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# INTRASPECIFIC INTERACTIONS *ASEMONEA TENUIPES*, A LYSSOMANINE JUMPING SPIDER (ARANEAE: SALTICIDAE) FROM SINGAPORE

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***ABSTRACT.*** **–** The display and courtship behaviour of a Singapore population of *Asemonea tenuipes* (O. P. –Cambridge, 1869) was studied. This is an iridescent lyssomanine jumping spider and the present study is the first to be carried out on this species under a full-spectrum light. A previous study was carried out on a population of this same species from Sri Lanka, but under light conditions lacking of UV. Findings from the present and the earlier study are, on the whole similar, but there are also some differences that may represent interpopulation variation or may be a consequence of the different lighting conditions. *A. tenuipes* is most often found on the underside of leaves in mangroves. Colours are sexually dimorphic. Males have bluish-purple iridescence and orange colour on the dorsal abdomen, while females are generally a pale whitish-green. Twenty-five major displays are described. While the intraspecific display repertoire of Singapore *A. tenuipes* was similar to the Sri Lanka population, the context (male-female, male-male and female-female interactions) in which certain displays were performed differed between the two populations. In addition, although zigzag dancing was not observed in the Sri Lankan population, a variation of this display was observed in the Singapore *A. tenuipes*. Rotated posturing is an aberrant display, observed in *A. tenuipes* but not other salticid species. Whether this display might function to advertise honestly male quality is discussed. One of the most interesting findings is that males of the Singapore *A. tenuipes* males often perform prolonged display posturing even when their anterior-median eyes are not aligned with the female. The anterior-median eyes of salticids are the part of the visual system responsible for seeing detail based on high spatial acuity. That *A. tenuipes* males display in the absence of detail from these eyes suggests that there is unusually strong reliance on chemical cues by this species during courtship.

***KEY WORDS.*** **–** Spider, *Asemonea tenuipes*, courtship, agonistic display, Lyssomaninae.

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## INTRODUCTION

Jumping spiders (Araneae, Salticidae) are the most diverse spider family with approximately 5,237 named species from 567 genera (Platnick, 2009). Most salticid species appear to be cursorial hunters that generally adopt stalk-and-leap predatory sequences rather than building webs to ensnare their prey (Forster, 1982a, b). Salticids have complex eyes and vision based on high spatial acuity (Land, 1969, 1985; Blest et al. 1990; Land & Nilsson, 2002) and, owing to their exceptional eyesight, salticids have distinctive vision-mediated predatory routines (Jackson & Pollard, 1996; Li & Jackson, 1996) and elaborate vision-mediated courtship and threat displays (Peckham & Peckham, 1889, 1890, 1894; Crane, 1949a, b; Drees, 1952; Forster, 1982a; Jackson, 1982).

The salticid's two anterior median (principal) eyes are especially large and they face forward. It is these eyes that are primarily responsible for seeing spatial detail, giving salticids remarkable ability to discriminate between classes of objects such as prey, mate, and conspecific of same sex (Foster, 1982a; Harland & Jackson, 2000, 2002), and the secondary (lateral and posterior) eyes primarily aid detection of long range movement (Land, 1985). The anterior-median eyes are also responsible for colour vision, with their retinas having, besides photoreceptors maximally sensitive to light in the range visible to the human eye, photoreceptors maximally sensitive to UV (Land, 1969; DeVoe, 1975; Yamashita & Tateda, 1976; Peaslee & Wilson, 1989; Nakamura & Yamashita, 2000). Recent experimental evidence has shown that many salticids reflect UV light (Lim & Li, 2006a; Li et al., 2008a), and that UV cues are not only necessary for agonistic (Lim & Li, 2006b) and courtship displays (Lim et al., 2007) but also important in female mate choice (Li et al., 2008b; Lim et al., 2008). Although this implies that the intraspecific interactions of salticids should be observed under full-spectrum light, the majority of previous studies have been performed under light conditions without UV wavelength.

Jackson & Blest (1982) proposed that salticids might have evolved from web-spinning spiders that had poor eyesight and that the unique, high-acuity visual system of salticids evolved in conjunction with ancestral web-building spiders becoming specialized spider-eating predators that used aggressive mimicry in the context of invading the webs of a wide range of other spiders with diverse kinds of webs. This hypothesis, which was suggested by an initial study of *Portia*, a genus from the salticid subfamily Spartaeinae, led to studies on other salticids, especially other spartaeine genera (see Su et al., 2007). However, comparative data from a wider range of salticids is critically important for evaluating this hypothesis.

The Spartaeinae appears to be a basal branch in salticid phylogeny (Su et al., 2007), but there is another basal subfamily (the Lyssomaninae) that has been largely neglected in the literature. This subfamily includes about 120 species in seven genera, and they are found in tropical and subtropical regions of the New World (*Chinoscopus* and *Lyssomanes*) and the Old World genera (*Asemonea*, *Goleba*, *Macopaeus*, *Onomastus* and *Pandisus*) (Platnick, 2009). Lyssomanine eyes have unusual characteristics, consistent with this subfamily having branched off early branching in salticid phylogeny (Blest, 1983, 1985; Blest & Sigmund, 1984; Su et al., 2007). However, details of lyssomanine behaviour are available for only 10 species from four genera (Crane, 1949a, b; Jackson & Hallas, 1986; Jackson, 1990; Jackson & Macnab, 1991).

In this study, we examined the intraspecific interactions of *Asemonea tenuipes* (O. P. – Cambridge, 1869), a lyssomanine species known from tropical Asia (specifically Andaman Islands, Burma, India, Sri Lanka, Thailand and Singapore; Murphy & Murphy, 2000; Platnick, 2009). This species is of particular interest because the males have iridescent markings. The only previous behavioural study on this species was based on a population from Peradeniya in Sri Lanka (Jackson & Macnab, 1991). Our study is different because we consider a different population (Singapore) and also because we consider, for the first time, the intraspecific interactions of a lyssomanine species under a full-spectrum light.

