

## Habitat-adapted communication in *Trite planiceps*, a New Zealand jumping spider (Araneae, Salticidae)

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**Abstract** The natural history and intraspecific interactions of *Trite planiceps*, a common New Zealand jumping spider (Salticidae), are described for the first time and discussed in relation to this salticid's unusual microhabitat – the rolled-up leaves of New Zealand flax (*Phormium tenax*) and similar plants. In many respects, *T. planiceps*' display and mating behaviour resembles other salticids. Males have conditional courtship and mating tactics, and the tactics used depend on the female's maturity and location. If in the light, the male uses vision-based courtship and mates in the open; if at a nest (inside a rolled-up leaf), the male uses vibratory courtship and mates inside the rolled-up leaf; if the female is immature but within c. 10 days of maturing, the male

cohabits until the female matures and then mates inside the rolled-up leaf. Regardless of which mating tactic is used, after males mount females there is a phase during which the pair are in physical contact and communicate using tactile signals ('post-mount courtship'). Other sex and age classes of *T. planiceps* also communicate using visual displays when in light, away from rolled-up leaves, and also sometimes employ tactile signals when at nests or during escalated contests in the light. In addition to these typical salticid characteristics, *T. planiceps* has some atypical display behaviours that appear to be adapted for communicating in its unusual habitat. Even when no conspecific has been encountered, *T. planiceps* males sometimes display when approaching openings of rolled-up leaves occupied by conspecific females. These displays closely resemble visual displays used while facing a conspecific in the light. Later, while entering the cavities within rolled-up leaves and while moving about inside simulated rolled-up leaves (glass tubes kept away from visible light and observed using infra-red video), males and females use vibratory displays, tapping the leaf surface with Legs I and vibrating their abdomens, even when no conspecific has been encountered. Finally, when spiders interact within simulated rolled-up leaves, they appear to communicate using both tactile signals and vibratory signals that are transmitted through nests or leaf surfaces. Many other salticids use nests as a medium for transmission of vibratory signals. However, *T. planiceps*' use of the leaves forming its nesting microhabitat for this function is unusual. This is the first study in which infra-red video has been used to observe interactions between salticids under conditions of total darkness for the spider, and also the first report of a salticid possessing a display repertoire for use in darkness but away from nests. We emphasise adaptation for typical habitat as a partial explanation for species differences in salticid communication systems.

**Keywords** communication; displays; salticid; spiders; *Trite planiceps*

## INTRODUCTION

Jumping spiders (Salticidae) have visual acuity unrivalled by other spiders (Land 1985; Blest et al. 1990) and are well-known for use of elaborate vision-based signaling during intraspecific interactions (Peckham & Peckham 1889, 1890; Crane 1949; Forster 1982a; Clark 1994). Salticids are also known for condition-dependent use of signaling based on other sensory modalities when at sites where visual signals would be ineffective (e.g., at nests or when touching conspecifics) (Jackson 1992; Richman & Jackson 1992). Although most salticids fit comfortably within this general scheme, closer inspection soon reveals considerable variation among species both in details of signal design (Crane 1949; Richman 1982) and in the relative importance of signaling based on vision versus other sensory modalities (e.g., Jackson & McNab 1991). Interspecific variation in salticid communication systems is poorly understood at present.

Guilford & Dawkins (1991) identified two main components of signal design, variation in either of which may help to explain species differences in salticid signaling. First, 'strategic design' is the signal's function (what the signal is 'for'). For example, the courtship displays of male spiders may be strategically designed to increase the likelihood that their potentially cannibalistic partners will accept them as mates rather than as meals (Jackson 1980a; Suter & Renkes 1984). Perhaps courtship behaviour varies depending on cannibalistic tendencies of conspecific females (Jackson & Pollard 1997). Second, 'tactical design' is the way in which signals are structured to be efficiently detected, discriminated between and remembered by receivers. Although strategic design has tended to receive the greater attention in studies of the signaling behaviour of animals (e.g., Moller & Pomiankowski 1993; Hasson 1994, 1997; Zahavi & Zahavi 1997), including salticids (e.g., Crane 1949; Jackson 1981; Jackson & Pollard 1997), recent studies suggest that both strategic and tactical features are important for a full understanding of signal design (Johnstone 1997).

Studies of tactical design have identified three variables that appear to be of prime importance: the receiver's sensory abilities (Fleishmann 1988, 1992), the receiver's psychology (Guilford & Dawkins 1991; Jackson & Pollard 1997) and features of the habitat through which signals must be transmitted (Endler 1992). Examples of potentially important habitat features include light intensity for optical signals and density of intervening foliage for audi-

tory signals. In salticids, small body size brings about adaptive trade-offs between the sensitivity and acuity of the principal eyes (Blest 1985). This suggests that, within the salticids, size-associated differences in visual abilities of receivers might partially explain interspecific variation in the visual signaling behaviours adopted by the sender (Crane 1949; Blest 1985). In relation to receiver psychology Guilford & Dawkins (1991) argue that animals evolve display behaviour adapted to each species' characteristic 'psychological landscape'. We currently have only limited understanding of what it would mean to discuss salticid psychological landscapes.

We acknowledge the likely importance of sensory ability and receiver psychology, but the focus of the present paper is on how a salticid's habitat may influence the communication system used. Evidence that habitat features may drive the evolution of signal design in animals has come especially from studies on fish, birds and lizards. In particular, colour and marking patterns are often adapted to contrast with the signaling animal's background and thereby increase signal apparency (Endler 1987, 1992, 1995; Marchetti 1993; Fleishman et al. 1993). Also, species and population differences in bird songs have been explained as adaptations related to constraints on sound propagation in typical habitat (Johnstone 1997). In the most detailed study of how habitat may influence signal design in spiders, Scheffer et al. (1996) showed that in two closely related North American wolf spiders (Lycosidae), *Schizocosa ocreata* and *S. rovneri*, species differences in the courtship signaling bear a strong relationship with habitat. Males of both species court females using vision-based (leg-waving) and also vibratory (stridulation) signals, but *S. ocreata* relies more heavily on the vision-based component. In these species, which of the two signaling channels is dominant appears to be an adaptation to the species' habitat: *S. rovneri* lives in a habitat where substrate vibrations carry across considerable distances, but *S. ocreata* lives in a habitat that impedes efficient transmission of similar signals. *Schizocosa ocreata*'s greater reliance on visual signaling appears to be an adaptive response to habitat-imposed constraints on vibratory signaling (McClintock & Uetz 1996).

Salticids occupy a wide range of terrestrial habitats. Common habitats in nature include surfaces of leaves in tropical rainforests (e.g., Jackson 1983, 1986a, 1988), sandy beaches next to the ocean (e.g., Jackson et al. 1990), and stones on the ground (Jackson & Griswold 1979). Many species also frequent houses and other man-made habitats (e.g.,

Jackson & Willey 1995). *Trite planiceps* is a widespread New Zealand salticid with an especially unusual habitat. This species lives primarily in association with New Zealand flax bushes (*Phormium tenax*) and similar plants (Forster & Forster 1973; Forster 1979). The leaves of *P. tenax* are typically 1–2 m long and 50–100 mm in width over most of their length. They taper to a point at the end. *Trite planiceps* hunts for prey and interacts with conspecifics on the surfaces of flax leaves, where ambient light levels permit vision-dependent behaviour (Forster 1977, 1982a), but *T. planiceps* also builds its nests and spends much of its time in the dark cavities formed by desiccating, rolled-up leaves (Forster & Forster 1973). For *Trite planiceps*, encounters between conspecifics potentially take place 1) in the open in the light (a universal context for all salticid species studied), 2) in the dark with nests present to carry silk-bourne vibratory signals (also known for most salticid species studied), and 3) in the dark without nests present to carry silk-bourne vibratory signals (a previously unreported context for encounters between salticids).

