THE RAFFLES BULLETIN OF ZOOLOGY 2002 **50**(1): 143-151

RIVET-LIKE NEST-BUILDING AND AGONISTIC BEHAVIOUR OF *THIANIA BHAMOENSIS*, AN IRIDESCENT JUMPING SPIDER (ARANEAE: SALTICIDAE) FROM SINGAPORE

Daiqin Li, Seow Hwa Yik and **Wee Khee Seah**
Department of Biological Sciences, National University of Singapore, 10 Kent Ridge Crescent, Singapore 119260. Email: dbslidq@nus.edu.sg

ABSTRACT. – This is the first detailed description of nest-building and fighting behaviour of *Thiania bhamoensis* Thorell, an iridescent jumping spider species, commonly known as fighting spiders in South-east Asia. Its nest-spinning behaviour is unusual for a jumping spider. *Thiania bhamoensis* built a silken nest by binding a pair of green leaves together with strong silken rivets. Spiders rested, moulted, and oviposited in the narrow space between the bound leaves. Egg sacs are usually flattened and densely woven for a salticids. However, the egg sac of *T. bhamoensis* was sealed to a leaf in the rivet-like nest but was not contiguous with the silken components (i.e., rivets) of the nest. Pairwise fights between males were staged in the laboratory and videotaped. Twelve major displays were identified, showing a large repertoire of agonistic displays of this species. The behaviour of *T. bhamoensis* is also discussed in relation to hypotheses concerning salticid evolution.

KEY WORDS. – Salticidae, *Thiania bhamoensis,* display, fighting spiders, rivet-like nest.

INTRODUCTION

A male's reproductive success generally depends on its ability to acquire or maintain access to prospective mates. Competition between males for mates is common in nature and conspecific males often communicate during the agonistic interaction through threat displays. These have been extensively studied for decades both theoretically and experimentally. However, actual knowledge about the meaning of agonistic displays and the fighting decision rules underlying their occurrence is poorly known (Mann et al., 2001). Male agonistic behaviour is common in many species of spiders, with best-known examples in jumping spiders from the Salticidae (Faber & Baylis, 1993; Taylor et al., 2000). Salticids are one of the few groups of spiders whose major mode of locomotion is, as the name implies, jumping. The Salticidae is the largest (nearly 5000 described species) and diverse family (Coddington & Levi, 1991; Zabka, 1993), with members on every continent (except Antarctica) and on most oceanic islands. These spiders are one of the major animal groups in which acute vision has evolved (e.g., Land & Nilsson, 2002). Visual acuity and jumping ability have enabled salticids to hunt their prey actively, instead of relying on silken snares. It is not surprising that their highly developed vision also plays an important role in the intraspecific interactions (Crane, 1949; Jackson & Pollard, 1997). All these, together with their complex behaviour, make salticids well representatives of ethological studies (Richman & Jackson, 1992).

Salticids have a pair of large anterior-medial eyes (AME), known as the principal eyes (Homann, 1928), and three pairs of smaller (`secondary') eyes responsible for movement detection (Land, 1971; 1974). The principal eyes, being responsible for acute vision (Land, 1969a, b), enable salticids, prior to contact, to discriminate between mates and rivals (Jackson & Blest, 1982; Harland et al, 1999; Harland & Jackson 2000a, b). Acute vision, made possible by the salticid's principal eyes, creates the potential for good assessment of the opponents (Taylor et al., 2000). Among salticids, all sex/age classes sometimes perform threat display and ritualized fights, but this type of behaviour is most pronounced in adult males (Crane, 1949; Jackson, 1982). Although salticids are assumed to highly develop such aggressive behaviour in conspecific males (e.g. Pechham & Peckham, 1889; Crane, 1949; Forster, 1982; Jackson & Pollard, 1997), only a small fraction of species in this large tropical family has been subjected to detailed studies of contest behaviour. However, information on the intraspecific interactions has been used to speculate the evolution of salticids (Jackson & Blest, 1982). To evaluate this, comparative

Received 28 Nov 2001 Accepted 22 Feb 2002

data from a wide range of species are needed. There are 73 described salticid species in Singapore (D. X. Song, J.X. Zhang & D. Li, unpublished data), but only three species, *Epeus flavobilineatus* (Doleschall) (Jackson, 1988), *Phaeacius malayensis* Wanless (Jackson & Hallas, 1986a) and *Thorellia ensifera* (Thorell) (Jackson & Whitehouse, 1989) have been studied so far.

Thiania is an Oriental salticid genus consisting of 17 described but poorly known species. *Thiania bhamoensis* Thorell are commonly known as fighting spiders in South-east Asia because males are known to engage in fighting behavior both in nature and the artificial situation (Rashid & Azirun, 1992). It is known that a spider that wins battle after battle attains the status of "first king" until its performance declines and is replaced by another champion. Fighting spiders are normally kept in matchboxes with a piece of green leaf and a spat of saliva to provide moisture. *Thiania bhamoensis* has an iridescent green-blue colouration, males being more blue and females more green. It is common belief that the darker the male is, the more aggressive it will be. Apart from a brief article describing male –male interactions in this jumping spider (Rashid & Azirun, 1992), no detailed studies of male-male interactions have ever been conducted. Furthermore, information on male-male interactions is needed for further investigation of factors that influence the outcomes of male-male contests. In the present study, the intraspecific display behaviour of *T. bhamoensis* from Singapore is investigated. The aberrant nest spinning behaviour and egg sacs of this salticid are also described in this paper.