## METHODS

***Collection and maintenance of spiders.*** **–** Our field site was mangroves at Lim Chu Kang mangroves in Singapore. Our laboratory observations were based on 143 individuals of *Asemonea tenuipes* (62 males and 81 females) collected in the field site (all collecting was in the morning, 0700–1000 hrs). The spiders collected were subsequently kept individually in cylindrical cages (diameter: 4.5 cm; height: 6.0 cm) in a controlled-environment laboratory (80–85% RH; 25 ± 1°C; light regime 12 hrs:12 hrs, lights switched on at 0800 hrs). Spiders were fed five fruit flies (*Drosophila melanogaster*) once a week. Testing procedure and terminology were similar to those in earlier studies of salticids (Jackson & Hallas, 1986b). These included the convention that expressions such as "usually" or "generally," "sometimes" or "occasionally," and "infrequently" or "rarely" were used to indicate frequencies of occurrence of >80%, 20–80%, or <20%, respectively. Voucher specimens have been deposited in the Raffles Museum of Biodiversity Research (RMBR), National University of Singapore.

***Inter- and intrasexual interactions.*** **–** Whenever intraspecific interactions of *A. tenuipes* were observed, we used a fresh leaf (Simpoh Air, *Dillenia suffructicosa;* length 24 ± 3 cm; width 13 ± 3 cm). The leaf was clamped to a stand and held horizontally 25 cm above a table top. Two individuals (a pair of males, a pair of females or one male and one female) were introduced onto the leaf at opposing ends (which spider introduced first decided at random. All interactions began on the adaxial surface of the leaf but before interactions began, individuals were first placed on opposite sides of the leaf for acclimatization to the experimental set-up (duration: 3 min). Subsequently, the individual on the abaxial surface was coaxed, by gently prodding, to the adaxial surface of the leaf to facilitate the start of interactions. As interactions never started until a few minutes after the prodding event, we considered the spiders that were originally on the abaxial surface to have had sufficient time to acclimatize to the other side of the leaf. Our procedure allowed us to make detailed and complete observations of progression from behaviour that occurred at a distance to behaviour that occurred while closer and the contact.

The leaf set-up we adopted was similar to that used in the previous study on *A. tenuipes* from Sri Lanka (Jackson & Macnab, 1991), but lighting conditions were different. In the earlier study, normal florescent lighting was used without UV. However, we used an arrangement of 10 equi-spaced Voltarc Ultra Light tubes (110W each) held 130 cm above the table was used to provide full-spectrum illumination (300–700 nm) during observations. The rationale for this was recent research (Lim & Li, 2006b) showing that the presence of ultraviolet light (300–400 nm) is important for enabling salticids to use UV signals. A total of 36 males and 50 females were used for these staged encounters. No male and no female spider were used more than twice (firstly in an intrasexual encounter and, subsequently, in an intersexual encounter). There was a rest period of at least three days between the two tests using any one spider was allowed before a spider was reused in a different test. All inter- and intrasexual interactions were video recorded and the video recordings were used for thorough observation of behavioural elements and determination of intraspecific interaction duration, copulation duration and palp insertion duration via video playback.

***Organization of behaviour.*** **–** Behavioural patterns occurring during intrasexual interactions were categorized and then further subdivided into stages. On this basis, increasing intensity of interactions could be discerned. *Watch* indicates the start of an interaction and the spider remains stationary when this occurs. *Distant displays* indicate periods during which the spider postures with one or a combination of behavioural elements: i.e. a raised body, flexed/bent abdomen (mostly for males) or leg postures (hunched and arched-out) when it is far away (more than 8 cm) from the other spider. The spider does not advance while it postures. *Approach* indicates periods when the spider moves towards the other spider, with or without concurrent displays. *Close proximity displays* occur only after *approach*. It is similar to *distant displaying* but also includes zigzag dancing and propulsive displays (long leap, strike) that did not result in contact. *Contact* refers to propulsive displays that resulted in the collision of spiders. Stage 1: *watch* and *distant displays*; Stage 2: a*pproach*; Stage 3: c*lose-proximity displays* and Stage 4: c*ontact*. We interpret progression from lower to higher stages as the spiders expressing successively higher levels of aggressiveness.

For male-female interactions, these categories are slightly modified and there are additional categories. *Close proximity displays* in male-female interactions refer to the earlier defined displays performed by males during male-male interactions and also includes rotated posturing, zigzag dance and side switching (alternating between two sides of the leaf). *Premount tap* refers to the male tapping the female with his legs as he attempts to mount the female. These categories were used to construct flow charts for female-female, male-male and male-female interactions.

## OBSERVATIONS

***Habitat.* –** *Asemonea tenuipes* was found in peripheral vegetation, especially on the undersides of the leaves of two common mangrove trees *Brugeria* and *Avicennia*. The mangrove environment was characterized by a high canopy cover and small gaps in the canopy that allowed patches of direct sunlight.

***Morphology.* –** *Asemonea tenuipes* is a small salticid (body length: adult male 4–5 mm; adult female ca. 4–6 mm). Sexual colour dimorphism is pronounced. Males were brightly coloured, they had stocky red palps (Figs. 1, 2) and the anterior portions of the male's abdomen had an iridescent dark bluish purple band covered (Fig. 5). This band seemed to be without pigment, colour coming instead from iridescence. The posterior portion of the male's abdomen had an orange band (covered by orange and brown pigmented scales) with a black tinged tip (Fig. 6).

The male had two types of scales, granular and clear. Clear scales were shiny and usually iridescent. The characteristic colour of granular scales came from pigments. The male's iridescent scales were transparent under light transmission microscopy and they were highly reflective under incident light.

Females were generally pale yellow in colouration (entire body), with greenish blue or brown spots on the abdomen (Figs. 3, 4). The female had short spinnerets, but the male's spinnerets were black and distinctive; the posterior pair being elongate and having curled terminal articles. The male's abdomen was slimmer than the female's, but the legs of both sexes were pale-yellow, long and slender. Sub-adult males (i.e. the instar one molt before maturity) resembled adult females and they acquired their striking colouration only after they molted and reached sexual maturity.