We consider whether the unusual physical qualities of *T. planiceps*' habitat has moulded the systems by which conspecifics communicate. Some details of *T. planiceps*' signaling and hunting behaviour are available from earlier studies (Forster 1977, 1979, 1982a,b; Jackson 1990; Jackson & van Olphen 1991; Tarsitano & Jackson 1992; Taylor et al. 1998), but this is the first detailed study concerned specifically with *T. planiceps*' interaction behaviour and natural history.

## METHODS

### Collection and maintenance of spiders

Spiders were collected from dense stands of New Zealand flax (*Phormium tenax*) near Christchurch, New Zealand. Standard procedures were used for maintenance and terminology, including the convention that the terms 'usually' or 'generally', 'sometimes' or 'occasionally', and 'infrequently' or 'rarely' indicate frequencies of 80% or more, 20–80%, and 20% or less, respectively (Jackson & Hallas 1986a). 'Male' and 'female' refer only to adults, 'subadults' are spiders in their penultimate instar, and 'juvenile' includes all active stages prior to the penultimate instar.

### Procedures for observing interactions in the laboratory

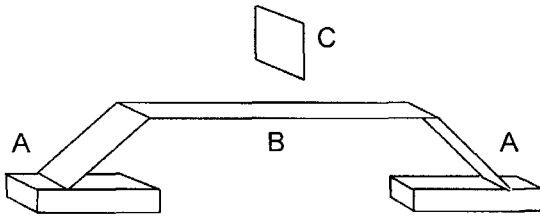
For all interactions, pairs of spiders were randomly selected from a laboratory stock, except that no individual spider was used more than three times in any particular interaction type (e.g., male-male) or allowed to interact more than once with any other conspecific individual. Interactions were video recorded, and they were never staged within 2 h of the beginning or end of the laboratory light phase (12L:12D; lights on at 0800 hrs).

Preliminary observations were staged in simple arenas using the procedures that have been standard in previous studies of salticid interactions (Jackson & Hallas 1986a). However, because we were especially interested in understanding how interactions and habitat are interrelated, we later staged interactions in special arenas designed to simulate the flax-leaf sites where interactions would normally take place in nature.

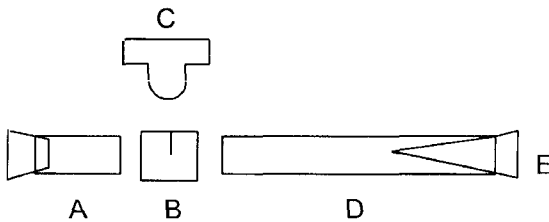
### In the light: Encounters on artificial flax leaves

In nature, encounters in daylight would normally take place on the long, narrow, leaves of flax plants. To simulate this habitat, we tested *T. planiceps* pairs on a polyacetate platform (70 mm wide, 300 mm long, Fig. 1) covered with opaque plastic insulating tape and connected at each end to a glass ramp (70 mm wide, 150 mm long) supported by a wooden base and angled up at 45° (entire set-up called the testing arena). To start a test, two spiders were released, one on each of the two ramps. Following release, the spiders usually walked up the ramp and onto the platform. Initially, an opaque partition was in place at the platform's mid-point. When both spiders were on the platform, the partition was removed (start of test) so that spiders could see each other and interact. Encounters staged on this platform are referred to as 'in the light'.

In previous studies, consideration has been largely restricted to encounters in which the spiders concurrently see (eyes fixated on the other spider) and react to each other ('interactions'). However, in preliminary observations of *T. planiceps*, it became evident that consideration should also be given to situations in which one spider might see the other without being seen itself. We refer to these encounters as 'spectations'. Interactions and spectations ended when one spider decamped and the other spider did not follow or when one spider left the arena



**Fig. 1** Diagram of testing arena used to stage *Trite planiceps* interactions that would in nature take place on leaf surfaces in daylight. (A) Ramp and base. (B) Platform. (C) Screen (raised). See text for details.



**Fig. 2** Diagram of testing arena used to stage *Trite planiceps* interactions that would in nature take place in dark cavities within rolled-up leaves. (A) Transfer chamber. (B) Collar with slit to take opaque screen. (C) Opaque screen (removed and rotated 90°). (D) Glass tube. (E) Cone. See text for details.

(platform and ramps). A spectation might also end when the other spider oriented so that the two spiders faced each other, thereby initiating an interaction.

#### In the dark: Encounters inside simulated rolled-up flax leaves

We allowed spiders to interact inside glass tubes in the absence of visible light. This simulated spiders in nature meeting conspecifics in the dark cavities of rolled-up flax leaves. The glass tubes, being 150 mm long and 10 mm in internal diameter, approximated the dimensions of the rolled-up leaves from which spiders were collected. In nature, rolled-up leaves taper at each end, and spiders inside rolled-up leaves might evade intruders by retreating into these narrow spaces. In the laboratory, a 60 mm-long cone at one end of the glass tube provided a narrow space into which spiders could retreat (Fig. 2). Interactions taking place inside the glass tubes were observed using an infra-red light source (GTE Mini-Kat) and an infra-red sensitive video (Burle TC300E) set up inside a light-proof cabinet and connected to a monitor outside. Because salticid eyes are not sensitive to infra-red light (Blest et al. 1981;

Yamashita 1985; Peaslee & Wilson 1989), this set-up was equivalent to total darkness.

Before testing began, one spider, the 'resident', was allowed to occupy the glass tube. To begin testing, another spider, the 'intruder', was released into the tube. Two groups of females were used: 1) females with no nest present; 2) females with a nest present in the tube. For group 1 (no nest), the resident was placed in the tube and the tube was placed inside the light-proof cabinet only 1 h before testing. For group 2 (nest present), the resident, while still in its cage, was given access to the tube 5 days before testing began by inserting the open end of the tube (i.e., the end not blocked by the cone) through a hole in the top of the spider's cage. The space inside the tube was kept dark by covering it with an opaque sheath. This being the only permanently dark space available for the spider, the tube was adopted by the spider as a nesting site. One hour before testing began, the tube containing the resident was removed from the cage, plugged, and placed in the light-proof cabinet. Thirty minutes later, another spider, the intruder, was taken from its cage into a clear plastic 'transfer chamber' (40 mm long, 10 mm internal diameter; Fig. 2). A removable opaque partition was inserted into a collar at one end of the transfer tube. Escape by the spider was prevented by a cork inserted into the other end.

By reaching through an opaque sleeve (made from heavy black satin) and using the infra-red video system for viewing, we could manipulate the tubes inside the light-proof cabinet. The collar of the transfer chamber was slid over the open end of the tube containing the resident. The partition was removed and, once the intruder left the transfer chamber and entered the resident's tube, the cork in the other end of the transfer tube was carefully removed. Removing this cork allowed either or both spiders to end the test by leaving the tube.

