering.

17. Short skittering. – Short skittering differs from skittering generally in the spider's posture during stepping and halting. When short skittering, the spider tended to remain stationary for about 0.4 s while legs were in a hunched position, and moved for about 0.2 – 0.4 s, at times maintaining their hunched posture even while moving. Routes taken mirror those of zigzag and stop-and-go skittering, except that distance covered between halts was shorter (<1 body length). Vibrating of palps during halts in short skittering was similar to that of males when posturing in front of females, with the exception of palps being more flexed (femur- tibia angle about 120˚) and never fully extended.

18. Decamp. – One spider decamped by either running or jumping away from the other spider (see Fig. 16d).

19. Block. – In an apparent attempt to prevent the female from running past, the male spider moved sideways so as to stay in front of the female. Blocking usually resembled a zig-zag skittering of short duration where the male skittered over the apparent decamping route of the female. However duration of blocking attempts by the male depended on locomotion and direction of the female's decamping.

20. Prod. – When the male decamped, the female chased after him, sometimes with her face intermittently coming into contact with the male's posterior abdomen.

21. Mounting and Postmount behaviour. – Upon contact and after creeping, the male used his extended legs I to tap the female's legs I. Next he proceeded to use legs I and II to tap the female's legs I and II. All this normally happened within c. 1s, with the female tapping back, before walking over the female. As the male walked over the female's cephalothorax, the female lowered her body. When the cephalothorax of the male was over the female's cephalothorax, the male then positioned himself either slightly to the left or slightly to the right of the female's body. He stroked with legs I on the female's abdomen on the same side as copulation (if male used right palp, then the right leg I stroked the right ventral side of the female's abdomen). Legs II were positioned over the female's abdomen, but did not stroke (Fig. 23). Slight movement of both of the male's palps could be seen during and after mounting, but details were not discerned. The female's abdomen was slightly raised and rotated 30˚- 60˚ to either the left or the right. Copulation (Fig. 24) started within 10 s after the male's first contact with the female.

22. Copulation. – Copulation ended when either spider decamped. In seven male-female interactions, a total of six separate copulations took place in 2 mating pairs. The males copulated with engaging of either one palp, or the engaging of one palp followed immediately by engaging of the other palp without the female decamping. Four separate copulations were recorded for one mating pair (the copulation durations were: (1) 25 s, one engagement (3 separate copulations); (2) 21.5 min, two engagements, 90 s, right palp, followed by 20 min left palp (1 separate copulation). Two separate copulations were observed for the other mating pair (the copulation durations were: (1) 10 min, one engagement; (2)

35 min, one engagement). The male and female faced opposite directions during copulation, with the right palp engaged under the right side of the female.

23. Hook and push down legs. – One spider used its legs I to hook and push down a leg of the other spider (the 'opponent') following an embrace (see Element 24). The legs used for hooking were held with the femur angled up and with both patella-tibia and tibia-metatarsus joint slightly flexed (tarsi pointed to the side). Contact with the other spider's legs was maximal along the tibia and metatarsus during attempts to hook each other. Initially each male appeared to try to raise its own legs I over the other's, and the male that succeeded in hooking its opponent (see Fig. 16c) will then push its opponent's legs 1 down.

24. Embrace. – When spiders embraced, both spiders' legs I were elevated in Position 2 with chelicerae and palps coming into contact (see Fig. 16b). Chelicerae were opened (Position 2) and palps were extended (Position 3). The spiders' bodies were raised, with the anterior part of the abdomen higher than the posterior. The duration of an embrace is about 0.5 – 1.0 s.

25. Grapple and push. – When spiders grappled and pushed (one spider forcing another spider backwards) each other, the spiders' legs I were in hooked position, chelicerae were opened (Position 2) and palps extended (Position 3), and faces tightly pressed together (see Fig. 16c). Bodies were usually raised. Femur-patella joints of legs III and legs IV were slightly flexed (more pronounced in legs IV), such that the posterior end of the spider was higher than the anterior. Legs II were almost fully extended, perpendicular to the sagittal plane of the body and touching the ground.

26. Lift up and throw. – With body positioned as when grappling and pushing, one spider (usually the larger male) raised its body and lifted up the other spider. The spider that did the lifting had the anterior part of the cephalothorax much higher than the posterior end (Fig. 16e). When one spider was lifted to the maximum height reached (all legs lost contact with substrate), the other spider suddenly released its legs I hook posture (see Element 23), such that it landed awkwardly upon contact with substrate, at times upending itself.