MATERIALS AND METHODS

Thiania bhamoensis were observed in nature and collected from Kent Ridge Park, Singapore Botanic Gardens and the National University of Singapore campus in Singapore. Thirty adults males were collected. Spiders were individually housed in plastic cylindrical containers (diameter: 9 cm, height: 6.5 cm). They were fed three adult *Drosophila melanogaster* three times a week. Green leaves were provided for spiders to build their nests. Leaves remained green in humid cages for up to two weeks and were replaced as they dried out. Water was provided via a cotton roll that penetrated through the floor of the cage and was dipped into a water-filled container outside the cage. Cages were cleaned once a week to remove any dead flies. Cardboard partitions shielded the spiders from one another so that they would not have any prior experience with conspecifics before testing. Lighting (12:12 L: D), temperature (25 ± 1°C), and humidity (70-80%) were controlled. Lights came on at 0800 h and went off at 2000 h.

To observe interactions, the leaf was removed from the cage and clamped to a stand and another male from another cage was put on the leaf with the resident male. The initial displays defined the beginning of the interaction; when one spider decamped and the other failed to follow defined the end, at which point the spiders were removed. The male-male interactions were videotaped for further descriptions. The descriptions were based on 45 male-male interactions. No individual male was used more than once per day or in the same pairing. All observations were carried out between 0900 h and 1800 h.