#### Measuring spider size

The influence of relative size on tendency to initiate and terminate spectations and interactions was investigated. While the spider was subdued under carbon dioxide, cephalothorax width was measured to the nearest 0.05 mm at the position of maximum width using an ocular micrometer. Maximum cephalothorax width is commonly used as a measure of spider size because cephalothorax dimensions are static within an instar (Hagstrum 1971), whereas measures that include the abdomen (e.g., mass and body length) vary from day to day in relation to feeding and reproductive state. By staging encounters

involving different classes of individuals (e.g., male-female, male-juvenile), the influence of a spider's sex and maturity on tendency to see the other spider first or tendency to incite or avoid interactions could be determined.

### Behaviour when entering rolled-up leaves

Leaves containing females on nests were collected in nature the day before testing. To set up a test, a leaf was clamped onto a laboratory stand so that it angled upward at 45° from the bench, this being the approximate vertical orientation of leaves in nature. A test spider (male or female) was then released at the bottom of the leaf by opening and inverting its cage, allowing the spider to jump onto the leaf. The spider then walked about freely until it entered the cavity of the rolled-up leaf. The test ended if the spider departed by walking or jumping off. Each rolled-up leaf was used only once.

### Statistical analyses

Continuous data sets failed assumptions of parametric tests and were instead compared using Mann-Whitney *U*-tests. For data sets related to frequency, where there were only two classes (i.e., binary), comparisons were made using binomial tests. When *N* was small ( $n < 35$ ), we used Table D in Siegal & Castellan (1988). When *n* was large ( $n > 35$ ), an approximation to the normal distribution (*z*) with correction for continuity was used (Siegal & Castellan 1988). When considering which spider saw the other first, 2-tailed *P*-values are given because we make no prediction about direction. However, previous studies of other salticids (e.g., Wells 1988; Jackson & Cooper 1991; Faber & Baylis 1993) lead us to predict that smaller individuals (in the light or in the dark) and intruders (in the dark) will tend to decamp first, and 1-tailed *P* values are given for these comparisons.

For tests of independence ( $2 \times 2$  contingency tables, 1 *df*), *G*-tests with William's correction were carried out as outlined in Sokal & Rohlf (1981).

## OBSERVATIONS

### Morphology and appearance

*Trite planiceps* adults have dark brown cephalothoraces and Legs I. Legs II-IV are amber and, in both sexes, Legs I are much longer and heavier than the other legs. When viewed from above, the abdomen has a central yellow longitudinal band, with a brown stripe on either side. The abdomen is brown

underneath and yellow on the sides. Juveniles resemble females, except that their Legs I are not so enlarged and darkened as those of adults, and they have a pale yellow medial stripe on the dorsal carapace. Males differ from females by having a dense row of dark hairs above the anterior median eyes, longer chelicerae and longer Legs I. Also, males have shorter abdomens in relation to cephalothorax length. Most males and females collected from nature were 2.7–3.1 mm in cephalothorax width and 8–10 mm in body length (minimum: 2.4 mm width, 6 mm length) (maximum: 3.6 mm width, 14 mm length). For a colour photograph of a *T. planiceps* female, see Moffett (1991).

### Locomotion and resting posture

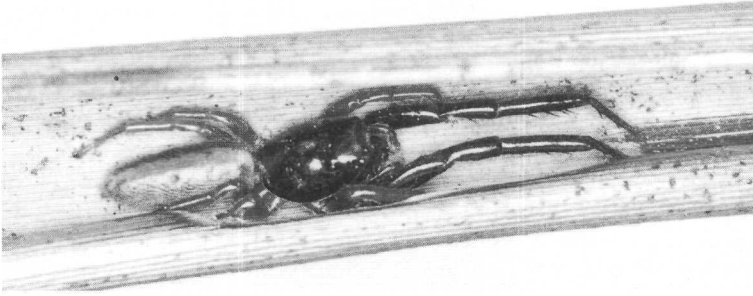
When no other route was available or when they had been startled, *T. planiceps* adults sometimes made leaps of 150 mm or more, but routine locomotion was usually by walking in intermittent bursts lasting 1–5 s and covering 150 mm or less. Pauses between bouts of stepping usually lasted less than 10 s, but infrequently lasted as long as 1 min. During pauses, spiders palpated the substrate and pivoted about.

Whether inside or outside a rolled-up leaf, *T. planiceps* tended to adopt a characteristic resting posture: the second and third pairs of legs were tucked in close to the body; Legs I extended forward and converged; Legs IV extended rearward; the body was held close to the substrate; palpal femora were raised and held together so that the distal palp segments hung straight down almost parallel in front of the chelicerae (Fig. 3). This resting posture contrasted with that of other salticids, which typically spread their legs outward, more or less evenly spaced around the body.

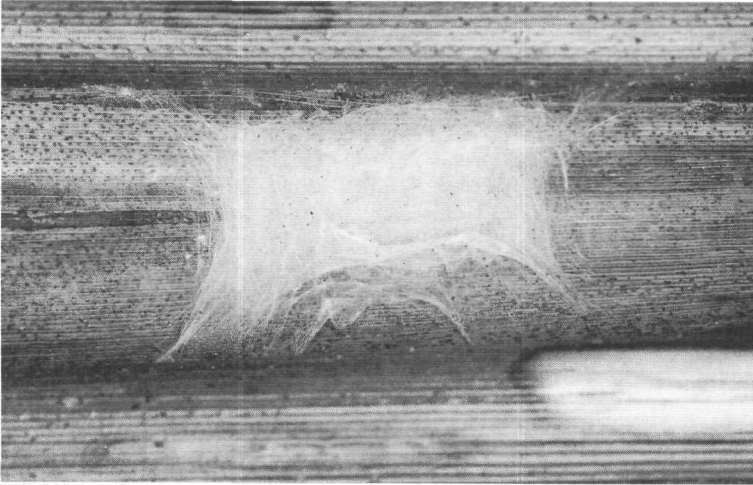
### Nesting sites and nest structure

In nature, juveniles, subadults and females were usually found resting in nests in the cavities formed by dead, rolled-up leaves. Nests built by juveniles and subadults were flat, tubular silk cocoons with a door at each end (Fig. 4). Such tubular enclosing cocoons are typical of many salticid species. Nests built by adult *T. planiceps* females, non-enclosing silken platforms (Fig. 5), were atypical for a salticid. In nature, *T. planiceps* females were usually found resting on their non-enclosing nests facing the opening of their rolled-up leaf. Normally, egg sacs were incorporated into the silk of these platforms.