27. Rapid extend & retract legs. – When extending and retracting, the femur-patella and tibia-metatarsus joints of legs I and II were flexed at 50-70˚, with the whole process lasting < 1 s, and one complete cycle (one extension and retraction of one side of legs I and II) at c. 0.08s. During extension phase, the femur-patella joints were slightly relaxed, such that legs I and II reached forward and away from body as both tarsi made contact and pointed downwards. During the retracting phase, both legs I and II had the femur-patella joints flexed and patella raised closer to body, such that both tarsi (not necessarily touching) were still pointing downwards but held further from substrate. Both pairs of left and right legs extend and retract in opposite direction (with femur held close to the face, segments distal to femur were held extended) such that tarsi pointed forward and diverged. Femur-patella joints of palps flexed at 85-90˚, such that palps made contact with legs I at the tarsi during extending and retracting (see Figs. 16f-g).

28. Lunge. – One or both spiders suddenly lunged forward or towards the other spider by raising the posterior end of its body and extending its rear legs, such that the posterior end of the spider is higher than the anterior end of the cephalothorax, with legs 1 elevated (Position 2). Distance between both spiders is about 1 to 1.5 body lengths (see Fig. 16a).

29. Clash. – When one or both spiders lunged towards the other or towards each other with elevated legs (Position 2), both spiders came into contact with leg I tarsi touching, resulting in either one or both spiders being pushed back.

Organization of behaviour

Inter- and intrasexual interactions (staged on leaves) began when one spider started to display (definition of display in male-female interactions: flexed-up abdomen, vibrating of palps and arched legs; definition of display in male-male interactions: hunched legs) to the other spider. After the initial display, observation of an interaction continued until one spider decamped, with the other spider failing to watch and follow, both spiders decamped and either one or both jumped off, or an interaction failed to occur within 30 min, after starting a test (i.e. both spiders placed together on the leaf). There was an interaction in 16 observations (male-male, 9 of 12; male-female, 7 of 12). Male-male interactions were much shorter than male-female interactions, with male-male agonistic interactions lasting from 0.15-0.5 min and male-female interactions lasting 0.15-10 min (time *in copula* excluded). In male-female interactions, females frequently decamped as soon as the male came into view, but the decamped female usually returned several seconds later. Decamping and returning by females and persistent courtship by males was repeated numerous times in both successful and unsuccessful male-female interactions. Cannibalism was never observed.

The male-female interactions

Skittering was the dominant element of the male's behaviour during male-female interactions. Females usually decamped immediately upon coming into view. There were variations in distance during male and female interactions, from four body lengths to ten body lengths. When the male initially faced the female, the male's behaviour became noticeably more 'excited'. He faced the female directly with body raised, abdomen flexed up, legs arched and palps vibrating. If the female did not decamp and instead faced the male, the male then proceeded to skitter with flexed up abdomen and vibrating its palps. Many skittering events, however, resulted in females decamping as males approached. Males however continued to skitter towards the on-looking female if it did not decamp or turn away. Sometimes the male drummed and scraped palps while he postured with flexed up abdomen and arched legs after the female had decamped or had turned away from him. After the female decamped, the male drummed or scraped the substrate only if the female was still in close proximity (about 5 body lengths or less away) and within sight of the male.

On some occasions the female bent her abdomen or prodded the male. In a few cases, when the female did not decamp after the male had appeared, she bent her abdomen, and the male either decamped immediately or only after persistent prodding by the female. Occasionally decamped females attempted to run past the male while the males were posturing or in the process of skittering. In these instances, the male normally attempted to block the female by skittering sideways to block her path. Males were never observed to bend their abdomens in any interactions with females, and on few occasions did it follow any females that had decamped or after an unsuccessful blocking.

If the female did not decamp, the male postured, skittered and crept towards her with legs I extended, and then mounted. Females always lowered their body prior to mounting and during copulation females might attempt to pull away, though this was seldom observed. Copulation effectively ended with females' successful attempt to pull away from the male. Duration of copulation was highly variable, but was noticeably longer in copulations involving simultaneous engagements of left and then right palps (see Element 22 Copulation on data on simultaneous palp engagements).

The male-male interactions

Male-male agonistic interactions began when one or both spiders started to display (raised bodies, hunched legs, and bent abdomens that were sometimes raised) at about 10-15 cm away. Both males then slowly short skittered towards each other with opened chelicerae (Position 1), vibrating their palps during pauses until they were about 2-3 body lengths apart. One or both spiders then lunged forward with legs elevated (Position 1), chelicerae opened (Position 2) and palps extended (Position 3). After a clash (see Element 29), majority of spiders that were pushed back eventually decamped, and the other spider chased after the decamping spider. If no spiders decamped, what proceeded next depended on size differences between the two males.