***Locomotion.* –** Like most salticids, *A. tenuipes* walked in a stop-and-go gait (usually moving 10–40 mm before pausing). In general, our observations of locomotion for the Singapore *A. tenuipes* resembled earlier observations on the Sri Lankan *A. tenuipes* (Jackson & Macnab, 1991). The Sri Lankan *A. tenuipes* males often flexed their abdomens up while stepping and during pauses between stepping bouts, and bobbed their abdomens during, or immediately after, each bout of stepping. For the Singapore *A. tenuipes*, bobbing of the abdomen was observed in all males but the tendency to bob during or immediately after each bout of stepping was not very pronounced. Bobbing, when it occurred, had the appearance of slow deliberate flexing down then up (0.5–1s; 10–20°) of the abdomen within the sagittal plane. Bobbing occurred regardless of whether or not the spider's abdomen was flexed up.

Males and females of the Singapore *A. tenuipes* behaved differently, with the female's gait being more rapid stop-and-go and based longer stepping distance up to 90 mm between pauses. Females were not observed to bob their abdomens (i.e. they generally kept their abdomens parallel to the substrate).

Spiders held their palps in front of the faces, thereby partially (females) or entirely (males) hiding their chelicerae. Palps were never observed to be fully extended or erected during normal locomotion. While at rest, palps were usually positioned in close proximity to each other but not touching the substrate. During normal locomotion, palps were sometimes waved (duration about 1s, moving up and down in matching phase).

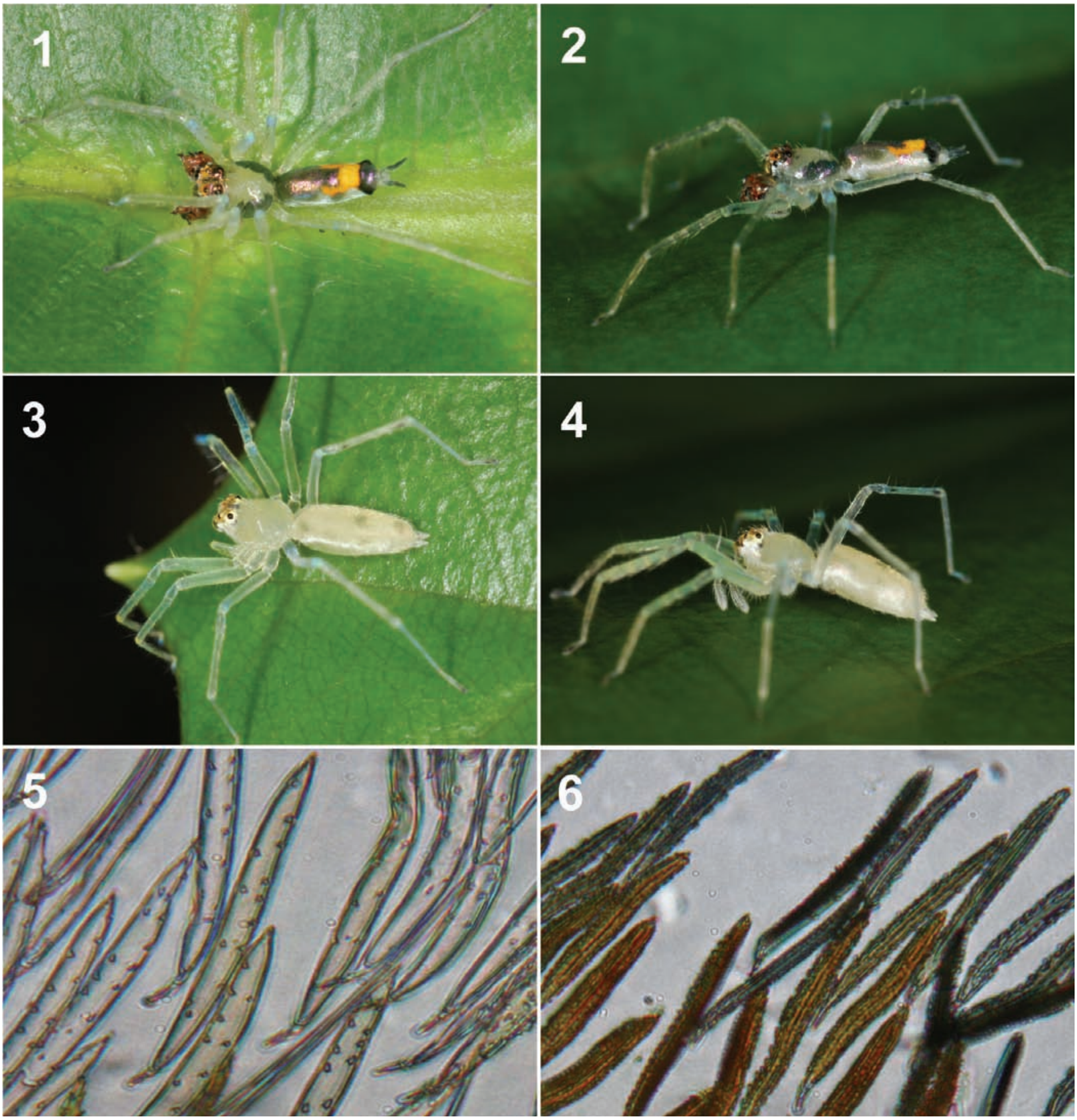
## RESULTS

***Behavioural elements.* –** Inter- and intrasexual interactions staged on leaves began when one spider "saw" another spider (definition: fixated the gaze of the anterior median eyes on another spider). Interactions ended when at least one spider decamped (Fig. 7) and the other spider failed to watch and follow. If no interaction took place within 30 min, the test was terminated and considered void.

Twenty five major elements of behaviour were observed (Table 1): (1) arched-forward legs (Fig. 8); (2) arched-out legs (Fig. 9); (3) charge; (4) elevated legs; (5) flexed up, flexed down, and bent abdomen (Figs. 10–12); (6) hunched legs; (7) jerk; (8) long leap; (9) lunge; (10) mounting; (11)

postmount tap with legs; (12) posturing; (13) premount tap with legs; (14) propulsive displays; (15) raised cephalothorax; (16) raised and lowered body (Figs. 13, 14); (17) rotate abdomen; (18) rotate cephalothorax; (19) rotated posturing; (20) scrape with palps; (21) strike; (22) stroke; (23) truncated leap; (24) waving of elevated legs; and (25) zigzag dance. For the contexts in which displays occurred, see Table 2.