In the laboratory, nests built by females in darkened glass tubes closely resembled nests built in



**Fig. 3** *Trite planiceps* male in resting stance. Legs held in line with the spider's body.



**Fig. 4** Nest built by *Trite planiceps* juvenile in cavity within rolled-up flax leaf (leaf unrolled to photograph).

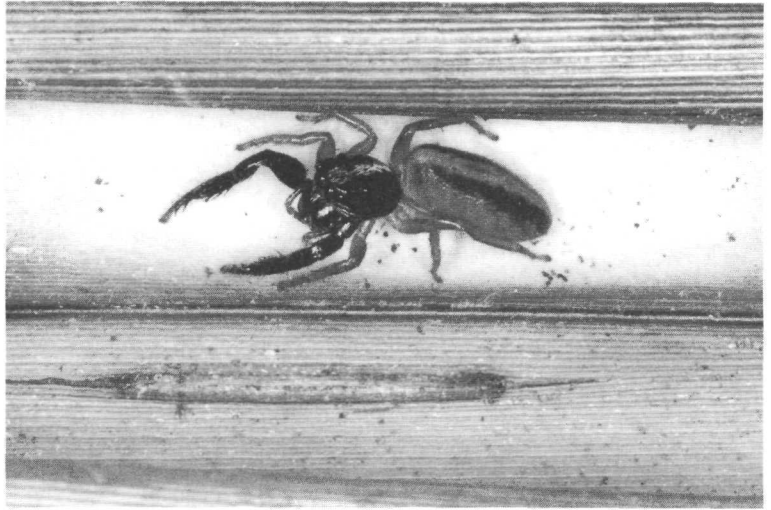
nature. Before ovipositing in the laboratory, females built a thin silk platform 1.5 and 2–3 times their own length and width, respectively. They next oviposited successive egg batches (each containing 8–40 eggs) on the same platform. Intervals between successive egg batches ranged from one day to many weeks. Each egg-batch was enclosed by its own silk casing, and fresh egg-batches were deposited immediately adjacent to, and partly overlapping, older egg batches. As many as 7 egg batches were observed in a single nest in nature, and a nest might simultaneously contain eggs, post-embryos and first instar juveniles (dispersal stage). If rolled-up leaves in nature or glass tubes in the laboratory were more than 10 mm in diameter, females sometimes built silk roofs connected to the leaf or glass surface opposite the nest. Roofs never touched nests, although the gap between nests and roofs was sometimes only just large enough for residents to pass through. Roofs were also built if leaves had been split open above the nest.

Except for recently moulted individuals (evident from pale coloration), males were observed in nests in nature or in the laboratory only when they were cohabiting with subadult females. Nests occupied by cohabiting males were similar to those built by juveniles and subadults, but were sparsely woven and never completely enclosed the spider. Both in nature and in the laboratory, cohabiting males usually were not in nests but instead simply stood between the subadult female's nest and opening of the leaf or glass tube. On five occasions in nature, two adult males were found cohabiting with one subadult female in a nest in a rolled-up leaf. In each case, one male was found at each end of the subadult female's nest. That is, one of the males would have to move past both the subadult female and the other male before it could leave the cavity in the rolled-up leaf.

#### **Elements of behaviour during intraspecific interactions**

1. **Cephalothorax lowered and raised.** The nor-

**Fig. 5** *Trite planiceps* female standing on her nest (leaf unrolled to photograph).



mal position of the cephalothorax was 1–2 mm above, and parallel to, the substrate. When lowered, however, the sternum touched or was less than 1 mm above the substrate. When raised it was held 2–4 mm above the substrate.

**2. Lean and tilt.** When in the normal standing posture, a spider's cephalothorax was positioned more or less in the centre of its leg span. To lean, a spider flexed its legs, without repositioning the tarsi, so that the cephalothorax was moved further anteriorly ('lean forward'), posteriorly ('lean backward') or to one side ('lean sideways') than its normal standing posture. To tilt, a spider either raised the anterior end of the cephalothorax so that it angled as much as 45° up from the posterior end ('tilt upward') or rotated the cephalothorax to one side by as much as 30° ('tilt sideways').

**3. Step in place.** When stepping in place, one or more leg tarsi were repositioned (but no more than once) so that the spider moved by less than 2 mm forwards, backwards or to one side.

**4. Bent abdomen.** When bent, the posterior end of the abdomen was directed as much as 45° to the left or right of the cephalothorax's sagittal plane and usually rested on the substrate.

**5. Twitch abdomen.** A spider twitched its abdomen by rapidly moving it up and down 5–20° from the pedicel (3–8 s<sup>-1</sup>) in bouts lasting 0.5–3 s. Within single bouts, rate and amplitude of twitching tended to vary without any apparent pattern.

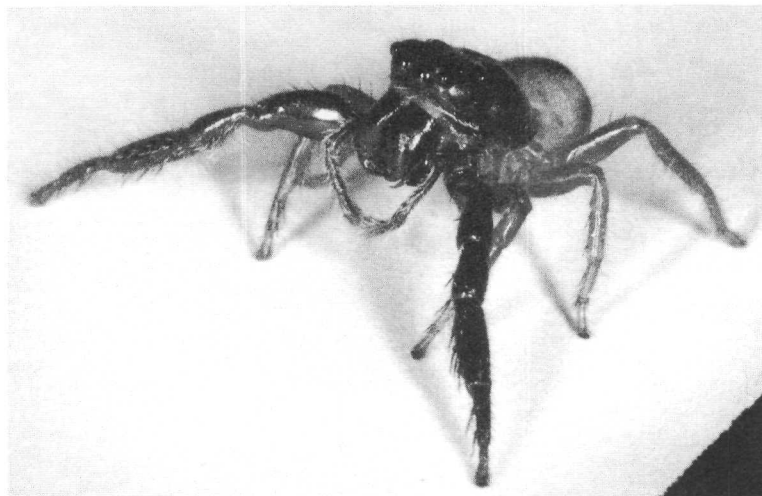
**6. Opened chelicerae and extended fangs.** Opened chelicerae were held with the basal segments spread

apart. Spiders with opened chelicerae sometimes also had their fangs extended, and the degree of fang extension was variable, ranging from barely perceptible to c. 90° from the resting position. Whenever spiders had their fangs extended, their chelicerae were also opened.

**7. Palp positions.** *Normal palps* were held with femora more or less parallel to the substrate and converging slightly in front of the spider's face, with the rest of each palp hanging either straight down alongside the chelicerae or so that the two palps converged slightly. *Femora of frontal palps* angled up and converged strongly so that the palpal patellae almost touched; distal palp segments hung straight down, obscuring the chelicerae. *Femora of arched palps* angled down and out to the side; from the femur to the tarsus, each palp was angled inward so that the tips converged beneath the chelicerae (Fig. 6). *Downward palps* were positioned straight down, more or less parallel to the chelicerae, with all joints close to full extension (Figs. 8, 11, 12). *Femora of raised palps* angled upward and slightly outward from the sagittal plane; the rest of the palp angled straight down alongside the femur.

**8. Palpate.** When palpating, spiders contacted the substrate with their moving palps. Three distinct patterns of palpating were discerned; 'flicking', 'sliding' and 'up-and-down' palpating. To flick, spiders moved their palps rapidly (cycle duration, c. 0.1 s) backward and forward 0.1–0.5 mm, primarily by flexion and extension at the femur-patella, making only very brief contact with the substrate during each cycle. Intervals between flicks within a bout were





**Fig. 6** *Trite planiceps* female posturing with cephalothorax raised, legs in type 2 erect position and palps arched.

highly variable (0.2–5 s). The whole palp moved when sliding so that the tarsus continuously and smoothly rubbed against the substrate. When up-and-down palpating, the whole palp was repeatedly and rapidly raised c. 0.5 mm and then lowered onto a nest (2–5 cycles  $s^{-1}$ ). Bouts of up-and-down palpating usually lasted 1–3 s and contact of the palps with the silk was forceful (distinct indentations could be seen in the nest surface). Spiders occasionally palpated with a single palp, but usually both palps were moving. Phasing of the two palps tended to be extremely variable during all types of palpating, although approximately alternating was the most common.