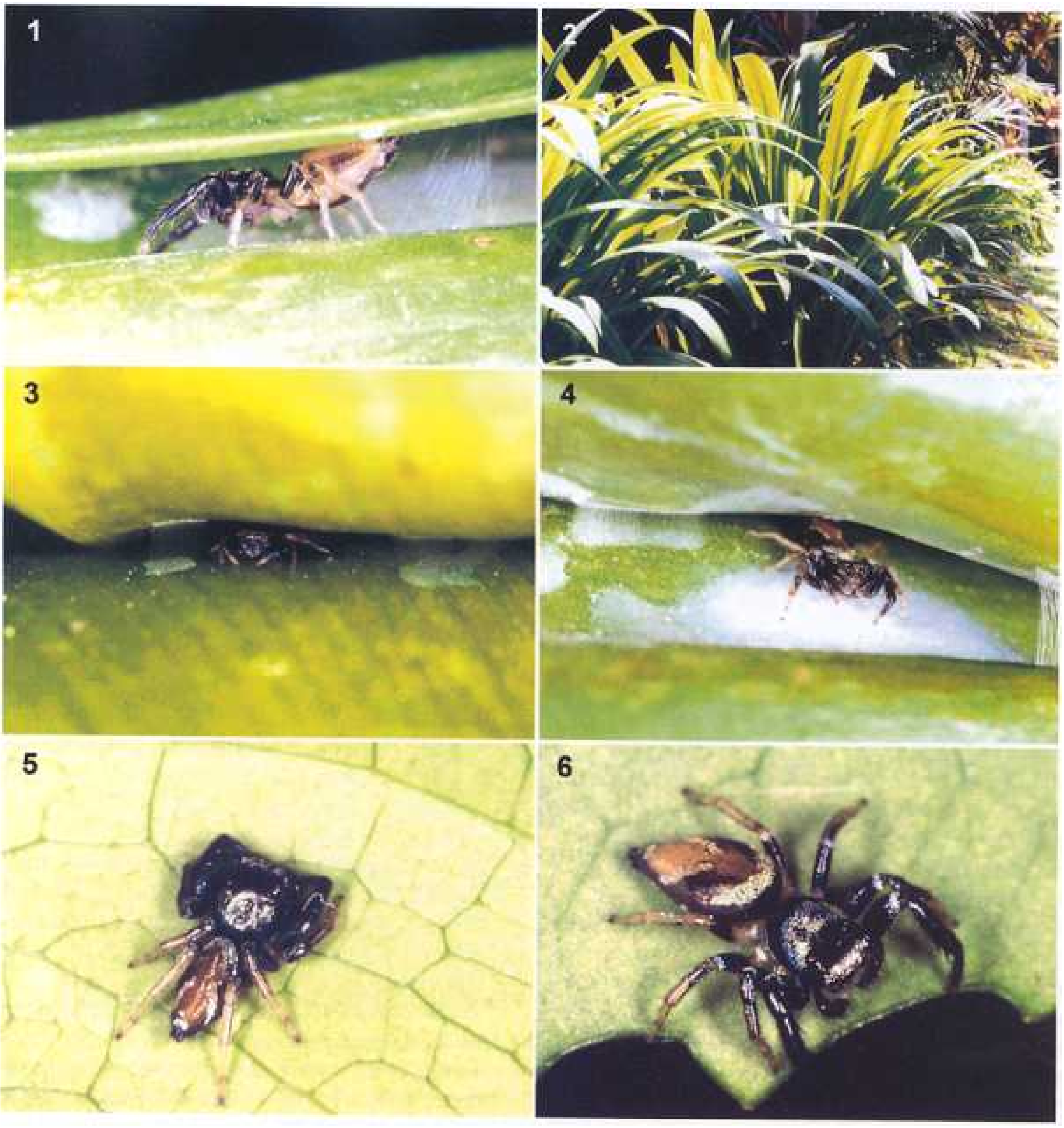
FIELD OBSERVATIONS

Nests and nest-building behaviour

The nest-building behaviour of *T. bhamoensis* is similar to that of *Thiania* sp. from Malaysia (Jackson, 1986a). In the laboratory, making a single rivet took *c.* 20-30 min and involved a variable number of cycles of making silk attachment discs to the leaf. Each cycle involved making three attachments. In a cycle, the spider first stood between two leaves, dorsal-side-up, facing into the nest. The spider then swept its abdomen from side to side 2-5 mm for a few times, laying strands of silk on the substratum, lowered the abdomen, and then moved the spinnerets back and forth fastening a thread. After a pause (0.5-1 s), the spider raised its abdomen and, at the same time, rotated *c.* 180°, bringing its spinnerets onto the upper leaf surface (Fig. 1). The spider moved its spinnerets back and forth, making the second attachment disc. Finally, the spider moved its abdomen back to the bottom leaf, making the third attachment disc close to the first. Each cycle took up to 1 min, with the spider gradually shifting its position for the next cycle. There was an interval of 0.5-3 min between two successive cycles. After completion of a rivet, the spider moved away for a certain distance, and either kept inactive for a while or immediately started building another rivet elsewhere.

In nature, *T. bhamoensis* were usually found between a horizontal pair of green leaves in a nest on most garden trees and shrubs but were especially common on *Crinum asiaticum* (spider lily) (Fig. 2). This plant is native to tropical Asia and is often cultivated in gardens for aesthetic purposes because of their stalked white flowers. The leaves are green, long and sessile with wide blades. Many leaves lay close together and *T. bhamoensis* built their nests in the space between the leaves (Fig. 3). When leaves were pulled apart, *T. bhamoensis* almost always escaped by making sudden leaps and subsequently remaining motionless, making it difficult to relocate.

The nest consisted of a space between two leaves and the perimeter was about 4-10 silken rivets arranged in a roughly circular or elliptical manner. The rivets were small or large. Most rivets were small and they were c. 1 mm wide × 2-8 mm long. Its long axis was generally facing the interior of the nest. The small rivets were formed by many closely packed vertical strands of silk (2-6 mm long) connecting the two leaves. Some effort was needed to break the rivets and pull the leaves apart (Fig. 3). Some nests had 1-3 larger rivets. The large rivets were c. 12 × 5 mm and had looser threads than the small rivets (Fig. 4). The leaf surface within and near the nest was rarely coated with silk threads so that wide, clear spaces between the rivets (doors) allowed the spider to enter and leave the nest. With many doors the spider was able to go in and out of the nest from almost any direction.



Figs. 1-6. (1) *Thiania bhamoensis* spinning a rivet. Standing between two leaves (facing left), it lifts and rotates abdomen to fasten line to top leaf (lateral view); (2) Spider lily (*Crinum asiaticum*), a tropical plant on which *Thiania bhamoensis* build the nests between two leaves; (3) *Thiania bhamoensis* at edge of nest peering out (front view). Note the silken 'rivets' on both sides of the spiders. Leaves have been partially lifted apart; (4) Female *Thiania bhamoensis* sitting above her egg sac (front view). Note the silken 'rivets' on the both left and right sides of the egg sac; (5) Male *Thiania bhamoensis* on leaf in cryptic rest posture. Facing up. Legs pressed against the surface of leaf; and (6) Male *Thiania bhamoensis* (dorsal view) walking on leaf.

Like adult males and females, juveniles also built rivet-like nests. However, adults commonly span larger nests (20 × 30 mm to 30 × 50 mm) while juveniles built relatively small nests. In nature, juveniles built their nests between the same sized leaves as adults. Nests were not built in the absence of paired leaves. Most times, only one individual was found in each nest. Occasionally, a male was found cohabiting with a juvenile female.

Egg sacs

In nature, all nests were found containing one egg sac each. The egg sac was *c.* 2-3 times larger than the spider body length. It was white (opaque) in colour and roughly elliptical in shape. The eggs were wrapped several layers of lower and upper densely woven silk sheets on the surface of the lower leave inside the nest (Fig. 4). The egg sac was unusually flattened. The lower silk sheet was generally larger than the upper sheet. The lower sheet sometimes extended about 5-8 mm out from the sides of the upper sheet, but the upper sheet always joined the lower sheet tightly.

NORMAL LOCOMOTION

When at rest, *T. bhamoensis* adopted the "flattened posture". When resting in the rivets between leaves, the flattened body and legs were pressed against the surface of the leaf (Fig. 5), with legs I arched, legs II angled forward, legs III arched-out and legs IV angled rearward. The palps angled ventro-mediately so that they obscured the view of chelicerae from the front.

Thiania bhamoensis had two modes of locomotion – walking and running (Fig. 6). The spider normally moved in a rapid stop-and-go gait typical of style of locomotion, stepping rapidly a few centimeters, and then standing for 0.5 – 1 s, then stepping forward again. The movement was rather rapid and agile, and the spider often alternated between walking and running, with walking predominating, although a spider almost always ran when disturbed (e.g., if a person attempted to push apart leaves. The spider also often waved its palps, but not so much as it was standing. There was little or no waving of legs when stepping or during pauses between steps.