On two occasions when a smaller male did not decamp after a clash, both males then approached each other with elevated legs (Position 1), opened chelicerae (Position 2) and extended palps (Position 3). Both males attempted to hook and push down each other's legs, grappled and pushed each other, and eventually the larger male lifted up the smaller male, held it up for about 2 s, and then threw the smaller male, after which the smaller male decamped while the larger male chased it. The duration of conspecific male interactions was generally shorter between males of different sizes than those of similar sizes.

When the two males were similar in size, the clash often ended with neither decamping. In these instances, both males then proceeded to extend and retract their legs rapidly. The two males always both performed rapid extending and retracting of legs, but not necessarily simultaneously. While one male was rapidly extending and retracting his legs, the other male sometimes scraped both palps on the substrate. Both spiders often would then raise their bodies as a preliminary to embracing, and then proceeded to elevate their legs (Position 2) so as to hook and push down each other's legs. Both spiders then grappled and pushed, with chelicerae opened (Position 2) and palps extended (Position 3). The duration of hooking and pushing legs down, grappling and pushing was about 2 s. Eventually one male succeeded in pushing back the other male, often proceeded by a chase after a decamp.

DISCUSSION

The size and complexity of the display repertoire of *Cosmophasis umbratica* from Singapore resemble that known for other salticids' intra-specific (i.e. male-male and male-female) interactions that have been studied in detail (e.g. Jackson, 1980, 1986a, 1986b; Jackson & Macnab, 1989; Jackson & Whitehouse, 1989; Li et al., 2002). In the male-male and male-female interactions of *C. umbratica*, a total of 18 'major displays' (see Moynihan, 1970) were performed away from nests: posturing with legs (1) arched, (2-3) elevated at Position 1 and 2, (4) extended, (5) hunched, (6) rapid extended and retracted, (7) clash head on, (8) creep, (9) embrace, (10) grapple and push, (11) lift up and throw, (12) lunge forward, (13) abdomen bent, (14) skitter towards a female, (15) short skittered towards a male, (16) drum palps, (17) scrape palps, and (18) vibrate palps. This is much more than the number of major displays away from nests estimated for *Epeus* from Singapore (8) (Jackson, 1988a), *Cobanus mandibularis* from New Zealand (9) (Jackson, 1989), *Cyllobelus rufopictus* from Kenya (12) (Jackson, 1986a), and *Cosmophasis micarioides* from Australia (13) (Jackson, 1986b). It is comparable to the number of major display away from nests estimated for *Thorellia ensifera* from Singapore (19) (Jackson & Whitehouse, 1989), *Jacksonoides queenslandica* (20) (Jackson, 1988b) and *Tauala lepidus* (21) (Jackson 1988c) from Australia, and *Corythalia canosa* (22) from America (Jackson & Macnab, 1989), but considerably fewer than those for *Bavia aericeps* from Australia (32) (Jackson, 1986c), *Holoplatys* from New Zealand (27) (Jackson & Harding, 1982), and *Phidippus johnsoni* (24) from America (Jackson, 1977).

The courtship and agonistic (male-male) displays of *C. umbratica* (Singapore) and *C. micarioides* (Queensland, Australia) (see Jackson, 1986b) away from nests are quite similar, though some differences exist. Skittering, as well as vibrating of palps and arched posture are the dominant courtship behaviours in both *Cosmophasis* species. When a female tried to decamp, both *C. micariodes* and *C. umbratica* males attempted to block her departure. If unsuccessful, only *C. umbratica* males continued scrapping and drumming the palps on the substrate, maintaining its courtship posture (of arched legs and flexed up abdomen). This courtship persistence of *C. umbratica* males, together with the drumming and scrapping of palps, suggests that vibratory courtship may be involved not only when males court females away from nest, but also when at nest.