**9. Normal leg posture.** When not displaying, *T. planiceps* usually held Legs I spread no more than  $20^\circ$  to the side with all joints flexed slightly and the tarsi resting on the substrate.

**10. Erect legs.** Erect Legs I were held with all joints close to fully extended so that they had a stiff appearance along their entire length. Four modal positions of erect legs were observed. ‘Type 1 erect legs’ were extended in front of the spider, within  $20^\circ$  of parallel to each other and the substrate (Fig. 12). ‘Type 2 erect legs’ were spread c.  $45^\circ$  to the side, with their tarsi directed downward and touching, or less than 1 mm above, the substrate (Fig. 6). ‘Type 3 erect legs’ were similar to type 2 except that their tarsi were held approximately parallel to the substrate, angling upward no more than  $20^\circ$  (Fig. 7). ‘Type 4 erect legs’ were like type 3 except that they angled  $20$ – $70^\circ$  upward.

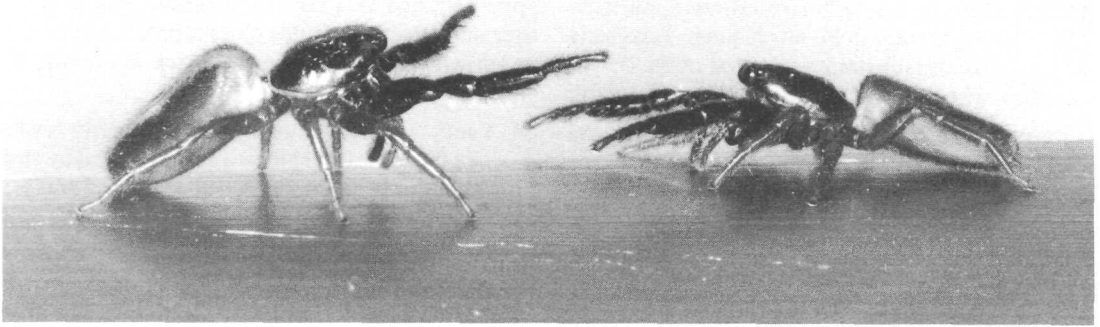
**11. Semi-erect legs.** Semi-erect legs were like corresponding erect legs except that the femur-patella joints were flexed  $10$ – $30^\circ$  (Fig. 8). Joints distal to the femur-patella were either fully extended or flexed only slightly so that each Leg I arched gradually along its entire length.

**12. Hunched legs.** When hunched, femora of Legs I angled upward c.  $45^\circ$  and were spread c.  $45^\circ$  outward from the cephalothorax’s sagittal plane. Legs I were flexed strongly at the femur-patella so that tibiae were directed straight down, perpendicular to the substrate, and the tibia-metatarsus joints were flexed so that tarsi converged. Tarsi of hunched legs either touched the substrate or were no more than 1 mm above it. Hunching spiders always held their cephalothoraces raised.

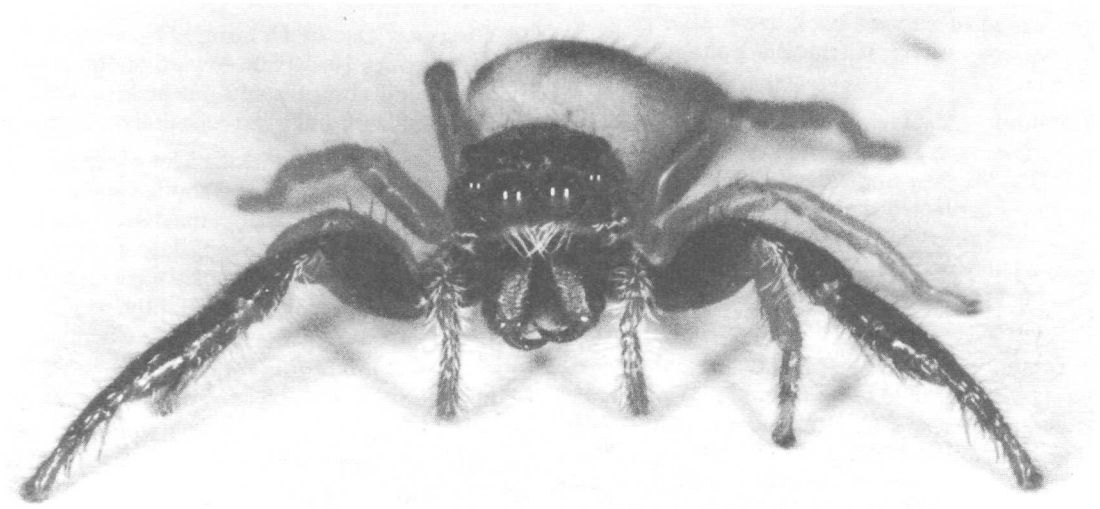
**13. Posture.** Spiders postured by standing still or walking with Legs I erect (‘erect posturing’), semi-erect (‘semi-erect posturing’) or hunched (‘hunched posturing’).

**14. Gesture.** To gesture, a spider displaying with Legs I erect or semi-erect (type 1, 2 or 3) moved Legs I so that they angled further upward, and then immediately, or after stepping 1–3 paces toward another spider, lowered them back down again. For example, a spider displaying with Legs I in the type 3 erect position might raise Legs I to the type 4 erect position and then return to the type 3 erect position. Sometimes, a spider raised Legs I from erect and lowered them to semi-erect, or vice versa. Upward movement tended to be faster than downward, and the whole cycle typically took 0.2–0.5s.





**Fig. 7** *Trite planiceps* females interacting. Female on left displaying with cephalothorax raised. Female on the right displaying with cephalothorax lowered. Both spiders' Legs I are in type 3 erect position.



**Fig. 8** *Trite planiceps* female displaying with palps downward and Legs I in type 2 semi-erect position.

**15. Stamp.** With Legs I in the type 2 erect or semi-erect position, a spider stamped by lifting both Legs I off the substrate  $10\text{--}70^\circ$  in matching phase and then immediately, or after walking 1–3 paces toward another spider, lowered them back down to the type 2 erect or semi-erect position. Upward and downward strokes were comparable in speed and the whole cycle took 0.1–0.2 s. Tarsi I usually struck the substrate forcefully on the downstroke. Although spiders sometimes stamped several times in rapid succession, there was usually a distinct pause of at least 0.5 s between stamps.

**16. Wave.** A spider posturing with Legs I in the

type 2 or type 3 erect or semi-erect position waved by moving Legs I up and down (matching or alternating phase). The legs remained spread c.  $45^\circ$  to either side throughout the cycle and at the highest point the legs angled as much as  $60^\circ$  upward from the substrate. Males raised and lowered Legs I faster than did females (cycle durations: 0.1–0.2 s for males, 0.2–0.5 s for females). Spiders sometimes first raised Legs I in matching phase, next waved the raised legs 2–4 times in alternating phase, then ended the bout by waving once or twice in matching phase.

**17. Swipe.** Spiders swiped by erratically raising and lowering Legs I by as much as  $70^\circ$ . All joints

distal to the femur tended to stay at close to full extension, and the up-and-down movement took 0.2–0.5 s. The spider swiped with one or with both legs simultaneously. When both legs moved simultaneously, phasing tended to be alternating. Tarsi only rarely touched the substrate at the end of the downstroke and, when they did, contact was not forceful.