ELEMENTS OF AGONISTIC BEHAVIOUR

Interactions between *T. bhamoensis* males consist of displays that involved movement patterns and those that involved postures, which were static, with the spider holding parts of its body in a particular stance for a sustained period. Each element of behaviour is described below. When referring to the legs of the spider, legs I are the most anterior pair; legs II, the next most anterior pair, etc.

1. ***Raised body.*** – Raised bodies were held higher than normal above the substratum (Fig. 7). The anterior cephalothorax was often held higher than the posterior, but the abdomen was held parallel to the substratum.

2. ***Abdomen flexed up or flexed down.*** – *Thiania bhamoensis* often held its abdomen flexed up (deflected up *c.* 45° from the cephalothorax) or flexed down (abdomen deflected down *c.* 45° from the cephalothorax) while displaying with its legs I. Very often, the cephalothorax was slightly raised when the abdomen was lowered.

3. ***Arched-out legs.*** – Legs II, III and IV were stretched outwards, raising up the body (Fig. 7).

4. ***Arched legs.*** – Only legs I were arched (Fig. 8). They were held roughly perpendicular to the sides of the body with the femur angled upward about 30°. The femur-patella and tibia-metatarsus joints were flexed slightly down so that the tarsus contacted the substratum. Legs were held about 120° apart. Occasionally, legs I were spread more than 120° (but less than 180°) apart.

5. ***Hunched legs.*** – Only legs I were hunched by being held to the sides of the cephalothorax with the femur angled upward about 50°. Legs were highly flexed at the femur-patella joints so that all segments distal to that joint pointed down and the tarsi contacted the substratum.

6. ***Bent abdomen.*** – The abdomen was frequently twisted at the pedicel and swivelled (c. 45°) to the left or right side of an individual's cephalothorax (Figs. 9,10, 11& 12).

7. ***Elevated legs.*** – Only legs I were elevated. The two most common positions were:

Position (1) – Arched legs I (see element 4) were raised off the ground. They were held to the side of the body about 120° or more but less than 180° apart (Fig. 10).

Position (2) – Legs I were held perpendicular to the side of the body, 180° apart and parallel to the substratum. All joints were fully extended, giving legs I a stiff appearance (Fig. 12).