Courtship versatility is common among salticid species (e.g. Jackson, 1980, 1986a; Jackson & Whitehouse, 1989; see also Jackson, 1986d), with vibratory courtship usually prevalent when a male courts a female at nest, and visual courtship while away from nest. Jackson (1986b) suggested that the act of skittering in *C. micarioides*, regardless of location, could have a dual function: as a visual courtship (primarily away from nest), and as a vibratory courtship (away and at nest). As plants are ideal substrate for transmitting vibratory signals (see Miklas et al, 2001; see also Rovner & Barth, 1981), vibrations from unique movements of males during courtship away from nests could indeed be transmitted through the leaves to the courted female, thus functioning as both visual (if females are within sight) and vibratory courtship. Examples of movements with such possibilities are zigzag dancing in salticids such as *Epeus* (see Jackson, 1988a), *T. lepidus* (see Jackson 1988c), *T. ensifera* (see Jackson & Whitehouse, 1989) and in primitive salticids *Cyrba algerina* (see Jackson & Hallas, 1986a) and *Cyrba ocellata* (see Jackson, 1990); juddering in *C. rufopictus* (see Jackson, 1986e), the successive approaches and withdrawals and jerking in the primitive salticid *Asemonea tenuipes* (see Jackson & Macnab, 1991) and on-erect tapping in *C. canosa* (see Jackson & Macnab, 1989). Another primitive jumping spider genus, *Portia* (Jackson & Hallas, 1986b) is known to use both vibratory and visual displays when interacting with conspecifics on webs, and use only visual displays when away from webs. Large tropical wandering spiders, *Cupiennius salei* (Araneae: Ctenidae) also engage in pre-copulatory communication by sending mainly vibrations through vertical movements of abdomens and scratching and drumming of palps on a leaf (Barth, 1993; Rovner & Barth, 1981). In wolf spiders, *Hygrolycosa rubrofasciata* females are known to respond faster to males with higher drumming rate and volume (Parri et al, 1997). In *C. umbratica*, the dominant male display elements of skittering, vibrating of palps and legs arching could probably serve as both vibratory and visual signals, since *C. umbratica* is observed to be a leaf-dweller and is also found on leafs of plants exposed to sunlight in the morning and evening. Though drumming and scraping on leaves in *C. umbratica* may indicate the possible web-building ancestry of the Salticidae, further observations are needed to investigate whether vibratory communications are involved in both *C. umbratica* inter- and intrasexual interactions (on the nests and near the vicinity of a female's nest).

The agonistic male interaction of *C. umbratica* is observed to generally follow a sequence but also exhibit variation in confrontations when dealing with competitors of different sizes. Conspecific male encounters generally occur in a temporal sequence (visual to tactile), progression of proximity (far to near), increasing energy expenditure and risk of injury (low to high). Variation in male agonistic behaviour may provide an avenue for both males to visually assess each other's physical strength, so as to avoid risk when conspecific competitors are of different sizes. In *Bavia aericeps* (see Jackson, 1986c), males postured to each other when within sight, and engagements escalated to physical contact, sometimes with one spider (always the smaller spider) being upended. In *C. umbratica*, smaller males are always the ones that are lifted up and thrown. Further examination, however, is needed to investigate variations in body size as possible factors that may influence male-male contest outcomes. In general, the threat displays of *C. umbratica* are similar to other salticids during conspecific male agonistic interactions: increase in apparent body size (elevated and hunched legs), weapons display (opened chelicerae), show of strength (hook, embrace, grapple and push, lift up and throw and clash) and movements intended for aggressiveness (lunge).

It is interesting that *C. umbratica* exhibits strong sexual colour dimorphism, where the iridescence coloration only prevails in adult males, and not in juveniles or females. The ornate colorations of *C. micarioides* (Jackson 1986b), *Thiania* (Jackson 1986f) and *Brettus cingulatus* (Jackson & Hallas, 1986a) were suggested to aid in concealment rather than intersexual selection in the spiders' natural surroundings. However, the possibility of a eucryptic nature in the colours of *C. umbratica* rather than colours derived from intersexual selection is unlikely, as both adult males and females have similar foraging niches (i.e. time of day and light microhabitat), and if the iridescent coloration was eucryptic, females may be at a greater disadvantage of being less cryptic than males. Moreover, the usually inactive and sudden rapid movements of *Thiania* and *B. cingulatus* during normal locomotion, coupled with their iridescence natures, is suggested to resemble iridescent reflections from sunlight penetrating the canopy and striking drops of water, providing effective camouflage in their natural environments. In contrast, both *C. micarioides* and *C. umbratica* are also highly active ornate spiders, prefer open habitats exposed to direct sunlight, with normal locomotion mainly characterized by rapid stop-and-go gaits and bobbing of abdomen. Therefore, the acquisition of bright coloration and high iridescence in sexually matured males, with both sexes' preference for niches exposed to open sunlight, coupled with high visual acuity and colour vision, suggests that *C. umbratica* (and possibly *C. micariodes*) may be a result of intersexual selection, and is therefore an ideal model for study of female mate choice and male-male competition studies, although the possibility of the coloration due to both intersexual selection and an eucryptic nature cannot be ruled out.

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