**18. Paw.** To paw, spiders lifted Legs I from the normal position until they were directed as much as 30° upward, and then immediately lowered them so that they gently touched another spider or the substrate (cycle duration 0.5–1 s). Leg movement was achieved mainly by flexion and extension at the trochanter-femur and at the femur-patella joints so that Tarsi I moved directly up, then forward and directly down, and finally back after touching the substrate. Spiders sometimes leaned or stepped forward immediately before or while lifting Legs I, and then leaned or stepped back again after pawing. Phasing was variable, but matching phase was most common.

**19. Pound.** A spider pounded by moving one or, more often, both Legs I up and down. The leg was lifted 30–70° then immediately lowered so that it forcefully contacted the substrate (cycle duration 0.1–0.3 s). Spiders sometimes stepped or leaned forwards as they pounded, but stepped or leaned back again after pounding. If both legs pounded, phasing tended to be matching.

**20. Drum.** To drum, a spider raised and lowered Legs I by 30–70° 2–3 times in rapid succession (cycle duration 0.1–0.2 s). Drumming legs forcefully contacted another spider or the substrate, usually in alternating phase. Spiders usually leaned or stepped forward, or walked forward several paces, immediately before or while raising legs at the beginning of a bout of drumming. They leaned, stepped or walked back again after drumming.

**21. Strike.** While walking toward another spider with cephalothorax raised, one spider struck another by repeatedly and rapidly raising and lowering Legs I 50–70° so that Legs I forcefully hit the other spider on the downstroke (2–5 s<sup>-1</sup>). There was no pause between up and down strokes, and the two legs moved in approximately alternating phase.

**22. Stalk.** Flies and other insects were stalked by slowly creeping forward with cephalothorax lowered, palps frontal, Legs I extended straight out in front of the body, and the abdomen raised parallel to the substrate (Forster 1977). Conspecifics were sometimes stalked in a comparable manner.

**23. Flicker.** To flicker, a stalking spider rapidly raised and lowered Legs I (alternating phase; c. 4 s<sup>-1</sup>; c. 2 mm amplitude at the tarsi). At the same time, the spider rotated its palps in matching phase, but in opposite directions (palps close together while moving downward, but further apart while moving upward).

**24. Veer.** Instead of taking a path directly toward or away from another spider, a spider veered by stepping to one side as it approached or backed away. A spider that was veering continuously faced the other spider.

**25. Zig-zag dance.** Males zig-zag danced while facing, and usually approaching, females. The dancing male repeatedly veered 5–30 mm to one side, paused for 0.5–5 s, then veered 5–30 mm to the other side, tending to get closer to the female in a series of arcs.

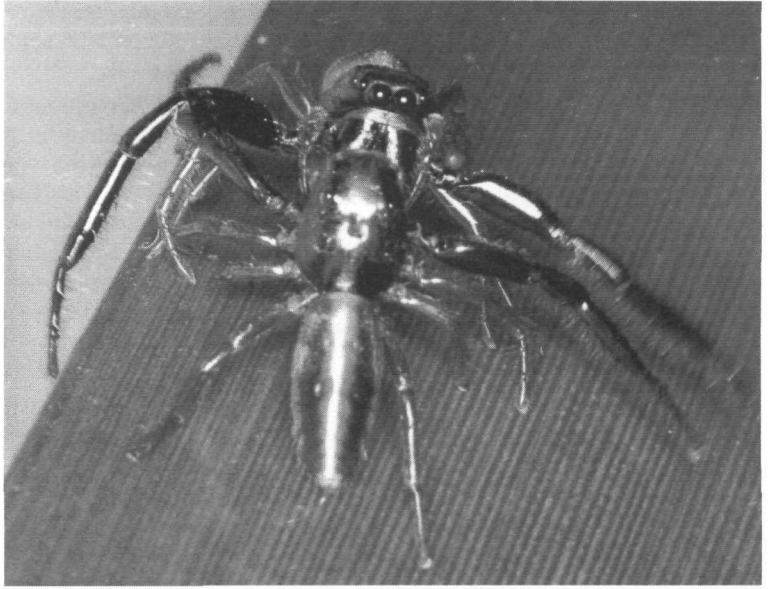
**26. Charge.** One spider charged by suddenly and rapidly running 10–40 mm toward another spider then stopping abruptly without making contact. Charging spiders usually had cephalothoraces raised.

**27. Long leap.** When making a long leap, one spider jumped 20–80 mm toward another spider. Upon landing, usually there was contact with the other spider. Just before making a long-leap, the spider repositioned Legs III and IV so they were close to the body then leaned backwards slightly. During the leap, all joints of Legs I and II were extended rapidly so that tarsi were directed upwards c. 30° in front of the spider's body.

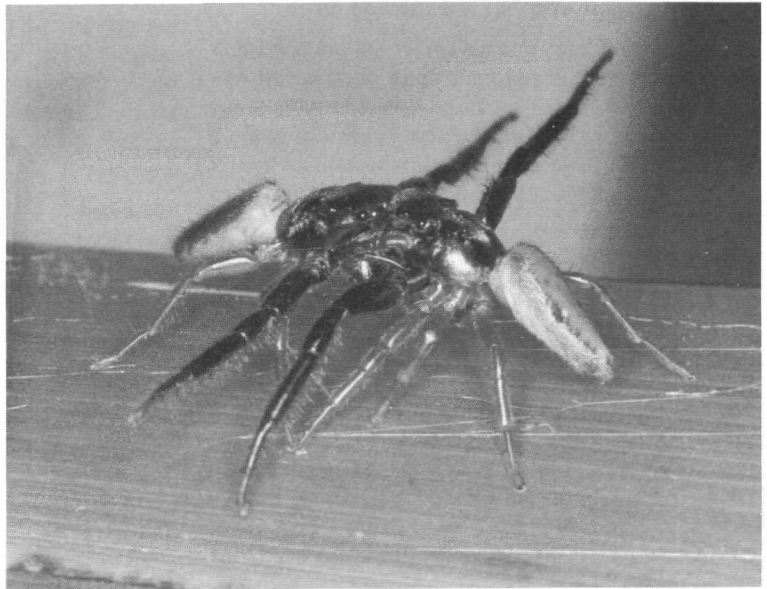
**28. Embrace.** Embracing spiders stood with faces touching. Each spider's palps were raised and extended forward, overlapping those of the other spider (Figs. 9, 10). Embracing spiders usually opened their chelicerae and extended their fangs. Two types of embracing (type 1 and type 2) were observed. When 'type 1 embracing', each spider's Legs I were perpendicular to the cephalothorax, approximately parallel to the substrate and with all segments distal to the trochanter pressed against the other spider's Legs I. While type 1 embracing, each spider sometimes also pressed its Legs II against those of the other spider, but contact between these legs was only at the tarsi. When 'type 2 embracing', each spider's Legs I were extended forward and loosely draped over the other spider (Fig. 9).

**29. Duel.** Embracing spiders duelled by waving fully extended Legs I up and down perpendicular to the sagittal plane (Fig. 10). Amplitudes (20–100°) and rates (2–8 s<sup>-1</sup>) were highly variable within each

**Fig 9** *Trite planiceps* males in type 2 embrace. Palps raised and overlapping. Faces touch. On one side, Legs I draped over the other spider. On other side, spiders duelling. Hooking and pulling with Legs II.