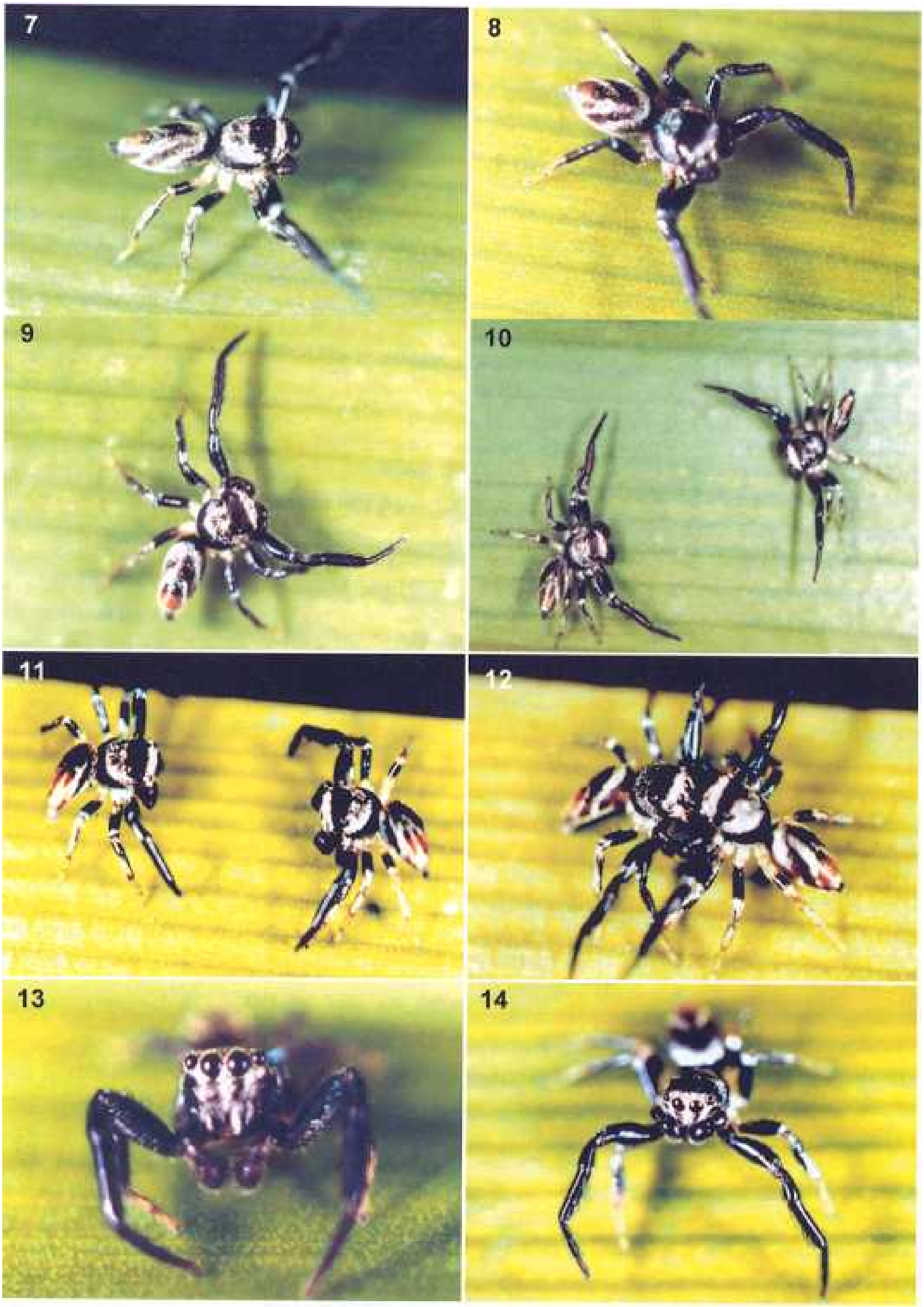


Fig. 7-14. (7) *Thiania bhamoensis* in a 'hunch' posture with arched out legs and raised body and cephalothorax (facing right). Palps in normal posture; (8) Male *Thiania bhamoensis* posturing with arched legs I. Palps in normal posture; (9) *Thiania bhamoensis* male posturing with arched legs I elevated in Position 1. Abdomen is bent to the right of the cephalothorax. Palps in normal posture; (10) Two *Thiania bhamoensis* males sparing with each other, each posturing with legs I arched and elevated in Position 1 and abdomen flexed up and bent to one side; (11) Two *Thiania bhamoensis* males approaching each other, with legs I arched and abdomen flexed up and bent to one side; (12) Same two *Thiania bhamoensis* males (as in Fig. 11) initiating an embrace. Each approaching the other with legs I elevated in Position 2. Palps laterally erecting and almost touching; (13) Front view of *Thiania bhamoensis* male. Palps held in normal posture: in front of the chelicerae, arched and hanging down; and (14) Front view of *Thiania bhamoensis* male. Palps in normal posture but with the femora angled slightly upward so that the palps hide the chelicerae from view (c.f. Fig. 13).

8. Jerky leg waving. – While stepping (forward or more often, to the side), males waved arched or elevated legs I (Position 1) by moving them up-then-down (by a small amplitude) in a sudden and rapid motion. There was only one wave for each step the spider took, with legs I remaining arched in between steps.

9. Normal palp posture. – The palps were held in front of the cephalothorax, arched and hanging down. The palp femora extended ventro-laterally alongside the chelicerae with the rest of each palp angled ventro-medially so that the tips of the two tarsi were 1-2 mm apart under the fangs (Fig. 13). Also, the femora were usually angled slightly up such that the rest of the palps obscured the view of the chelicerae from the front (Fig. 14).

10. Erect palp. – Palps were stiffly extended and in the *lateral erect* posture where they were held to the sides of the chelicerae about 120° away from each other (Fig. 12).

11. Embrace. – The spiders approached each other with legs arched or elevated in Position 1, moving them into Position 2 when they got closer. They continued to advance and brought their laterally erect palps into contact to initiate an embrace (Fig. 12).

12. Palpal pushing. – During embrace, with legs extended in Position 2, palpal pushing occurred with laterally erect palps. Each palp touched the palp of the facing spider then each spider moved or attempted to move forward. When pushing, legs I of both spiders touched when they fluttered back and forth and appeared to be a blur. Also, during this period, the anterior end of the cephalothorax tended to tilt up a little with the bodies of both spiders forming a 'tent' structure.

13. Grapple. – From embrace, both spiders pressed their faces tightly together and moved their legs forward over each other so that they interlocked. The legs I of one spider appeared to wrap around the body of the other spider in a bid to pin it down to the substratum.

14. Step-to-the-side and forward-and-backward. – Spiders faced but never ran directly into each other (charge). Instead, when approaching, they stepped to the left or right or stepped forward or backward a few millimetres. When performing these behaviours, the spider usually postured (Position 1) or waved its legs I. While stepping to the side, the spider's abdomen was often bent away from the direction of stepping.

15. Decamp. – To decamp, one spider ran or leapt away from the other.

ORGANIZATION OF MALE-MALE AGONISTIC BEHAVIOUR

When spiders were not interacting with conspecifics, a male normally postured by standing or walking as it held its stationary legs erect, hunched, or arched. Interactions began when both males faced each other from as far as 14 cm apart. Generally, they adopted the 'hunch' posture where legs I were *hunched* and legs II, III and IV were *arched out,* raising up the body. This appeared to be a defensive and alert stance. Both males approached one another maintaining this posture or sometimes one male remained stationary at this posture and visually tracked its opponent.

Next, sparring began. The legs I of one male was *arched* and the anterior cephalothorax lowered from the 'hunch' position (Fig. 8). The other male usually matched this display. As they got closer to each other, legs I were *elevated in position 2* (Figs. 9 & 10). Both males usually held their abdomens *flexed up/down and bent to the side* while they sparred with each other. The palps were held in their *normal position.*

When both spiders approached, they usually *stepped forward and backward* or sometimes *to the side* and tended to *wave* their legs I. Within about 1 body length of each other (Fig. 11), the legs I of both spiders were suddenly straightened and *elevated in position 2.* They faced each other with legs I in this position and parallel to each other (Fig. 12).