***General trends during intraspecific interactions.* –** Male-male and female-female interactions were much shorter than male-female interactions, with male-male agonistic interactions (18 pairs) lasting up to 4.65 min, female-female (25 pairs) lasting up to 5.48 min and male-female (37 pairs) lasting up to 21 min (time *in copula* excluded; Table 3). Median male-male interaction duration was two times longer



Figs. 1–6. Adult *Asemonea tenuipes* male and female as well as scales from adult male. Male *A. tenuipes* (1) (dorsal view) possess a bluish-purple iridescence and orange colour on the dorsal abdomen with the former hue also on the lateral carapace (2) (lateral view) with distinctive reddish-brown enlarged palps. Female *A. tenuipes* (3) (dorsal view) are generally paler in colouration (whitish-green) and (4) possess a short and plump abdomen in contrast to the slim and elongated abdomen of males. (5) Scales were gently removed from the spider with a sticky tape and placed on a glass slide for viewing under light microscope: 40× magnification scales on the bluish-purple region of the male anterior dorsal abdomen. The scales are translucent. (6) Light microscope: 40× magnification scales on the orange region of the male posterior dorsal abdomen.

Table 1. Elements of behaviour (listed alphabetically) during intraspecific interactions of Singapore *Asemonea tenuipes* (adapted from Jackson & Macnab, 1991).

| No. | Element | Description |
|---|---|---|
| 1 | Raised cephalothorax | A raised cephalothorax was held higher than normal above the substrate; the anterior end of cephalothorax was often held higher than the posterior. |
| 2 | Flexed up, flexed down, and bent abdomen | From the cephalothorax, the abdomen was held down c. 20° (flexed down, Fig. 10), tilted up 20–80º (flexed up, Fig. 11), or 20° to either side (bent, Fig. 12). Often, A bent abdomen was also flexed down or flexed up. Bent abdomens usually were also lowered. The cephalothorax was always raised when the abdomen was flexed down. |
| 3 | Raised and lowered body | A lowered body was held near or on the substrate (Fig. 13). A raised body was held higher than normal above the substrate, with the anterior cephalothorax was occasionally held higher than the posterior. The abdomen was held about parallel to the substrate (Fig. 14). |
| 4 | Elevated legs | Erect and semi-erect are referred to jointly as elevated legs. Erect legs appeared stiff since all joints were fully extended than in semi-erect legs. Only legs I alone were held erect. Two modal positions were observed. *Position 1*. Legs were fully extended forward about parallel to the substrate and to each other. In Position 1, legs were always erect. *Position 2*. Legs extended 20–45° to the side and 10–45° up. In Position 2, legs were either erect or semi-erect. |
| 5 | Waving of elevated legs | Elevated legs were waved up and down in matching-phase 20–60° at 1–3/s (femoral movement; no alteration of femur-patella joints). Legs were held in *Position 1* or *Position 2* while elevated waving. |
| 6 | Hunched legs | Hunched legs (I, or I & II) were held in a plane perpendicular to the sagittal plane of the body or as much as 45° forward (Fig. 20). They were highly flexed at the femur-patella joints. Tarsi pointed down and sometimes medially. Tarsi were only slightly off or touching the substrate. The cephalothorax was usually raised, with abdomen flexed down and bent. |
| 7 | Arched-out legs | Legs I and II were arched-out. Patella and tibia usually remained nearly parallel to the substrate but may angle downward by as much as 45°. Femora of arched-out legs (Fig. 9) angled up c. 45° and forward by no more than 45°. Metatarsus and tarsus extended sharply downward to the substrate. Tarsi I and II were sometimes held c. 1 mm above the substrate; more often, they remained on the substrate. Arched-out legs I were held out to the side 45–90° with legs II being more or less parallel to legs I whether or not they were also arched out. |
| 8 | Arched-forward legs | Arched-forward legs were similar to arched-out legs except that arched-forward legs I angled forward more or less parallel to the body's sagittal plane (Fig. 8). Legs II may also be arched-forward and held about parallel to legs I. A more extreme version of arched-forward posturing with femora more or less perpendicularly up is commonly adopted. |
| 9 | Posturing | A spider postured by standing or stepping while holding its legs arched-out (arched-out posturing), arched-forward (arched-forward posturing), elevated (elevated posturing), or hunched (hunched posturing). |
| 10 | Rotate cephalothorax | A spider tilted its cephalothorax over to the left or right so that the sagittal plane of the cephalothorax was c. 45° to the substrate when rotating. The spider held its abdomen normally aligned to the substrate (i.e. cephalothorax's and abdomen's sagittal planes were c. 45° to each other). |
| 11 | Rotated posturing | A spider held its cephalothorax rotated and abdomen raised for the two types of rotated posturing. When arched rotated posturing, legs I (or I & II) on the other side of the cephalothorax were arched-forward. When erect rotated posturing, these legs were erect in *Position 1*. The other side of the spider's cephalothorax was on or very near the substrate. Legs I and II on this side extended forward, legs I sometimes being erect but on the substrate. Switching back and forth between arched and erect rotated posturing was very common. |
| 12 | Jerk | A spider jerked by suddenly and rapidly moving its body up then down 2–3 mm (cycle duration less than 0.1 s). |
| 13 | Zigzag dance | A spider zigzag danced by stepping sideways and spiralling towards its partner, with legs raised. Stepping was deliberate and smooth. The abdomen was bent away from the side toward which it stepped while dancing. |
| 14 | Strike | The spider held its legs I elevated just before striking. A strike was executed by very rapidly stepping 20–50 mm toward the other spider, and simultaneously, bringing legs I rapidly and forcefully down and forward onto the substrate or the other spider. |
| 15 | Charge | In charging, a spider suddenly and rapidly ran 20–40 mm forward, then suddenly stopped 10–20 mm in front of the other spider. |

Table 1. Cont'd.