**Fig. 10** *Trite planiceps* males duelling. Legs I waving up and down perpendicular to sagittal plane while spiders push against each other.



bout. Spiders sometimes duelled with only one Leg I, but they usually used both.

**30. Push down legs.** To push down another spider's legs, a duelling spider moved one fully raised Leg I (approximately perpendicular to the substrate) forward c.  $10^\circ$  then lowered it straight down to the side so that it contacted the other spider's Leg I, pushing it downward. Sometimes there was little or no down-

ward movement, apparently because the other spider resisted. However, a spider sometimes pushed the other spider's Leg I down to the substrate and held it there for c. 1 s, after which duelling resumed.

**31. Hook and pull.** To hook, a spider in a type 2 embrace used one or both Legs I, and sometimes also one or both Legs II, to reach around the legs, abdomen, or cephalothorax of the other spider (Fig. 9).

The spider then pulled by flexing the hooking legs. While hooking and pulling, the spider sometimes lifted the other spider's legs off the substrate or pulled the other spider's cephalothorax abruptly forward.

**32. Push.** Embracing spiders pushed against each other by attempting to step forward. One spider usually managed, apparently against considerable resistance, to force the other to step or slide backwards.

**33. Decamp.** To decamp, one spider walked, ran or jumped away from the other. Walking was usually forwards (i.e., decamping spider faced away from other spider). However, spiders also sometimes decamped by walking backwards (i.e., a decamping spider faced the other spider while moving away). Spiders that decamped by backing away usually postured with type 4 erect legs until 80–100 mm from the other spider, then turned and ran away.

**34. Watch and follow.** A spider watched by turning to maintain orientation toward the other spider. A spider followed by running, walking or stalking toward a conspecific that was moving away.

**35. Lunge and grab.** One spider lunged at another by suddenly and abruptly leaning or stepping forward (duration c. 0.1 s). Legs I were extended upwards and forwards during the lunge. To grab, a lunging spider extended Legs I over another spider while leaning forward and then rapidly flexed Legs I, grasping at the other spider. Spiders usually leaned backwards immediately after lunging or after lunging and grabbing. If they grabbed, backward movement was rapid (c. 0.1 s). However, if they did not grab, backward movement tended to be much slower (c. 0.5 s).

**36. Thrust.** Thrusts resembled lunges except that the spiders kept their cephalothoraces raised and the tarsi of all legs remained on the substrate. Flexing Legs I, the spider leaned forward and brought its face forward approximately to the position of Tarsi I. Bouts were usually of two or three thrusts 1–5 s apart.

**37. Chew and tug.** After inserting its extended fangs into the silk of a nest, the spider chewed by opening and closing its chelicerae. Chewing spiders sometimes used their palps or Legs I to push silk between the chelicerae. While gripping the silk with its chelicerae, a spider tugged by moving its cephalothorax up and down 2–4 mm.

**38. Probe.** While probing, Legs I rested on the nest surface. By moving its Legs I backwards and for-

wards, usually in matching phase, 1–2 mm at 1–2 s<sup>-1</sup>, the probing spider repeatedly pushed and pulled on the silk.

**39. Pre-mount tap with legs.** A male, while standing directly in front of a female, began pre-mount tapping with legs by reaching Legs I over the female, lowering his Tarsi I onto the female's legs, cephalothorax or abdomen. Then, while in this posture, the male tapped the female either by moving the whole Leg I up and down 1–2 mm or, more commonly, by flexing and extending the tibia-metatarsus (4–6 s<sup>-1</sup>). Phasing was sometimes variable, but usually approximately alternating.

**40. Pre-mount tap with palps.** While pre-mount tapping with legs, males sometimes also pre-mount tapped with palps: the entire palp, while extended forward, was repeatedly raised and lowered c. 0.5 mm at 2–4 s<sup>-1</sup>. While tapping, palp tarsi repeatedly touched the female's palps, chelicerae or cephalothorax.

**41. Mount and post-mount courtship.** Males mounted by walking onto females (Fig. 12). Usually, the female was facing toward the male when he mounted her, but males infrequently mounted females that were facing to the side or even directly away. The male's behaviour while mounted, but excluding copulation, is referred to as 'post-mount courtship'.

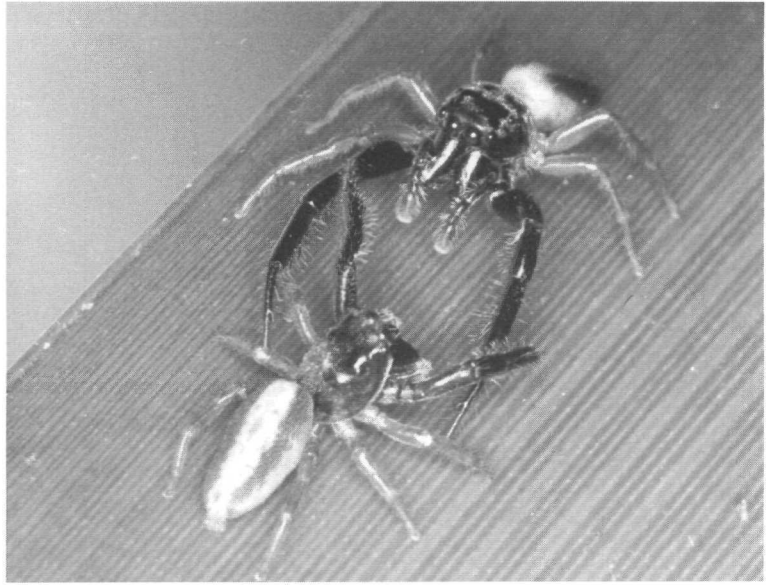
**42. Fend.** Females sometimes fended off males that tried to mount by raising one or, more often, both Legs I, thereby preventing mounting (Fig. 11). When fending males off, females usually tilted their cephalothoraces upward.

**43. Spin.** To spin, a spider deposited draglines by sweeping its abdomen from side to side. Males spun when walking over areas that had been recently walked across by females (female's draglines present) and when mounting. When he was spinning while walking over areas covered by a female's draglines, the male usually swept his abdomen only once per step. However, when spinning while mounting, males sometimes swept their abdomens at rates as rapid as 4 cycles per step. Males rarely spun while standing in place.

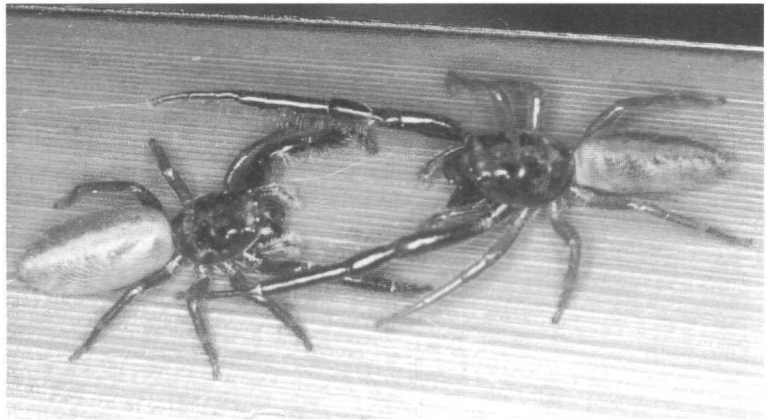
**44. Shudder.** After mounting, a male shuddered with Tarsi I touching the female's abdomen. During the shudder, his whole Leg I moved up and down rapidly at low amplitude (amplitude 0.1–0.5 mm; rate 5–10 s<sup>-1</sup>) in bouts lasting 0.2–2 s (Fig. 13).