They moved closer together, paused momentarily face-to-face and *embraced* to engage in *palpal pushing.* With their bodies in such close proximity, both males occasionally started to *grapple.* Eventually, the interaction ended when the dominant male caused its opponent to break away and *decamp.*

LEVELS OF CONTEST INTENSITY

The following stages were viewed as representing a sequence of increasing levels of intensity within agonistic encounters based on consideration of proximity of males to each other and risk of injury. Transitions from one stage to the next were viewed as escalations in encounter intensity.

Level 1. – The sparring distance between the two males was about four body lengths or more. Usually, one male approached the other that remained stationary and they sparred at that distance.

Level 2. – The sparring distance between the two males was about two body lengths or less. In most cases, this proximity was due to the two males approaching each other.

Level 3. – Both males embraced to engage in palpal pushing.

Level 4. – Males were involved in a grapple with each other.

DISCUSSION

Nests and egg sacs

Like the tubular nests spun by typical salticids, the opened, rivet-like nests of *Thiania bhamoensis* may serve as resting sites and as sites for moulting, mating and oviposition. However, the nests of *T. bhamoensis* are morphologically different from the tubular nests of most salticids: *T. bhamoensis* made silken rivets and sandwiches itself between two leaves rather than enclosing itself in silk (also see Jackson, 1986a). Furthermore, typical salticids spin their egg sacs by covering a few layers of dense silk that is continuous with the enclosing silk of a tubular nest (Jackson, 1979) while *T. bhamoensis* encloses its egg sac between two leaves in the rivet silk that is not continuous with the silk of egg sac. Why do the species from the genus *Thiania* (Jackson, 1986a) build this aberrant form of nests and egg sacs? One explanation has been proposed for this form of nest (Jackson, 1986a). These opened, rivet-like nests may function as a significant anti-predator measure (Jackson, 1986a) because these nests have many doors so that spiders can escape from almost any direction. However, to test hypothesis we need to show, for example, that *Thiania* that spin the opened, rivet-like nest has higher survival rate compared to salticids that make the enclosed nests. This hypothesis is now being investigated.

Other interesting questions also arise regarding the evolution of salticids. For example, is the spinning behaviour of *T. bhamoensis* primitive among the Salticidae or modified from typical tubular nests built by majority of salticids? If the nest and egg sac spinning behaviour of *T. bhamoensis* is primitive, the nests and/or egg sacs of *T. bhamoensis* should be similar to those of primitive salticids. *Lyssomanes viridis* and all spartaeine salticid genera (*Portia, Brettus, Cyrba,* and *Phaeacius*) studied so far are putatively primitive (Hallas & Jackson, 1986; Jackson & Hallas, 1986a, b). *Thiania bhamoensis* does resemble *L. viridis* and the spartaeines in making egg sacs that are not contiguous with the silk of a nest. However, unlike *L. viridis* and the spartaeines that make the more transparent egg sacs, *T. bhamoensis* spins the flat, densely woven egg sacs, differing from most typical salticid egg sacs. These findings suggest that the non-contiguousness of nest and egg sac silk might be a primitive trait and the typical enclosed nests might be an advanced trait of salticids. If this hypothesis is correct, the ancestors of *T. bhamoensis* were salticids that made typical tubular nests but also kept the primitive trait in which the nest and egg sac silk is not contiguous. The spinning behaviour of *T. bhamoensis* might modify in conjunction with its becoming specialized at living between leaves (Jackson, 1986a), representing a transition from primitive to advanced salticids. However, the phylogeny of salticids is little known.

Interestingly, like *T. bhamoensis, Holcolaetis* and *Euryattus,* two genera of more advanced salticids, also build egg sacs that are not contiguous with the silk of a nest (Jackson, 1985, 1986a). Furthermore, *T. bhamoensis* resemble *Holcolaetis* and *Euryattus* in spinning flat and densely woven egg sacs, and none of these three genera build the typical tubular nests (Jackson, 1986a). This suggests a possible phylogenetic affinity of these three genera (*Thiania, Holcolaetis* and *Euryattus*). However, unlike *T. bhamoensis* that spins the egg sacs between leaves, *Holcolaetis* lays the egg sacs on the trunks of trees and *Euryattus* in rolled up leaves. This may be because of different selective pressures the spiders from these three genera may have evolved the spinning behaviour to use the tree trunk or a leaf, instead of silk, to prevent the nest and thus its egg sac is attached the trunk leaf instead. However, nothing is known about the selective pressures on the spinning behaviour of these three genera. In addition, the phylogenetic affinities of these three genera are also not clear. Obviously, much more comparative information on the biology of salticids is needed.

Agonistic behaviour

In those salticids that have been studied in details, males have large and complex display repertoire (Jackson, 1977a, b, 1980, 1986b, 1989), comparable to the maximum repertoire sizes recorded for mammals, birds, fish and social insects (Moynihan, 1970; Wilson, 1975; Smith, 1977). In its male-male interactions, *T. bhamoensis* performed 12 'major displays' (according to Moynihan's (1970) definition): Hunched posturing

(1), posturing with legs I arched (2) or elevated in Positions 1 and 2 (3, 4), waving with legs I arched (5), bent abdomen (6), abdomen flexed up or down (7), embracing (8), palpal pushing (9), grapple (10), stepping-to-the-side (11), stepping-forward-and-backward (12). This is comparable to repertoire sizes that have been estimated for numerous other salticids (see Jackson, 1988). These crude estimates suggest that complex display repertoires are widespread in Salticidae.