| No. | Element | Description |
|---|---|---|
| 16 | Lunge | A spider lunged by suddenly and rapidly moved its body forward 3–4 mm by extending its rear legs. A lunging spider did not leap (i.e. tarsi of rear legs did not leave the substrate) but always moved its body back to its original position immediately after lunging. A spider arched-out or elevated postured while it lunged and may contact the other spider with its legs during the forward motion of the lunge. A spider sometimes charged immediately before it lunged. |
| 17 | Truncated leap | A truncated leap was made by suddenly leaping 2–5 mm toward the other spider, but making no contact with the other spider. A spider might make as many as five truncated leaps in rapid succession, but despite the number of leaps it made, a truncated leaping spider usually stopped only 2–5 mm away from its rival. |
| 18 | Long leap | A spider executed long leaps by suddenly propelling itself forward 20–80 mm and either contacting (mostly face-on), or landing within 5 mm of, the other spider. |
| 19 | Propulsive displays | Striking, charging, lunging, truncated leaps, and long leaps, each of which involved sudden and rapid forward locomotion of the spider, are termed "propulsive displays". Propulsive displays were performed intermittently and seemingly unpredictably, the spider usually turning and running away immediately afterwards. |
| 20 | Premount tap with legs | With legs I up and down (ca. 2/s; 1–2 mm; femoral; alternating phase; bout lengths 1–2 s), males premount tapped over a female repeatedly, bringing their tarsi into contact with her carapace or, less often, her legs I, palps, chelicerae, or abdomen. |
| 21 | Mounting | Males mounted by walking over females, usually premount tapping as they did so and usually with two spiders face-to-face. |
| 22 | Postmount tap with legs | Males flexed legs I more and more as they moved over females. When a female faces him, then the male's femur-patella and tibia-metatarsus joints were flexed 90–135° by the time his cephalothorax was over her anterior abdomen. Once mounted, a male tapped the female's abdomen by moving his highly flexed legs I up and down in the same fashion as during premount tapping, except that phasing was now usually matching. By doing so, the male lifts her abdomen towards him such that her abdomen is now flexed up 70–80°. |
| 23 | Stroke. | A male leaned to one side and stroked with the opposite leg I or vice versa; he stroked by moving tarsi of legs repeatedly across the female's ventral abdomen (1–3 mm; 1–2/s) with tarsi not flexed up from metatarsi. |
| 24 | Rotate abdomen | A female's abdomen rotated to the left or right while a male stroked, so that the ventral surface of her abdomen was brought closer to the male's stroking leg. |
| 25 | Scrape with palps | A male moved his palps back and forth across the ventral surface of a female's rotated abdomen in the vicinity of her epigynum before engaging his palps and starting to copulate. Males often continued to stroke while scraping with palps. |

than median female-female interaction. Median male-female interaction duration when the female was receptive (i.e. copulation resulted) and when the female was unreceptive was similar (Table 3). No instances of cannibalism were observed for any of the interactions.

***Intrasexual interactions (Figs. 15 & 16).*** **–** In 8% of the male-male and 12% of the female-female interactions, the spiders apparently ignored each other throughout the test. During intrasexual interactions, spiders usually postured while standing or while repeatedly stepping toward then away from each other. The most common sequence of behaviour for females was to watch and display for a few seconds before decamping. For males, however, it was to watch and posture, followed by a zigzag dance before decamping. When a male zigzag dances, he was mirrored by his test partner. About 60% of the observed female-female interactions ended at stage 2 compared to about 39% of the male-male individual interactions ending at stage 2. That is, a larger proportion of male-male interactions escalated to the more intense stages (i.e. stage 3 and 4). Contact was rare in male-male and in female-female interactions (5.6% for males and 14% for females).

Male-male agonistic interactions began when one or both spiders started to display (raised bodies, arched-out or hunched legs and flexed-up abdomens, abdomens sometimes also bent) at about 10–15 cm away. Both males then slowly zigzag danced towards each other until they were about 1–3 body lengths apart. Males zigzag danced by adopting an arched-out posture and flexing-up their abdomen (60–80°) while stepping sideways. Stepping sideways involves a left-right sideways motion in a semi-circle arc that progressively closes the distance from his partner. Abdomens were bent away from the direction of stepping and the degree of abdomen flexion increased with decreasing distance from the

Table 2. Types of interactions during which different displays (listed alphabetically) were performed by Singapore *Asemonea tenuipes* (A). X: did not to occur.

| | **Male-female*** | **Male-female**** | **Male-male** | **Female-female** |
|---|---|---|---|---|
| Arched-forward posturing | A | X | A[1] | X |
| Arched-out posturing | A | A | A | A |
| Charge | X | A | X | A |
| Elevated posturing | A | A[1] | A[1] | X |
| Position 1 | A | A[1] | A[1] | X |
| Position 2 | A | A[1] | A[1] | X |
| Erect | A | A[1] | X | X |
| Semi-erect | A[1] | X | A[1] | X |
| Flickering of elevated legs | X | X | X | X |
| Flickering of erect palps | X | X | X | X |
| Hunched posturing | X | A | A | A |
| Jerk | A | X | X | X |
| Long Leap | X | X | A | A |
| Lunge | X | A | X[2] | X[2] |
| Postmount tap with legs | A | X | X | X |
| Premount tap with legs | A | X | X | X |
| Rotated posturing | A | X | X | X |
| Scrape with legs | X | X | X | X |
| Scrape with palps | A | X | X | X |
| Strike | X | A[1] | A[1] | A |
| Stroke | A | X | X | X |
| Truncated leap | X | X[2] | X | A |
| Twitch abdomen | A | A | A | A |
| Waving of elevated legs | A[1] | A | A[1] | X |
| Zigzag dance | A[1] | X | A[1] | A[1] |

*Displays performed by males during male-female interactions.
**Displays performed by females during male-female interactions.
[1] Observed in this study but not in the Sri Lankan population (same species) by Jackson & Macnab (1991).
[2] Observed by Jackson & Macnab (1991) but not in this study.

Table 3. Durations (sec) of intraspecific interactions (see text).

| | **Male-female (female receptive)*** | **Male-female (female unreceptive)** | **Male-male** | **Female-female** |
|---|---|---|---|---|
| Median | 158 | 165 | 62 | 38 |
| Maximum | 1215 | 1327 | 279 | 329 |
| Minimum | 21 | 51 | 13 | 5 |
| No. | 8 | 29 | 18 | 25 |

*Interaction duration before copulation.

other spider. The interaction usually ended with one male suddenly decamping by running off. There were two instances of *Contact* (strike or long leap at the other male).