Our data also showed that the agonistic behavior of male *T. bhamoensis* has characteristics in common with that of other salticids (Jackson, 1977a, b, 1980, 1986b, 1989). As in many species of salticids, web-building spiders and other animals, males of *T. bhamoensis* apparently avoid fights by using displays to visually assess the fighting ability of their opponents to win fights. There was a consistent sequence to the contests. All contests began with non-contact displays when participants were at a distance from each other. Display such as the spreading open of the first legs (hunched legs, arched legs and elevated legs) seems to facilitate visual assessment of opponent size. As males of almost all salticid species that have been studied have relatively longer first pairs of legs that are known to be heavily involved in the male agonistic interactions. Clearly, the investigation of the effect of the size of legs on contest outcomes in jumping spiders is needed.

When closely size-matched males of *T. bhamoensis* contacted each other with their palps, they probably used tactile cues (e.g. mass) to assess their relative sizes. In this position, pushing of each other might transmit information to contestants about their relative strength and endurance. Encounters that ended in this manner always occurred in the same temporal sequence (from visual to tactile) and followed a progression of proximity (from far to near). They also appeared to follow a progression of increasing energy expenditure and risk of injury (from lower to higher). The sequence of escalation in fights in *T. bhamoensis* is similar to reports of agonistic interactions in other species of salticids (Wells, 1988; Faber & Baylis, 1993). However, studies of factors such as body size that influence the outcomes of concspecific contests are needed.

ACKNOWLEDGEMENTS

This work was supported by grants to DLi (R-154-000-060-112 and R-154-000-072-112) from the National University of Singapore. We are grateful to the assistance of K. T. Ang for keeping the spiders alive with his ready supply of fruit flies and houseflies. We thank H. K. Yip for his photographic assistance. Some photographs (Figs. 5 & 6) were kindly taken by Robert R. Jackson. Comments and suggestions from Naomi Diplock, Wan She Lee, Lek Min Lim and one anonymous reviewer greatly improved the quality of this manuscript.

LITERATURE CITED

Coddington, J. A. & H. W. Levi, 1991. Systematics and evolution of spiders (Araneae). *Annual Review of Ecology & Systematics*, **22**: 565-592.

Crane, J., 1949. Comparative biology of salticid spiders at Rancho Grande, Venezuela. Part IV. An analysis of display. *Zoologica, New York*, **34**: 159-214.

Faber, D. B. & J. R. Baylis, 1993. Effects of body size on agonistic encounters between male jumping spiders (Araneae: Salticidae). *Animal Behaviour*, **45**: 289-299.

Forster, L. M., 1982. Vision and prey-catching strategies in jumping spiders. *American Scientist*, **70**: 165-175.

Hallas, S. E. A. & R. R. Jackson, 1986. Comparative study of Old and New World 'lyssomanines' (Araneae: Salticidae): utilisation of silk and predatory behaviour of *Asemonea tenuipe* and *Lyssomanes viridis*. *New Zealand Journal of Zoology*, **13**: 543-551.

Harland, D. P. & R. R. Jackson, 2000a. 'Eight-legged cats' and how they see – a review of recent research on jumping spiders (Araneae: Salticidae). *Cimbebasia*, **16**: 231-240.

Harland, D. P. & R. R. Jackson, 2000b. Cues by which *Portia fimbriata*, an araneophagic jumping spider, distinguishes jumping-spider prey from other prey. *Journal of Experimental Biology*, **203**: 3485-3494.

Harland, D. P., R. R. Jackson & A. M. Macnab, 1999. Distances at which jumping spiders (Araneae: Salticidae) distinguish between prey and conspecific rivals. *Journal of Zoology, London*, **247**: 357-364.

Homann, H., 1928. Betrage zur Physiologie der Spinnenaugen. I. Untersuchungsmethoden, II. Das Sehvermoen der Salticiden. *Zeitschrift für Vergleichende Physiologie*, **7**: 201-268.

Jackson, R. R., 1977a. Courtship versatility in the jumping spider *Phidippus johnsoni* (Araneae: Salticidae). *Animal Behaviour*, **25**: 953-957.

Jackson, R. R., 1977b. An analysis of alternative mating tactics of the jumping spider *Phidippus johnsoni* (Araneae: Salticidae). *Journal of Arachnology*, **5**: 185-230.

Jackson, R. R., 1979. Nests of *Phidippus johnsoni* (Araneae: Salticidae): characteristics, pattern of occupation, and function. *Journal of Arachnology*, **9**: 87-92.

Jackson, R. R., 1980. The mating strategy of *Phidippus johnsoni* (Araneae: Salticidae): III intermale aggression and a cost-benefit analysis. *Journal of Arachnology*, **34**: 381-409.

Jackson, R. R., 1982. The behavior of communicating in jumping spiders (Salticidae). In: Witt, P. N. & J. S.

Rovner (eds.), *Spider Communication: mechanisma and ecological significance.* Princeton, New Jersey, Princeton University Press. Pp. 213-247.