Although the beginnings of female-female and male-male agonistic interactions were similar, there were some interesting differences. The *distant displays* of males were raised body, flexed-up abdomens, and hunched legs. Females tended to not flex their abdomens as often as males and, when they did, the abdomen was raised 20–50° (60–80% for males). Instead of zigzag dancing to approach another female, females usually stayed still or approached by rapid stepping. Females usually made c*ontact* by charging and they adopted especially pronounced hunched posture (raised

Table 4. Data from copulations (mean ± SE).

| | *Asemonea tenuipes* |
|---|---|
| No. of pairs that copulated | 8 |
| No. of copulations | 18 |
| Copulation duration | 2.1 ± 0.26 min |
| Palp engagement duration | 1.8 ± 0.23 min |

body and slightly flexed-up abdomen) before charging. Occasionally, the other spider decamped just before a female charged. Most intrasexual interactions ended after the first instance of decamping.

***Intersexual interactions (i.e. male-female interactions) (Fig. 17). –*** The primary behaviour of males was to posture while standing, while stepping nearer or while stepping away from a female. Females, on the other hand, usually watched displaying males for a few seconds before decamping. Males were always the first to initiate an interaction (*watch, distant displays and approach),* after which, 76% proceeded to close-proximity displays. Rotated posturing was the most common close-proximity display (86%) performed by males and it occurred in all interactions that resulted in copulation. About 30% of the interactions ended after close proximity displays when males decamped. Another 38% proceeded from c*lose proximity displays* to *embrace*. The sequence of events after *embrace* was varied considerably, with 43% of these proceeding to *mount*. Some males then failed to initiate and only 11% of all interactions resulted in copulation.

Males usually approached and backed away repeatedly from females that remained more or less stationary, often switching repeatedly from rotated to arched-up posturing. They also zigzag danced (with abdomen flexed up, stepping sideways while progressively moving closer to the female). Regardless which side of the leaf the female was on (usually underside of the leaf), males often alternated between two sides of the leaves while courting a female He usually remained motionless on the side of the leaf without the female but posture once he returned to the side with the female and, in most cases, he started rotated posturing if the female was watching. Usually, males stopped posturing altogether when losing sight of females that moved away.

Females always initiated contact in intersexual interactions. Females usually attacked males by charging or, rarely, by striking or lunging during close-proximity displays or while males tried to embrace them. Although intrasexual int±eractions generally ended as soon as one spider decamped, sometimes males followed again immediately after the female or they themselves decamped, with the male displaying again if the female stopped. However, he soon ceased to follow if she did not stop.

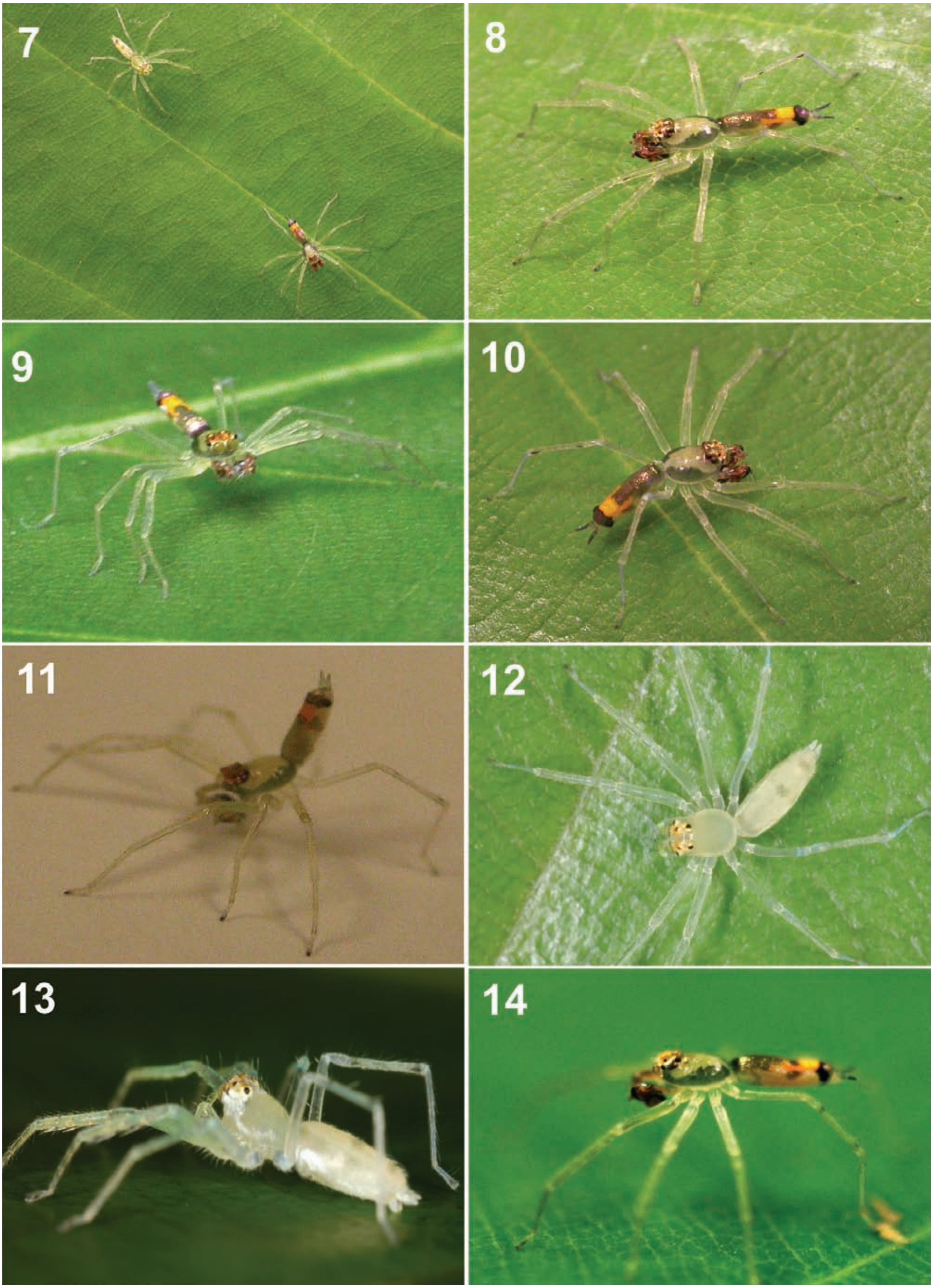
***Mounting and postmount behaviour. –*** While attempting to mount females, males switched from an arched rotated posture to erect rotated posturing (Position 1). The male premount tapped the female as he tried to mount. Males tended to lean to the left or right and usually engaged their palps soon after mounting. A male usually backed away when the female's abdomen did not rotate. Males sometimes mounted females without initiating palp engagement and later decamped voluntarily before the female became active.

***Copulation. –*** There were eight pairs that copulated and copulation always took place on the leaf underside. Data on copulation duration and palp engagement duration are presented in Table 4. While copulating, the female usually had her abdomen raised 20–45° and rotated 45–90°, with her cephalothorax lowered and resting on the substrate. Copulatory posture was similar to that described in the Sri Lanka population directions [copulatory posture No. 2, (Gerhardt & Kaestner, 1938); male standing over and leaning across the female, spiders facing in opposite directions].

Unlike many other species, and unlike the Sri Lanka *Asemonea tenuipes*, copulations did not end when the female became active and decamped but, instead, it usually ended because males that decamped first. The males usually quickly move away from the female while the female remained still in her characteristic copulatory posture. Eight pairs copulated, with three copulating only once and five copulating two to four times. In these cases, after the males decamped, they attempted to court the female again by performing close proximity displays such as rotated posturing before mounting her again. In the subsequent copulation for multiple mating, copulating males sometimes switched over to a different palp from the one used previously.

## DISCUSSION

***Comparison of findings from this study and the earlier study. –*** On the whole, the size and complexity of the display repertoire of the Singapore *A. tenuipes* observed under full-spectrum light largely resembles that of the Sri Lanka population observed under light conditions lacking of UV light (Jackson & Macnab, 1991). However, there were some differences and we need first to consider whether having adopted somewhat different definitions for elements of behavior might have been important. Zigzag dancing is an example. Jackson & Macnab (1991) used the term 'zigzag dance' for male courtship behaviour seen for other salticids (Jackson & Pollard, 1997), including other lyssomanine species. It referred to specifically instances of the male stepping sideways and spiraling towards its partner in conjunction with other courtship display (e.g. erect forelegs). For the Singapore population of *A. tenuipes*, we observed the spider perform sideways stepping in same-sex interactions while spiraling towards its partner, but without the spider doing this in conjunction with other display behavior such as erect legs. With definitions being somewhat different, it is not so simple to say the use of zigzag dancing is unique to the Singapore *A. tenuipes*. However, terminology notwithstanding, the zigzag approaches reported here for same-sex interactions were not reported in the study on the Sri Lanka population, a spiraling stepping pattern in the absence of other display behaviour was not reported in the study on



Figs. 7–14. (7) Left: female; Right: male. Male decamped just after performing a close proximity display. (8) Male (facing left) displays with arched-forward legs. (9) Male (facing to right) displays with raised body, arched-out legs and flexed-up abdomen. (10) Side view of male: displays with flexed-down abdomen. (11) Female: bent abdomen to her right. (12) Side view of male: displays with highly flexed-up abdomen and arched-forward legs. 17, 18. Raised and lowered body postures. (13) Female (side view, facing to left) with lowered body and raised cephalothorax. (14) Male (side view, facing to left) with raised body parallel to substrate.

the Sri Lanka population. Unfortunately, the absence of a report of this behaviour cannot so simply be taken as being evidence that this behaviour did not occur. For example, taking a spiraling path might be less conspicuous than the display-associated zigzag dancing during the courtship rituals of many salticid species and that might have led to it being overlooked. This highlights a difficulty with basing comparisons on what is and in not reported in the literature. Statements about what was observed and recorded can be made with considerable confidence, but concluding that something does not occur on the basis of it not having been reported is usually subject to considerably less confidence. It would be of interest to repeat the study on the Sri Lanka *A. tenuipes* now that we have the study on the Singapore *A. tenuipes* to inform us of what to look for.

On the whole, the present study of the Singapore *A. tenuipes* has revealed new elements of behaviour more often than there having been elements of behaviour recorded for the Sri Lanka *A. tenuipes* that were not observed for the Singapore *A. tenuipes* (Table 1). This suggests that full-spectrum light made the spiders inclined to perform behaviour that was not performed when UV was lacking. It is particularly striking that almost all the new elements observed under full-spectrum light were leg postures while the elements present only in the absence of UV were propulsive displays (truncated leap and lunge). An intriguing possibility is that, as showed in

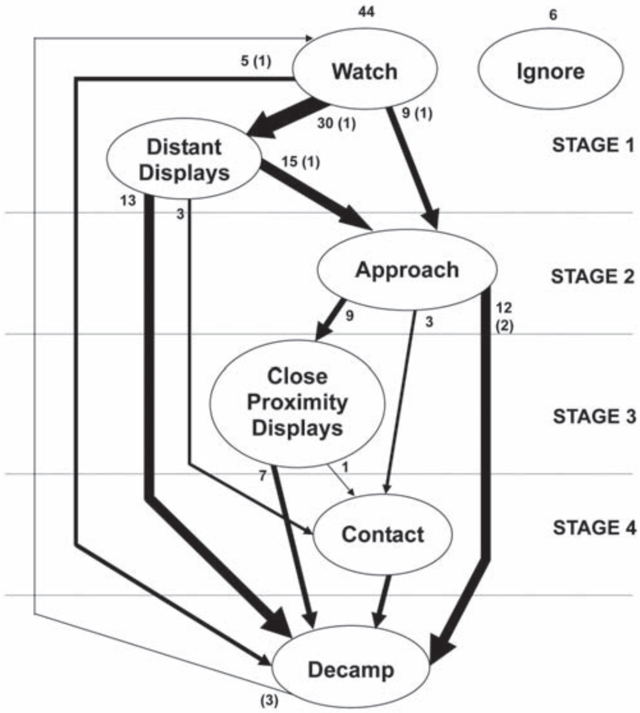


Fig. 15. Summary of interactions by 50 individuals (25 pairings) between adult females on leaf. Distant displays predominantly refer to raised body and leg postures (hunched and arched-out). Approach includes both with and without concurrent displays. Close proximity displays for females are similar to above defined displays but also include propulsive displays (truncated leap, charge) that did not result in contact unlike in Contact. Unbracketed numbers refers to the number of individuals that proceeded to the next category while bracketed numbers refer to the number of interactions that proceeded after the first decamp.