Jackson, R. R., 1985. The biology of *Euryattus* sp. indet., a web-building jumping spider (Araneae: Salticidae) from Queensland: utilization of silk, predatory behaviour and intraspecific interactions. *Journal of Zoology, London (B),* **1**: 145-173.

Jackson, R. R., 1986a. Silk utilisation and defensive behaviour of *Thiania,* an iridescent jumping spider (Araneae: Salticidae) from Malaysia. *New Zealand Journal of Zoology,* **13**: 553-561.

Jackson, R. R., 1986b. The display behavior of *Bavia aericeps* (Araneae: Salticidae), a jumping spider from Queensland. *Australian Journal of Zoology,* **34**: 381-409.

Jackson, R. R., 1988. The display behaviour and silk utilisation of *Epeus* sp. indet., a jumping spider (Araneae: Salticidae) from Singapore. *New Zealand Journal of Zoology,* **15**: 455-460.

Jackson, R. R., 1989. Display behaviour of *Corythalia canosa,* an ant-eating jumping spider (Araneae: Salticidae) from Florida. *New Zealand Journal of Zoology,* **16**: 169-183.

Jackson, R. R. & A. D. Blest, 1982. The biology of *Portia fimbriata,* a web-building jumping spider (Araneae: Salticidae) from Queensland: Utilisation of webs and predatory versatility. *Journal of Zoology, London,* **196**: 255-293.

Jackson, R. R. & S. E. A. Hallas, 1986a. Predatory versatility and intraspecific interactions of spartaeine jumping spiders (Araneae: Salticidae): *Brettus adonis, B. cingultus, Cyrba algerina* and *Phaeacius* sp. indet. *New Zealand Journal of Zoology,* **13**: 491-520.

Jackson, R. R. & S. E. A. Hallas, 1986b. Comparative biology of *Portia africana, P. albimana, P. fimbriata, P. labiata and P. schultzi,* araneophagic, web building jumping spiders (Araneae: Salticidae): Utilisation of webs, predatory versatility, and intraspecific interactions. *New Zealand Journal of Zoology,* **13**: 423-489.

Jackson, R. R. & S. D. Pollard, 1997. Jumping spider mating strategies: sex among cannibals in and out of webs. In: Choe, J. C. & B. J. Crespi (eds.), *The evolution of mating systems in insects and arachnids.* Cambridge, Cambridge University Press. Pp. 340-351.

Jackson, R. R. & M. E. A. Whitehouse, 1989. Display and mating behaviour of *Thorellia ensifera,* a jumping spider (Araneae: Salticidae) from Singapore. *New Zealand Journal of Zoology,* **16**: 1-16.

Land, M. F., 1969a. Structure of the retinae of the eyes of jumping spiders (Salticidae: Dendryphantinae) in relation to visual optics. *Journal of Experimental Biology,* **51**: 443-470.

Land, M. F., 1969b. Movements of the retinae of jumping spiders (Salticidae: Dendryphantinae) in response to visual stimuli. *Journal of Experimental Biology,* **51**: 471-493.

Land, M. F., 1971. Orientation by jumping spiders in the absence of visual feedback. *Journal of Experimental Biology,* **54**: 119-139.

Land, M. F., 1974. A comparison of the visual behaviour of a predatory arthropod with that of a mammal. In: C. A. G. Wiersma (ed.), *Invertebrate neurons and behaviour.* Cambridge, MIT Press. Pp. 411-418.

Land, M. F. & D. E. Nilsson, 2002. *Animal eyes.* Oxford, Oxford University Press. 234 pp.

Mann, M. E., T. G. G. Groothuis & J. Wittenberg, 2001. Escalated fighting despite predictions of conflicts outcome: solving the paradox in South American cichlid fish. *Animal Behaviour,* **62**: 623-634.

Moynihan, M., 1970. Control, suppression, decay, disappearance and replacement of displays. *Journal of Theoretical Biology,* **29**: 85-112.

Peckham, G. W. & E. G. Peckham, 1889. Observations on sexual selection in spiders of the family Attidae. *Occasional Papers of the Wisconsin Natural History Society,* **1**: 3-60.

Rashid, N. Y. & M. S. Azirun, 1992. Agonistic behaviour of male fighting spiders *(Thania bhamoensis). Nature Malaysia,* **17**: 121-123.

Richman, D. B. & R. R. Jackson, 1992. A review of the ethology of jumping spiders (Araneae: Salticidae). *Bulletin of British Archnological Society,* **9**: 33-37.

Smith, W. J., 1977. *The behavior of communicating.* Cambridge, Massachusetts, Harvard University Press. 545 pp.

Taylor, P. W., O. Hasson & D. L. Clark, 2001. Body postures and patterns as amplifiers of physical condition. *Proceedings of the Royal Society of London, B* **267**: 917-922.

Wells, M. S., 1988. Effects of body size and resource value on fighting behaviour in a jumping spider. *Animal Behaviour,* **36**: 321-326.

Wilson, E. O., 1975. Sociobiology: *The new synthesis.* Cambridge, Massachuetts, Harvard University Press. 697 pp.

Zabka, M., 1993. Salticidae (Arachnida: Araneae) of the Oriental, Australian and Pacific Regions. IX. General *Afraflacilla* Berland & Millot 1941 and *Evarcha* Simon 1902. *Invertebrate Taxonomy,* **7**, 279-295.