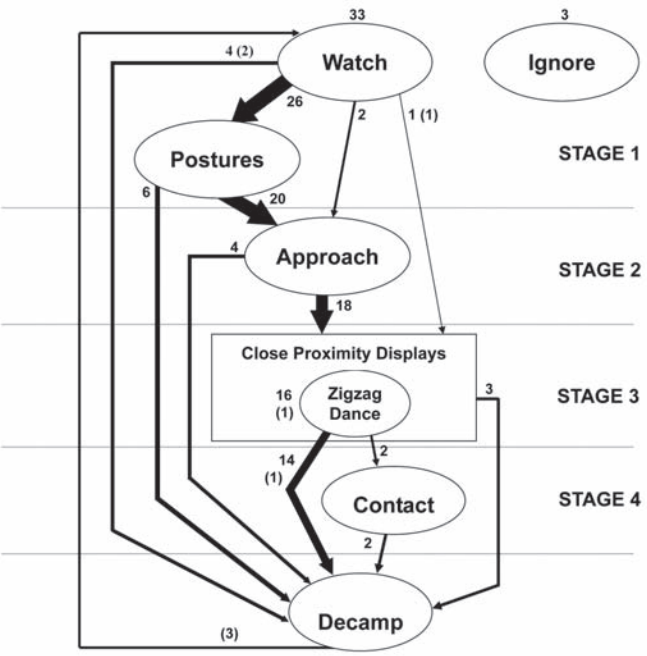


Fig. 16. Summary of interactions by 36 individuals (18 pairings) between adult males on leaf. Distant displays predominantly refer to raised body, flexed/bent abdomen and leg postures (hunched and arched-out). Approach includes both with and without concurrent displays. Close proximity displays for males are similar to above defined displays but also include zigzag dance and propulsive displays (long leap, strike) that did not result in contact unlike in Contact.

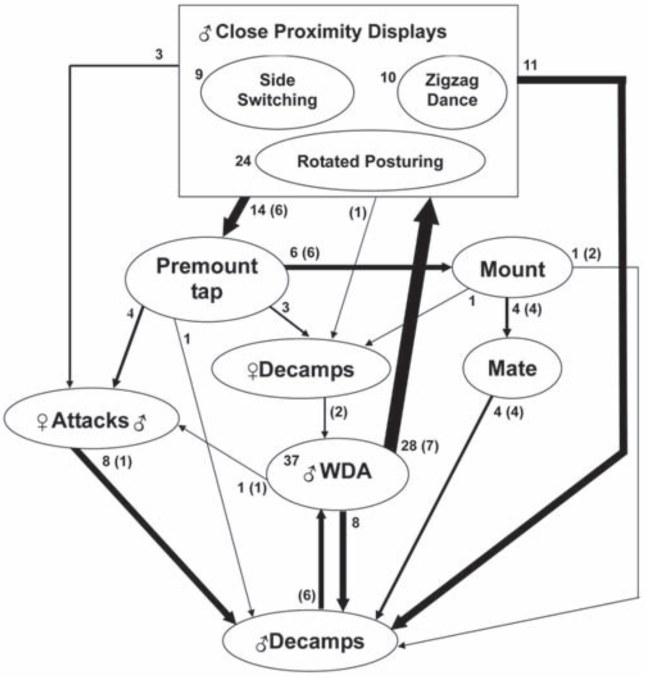


Fig. 17. Summary of 37 interactions between adult males and females on leaf. WDA is the summation of the Watch, Distant displays and Approach categories of the intra-gender specific interactions. Close proximity displays for males include raised body, flexed/bent abdomen and leg postures (hunched and arched-out), rotated posturing, zigzag dance and side switching. Females predominantly attack males by charging or rarely, by striking or lunging.

*Cosmophasis* (Lim & Li, 2006b; Lim, 2007), the presence or absence of UV light has a strong influence on the level of aggressiveness exhibited during interactions.

***Rotated posturing.*** **–** Rotated posturing is of particular interest because, although the rest of the repertoire of *A. tenuipes* consists of behaviour similar to behaviour reported for other salticids, rotated posturing has never been recorded for any other salticid species. It was observed for both the Singapore and the Sri Lanka *A. tenuipes* and, observing *A. tenuipes* males in the rotated posture, it is easy to suggest as a hypothesis that males of low quality would have difficulty sustaining this posture (Jackson & Macnab, 1991). Testing this hypothesis, however, will require experiments that have not yet been carried out, and the hypothesis will probably need refinement. Perhaps simply the ability to adopt this posture is not what is important. After all, this unusual posture preceded all observed copulations. However, for the female, what matters might be details concerning how the male expresses this display, with these details varying with male quality.

***Displaying by males when no other spider is in view.*** **–** The typical pattern in salticids is for males, when they encounter females in nests, to adopt displays that do not depend on vision (Jackson & Pollard, 1997). However, when they encounter females out in the open, they typically display specifically at a female that is in sight (Crane, 1949a; Drees, 1952). Lyssomanines may be different. In the earlier study (Jackson & Macnab, 1991), the males of three lyssomanine species, *A. tenuipes*, *Goleba puella* and *Lyssomanes viridis*, sometimes initiated courtship displaying before they made eye contact with a female, and males readily held display postures during the interaction even at times even when a female was not within his line of sight. On the whole, the observations in the present study of the Singapore *A. tenuipes* are consistent. The Singapore *A. tenuipes* males also held their posture for up to a minute even when there was no direct eye-contact with females during interactions or after a female decamped. A hypothesis currently being investigated is that lyssomanine males rely especially strongly on olfactory pheromones from females.

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