**45. Post-mount tap with palps.** Males post-mount tapped females with their palps by repeatedly

**Fig. 11** *Trite planiceps* female fending off a mounting male. Male's palps downward.



**Fig. 12** *Trite planiceps* male mounting receptive female. Male's palps downward and Legs I in type I erect position. Female's cephalothorax lowered.



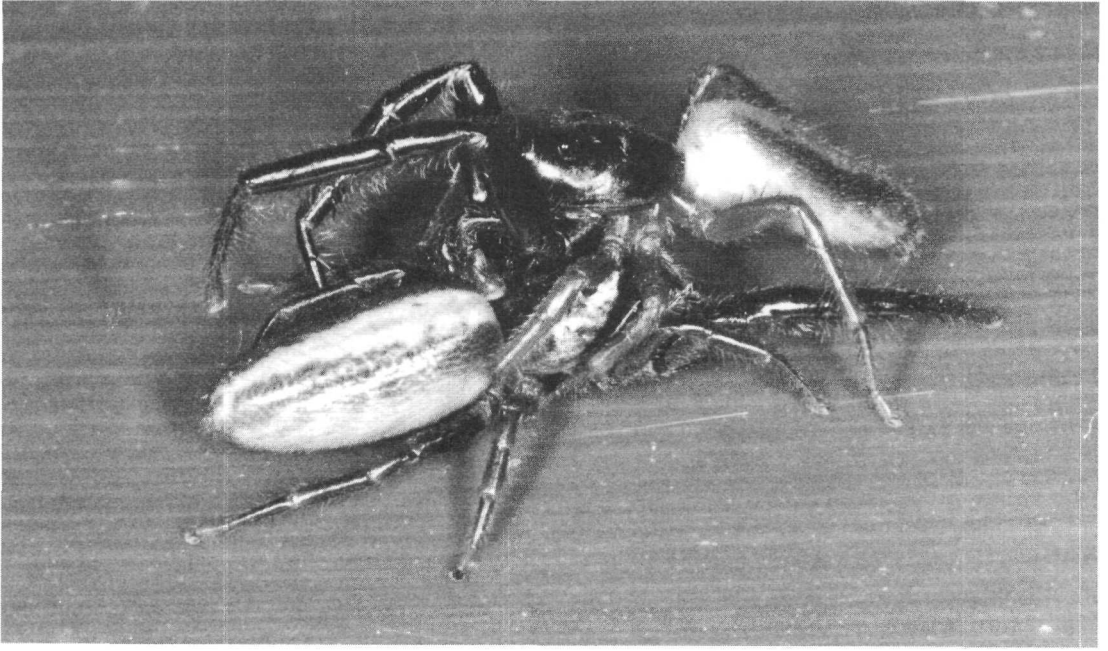
moving them up and down c. 0.5 mm so that their tarsi contacted the female more or less in alternating phase ( $2-4\text{ s}^{-1}$ ) (Fig. 13). Tapping began on the carapace, but later progressed to the abdomen as the male mounted.

**46. Lift leg IV and rotate abdomen.** While tapping the female's abdomen with his palps and shuddering, a male leaned to one side of a female. The female eventually lifted Leg IV on the side over which the male leaned. When lifted, the female's Leg IV was directed c.  $30^\circ$  upward (Fig. 14). Next, with his Legs I, the male reached under the female's abdomen, which rotated  $45-90^\circ$  at the pedicel so that the ventral surface came closer to the male's palp.

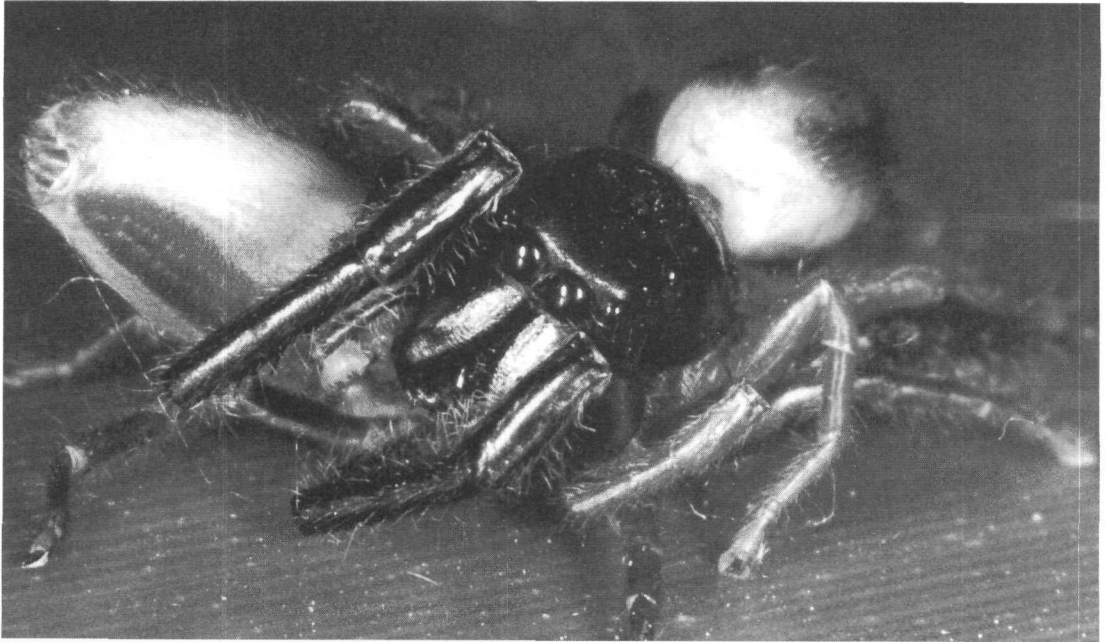
**47. Scrape.** Once her abdomen was rotated, the male scraped by moving his closer palp backward and forward  $1-2\text{ mm}$  ( $2-4\text{ s}^{-1}$ ) against the female's ventral abdomen in the region of the epigynum. Scraping was in bouts lasting  $1-10\text{ s}$ , after which there was a pause of  $1-10\text{ s}$  before the next bout of scraping began.

**48. Apply palp.** A male's palp was by definition applied when the palpal organ was positioned on a female's genital opening and scraping ceased (Fig. 14). While applied, the palp haematodocha was repeatedly inflated and deflated, and presumably the embolus was inserted during this time.

**49. Copulation.** Copulation was defined as the



**Fig. 13** Postmount courtship by *Trite planiceps*. Male leaning to right while shuddering with Legs I and post-mount tapping with palps. Female's left Leg IV raised.



**Fig. 14** *Trite planiceps* copulating. Male facing. Female's Leg IV raised and abdomen rotated. Male holding female's abdomen with both Legs I. Male's closer palp applied.



time during which palps were applied, excluding periods between successive applications. *Trite planiceps* adopted the copulatory position typical of salticid spiders (Fig. 14): the two spiders facing opposite directions with male's ventral surface against female's dorsal surface (Gerhardt & Kaestner 1937).

### Organisation of behaviour

Only general trends are described here because details of the sequences of behaviour during spectations and interactions were highly variable. Interaction durations are presented in Table 1.

### Male-female interactions in the light

Males were generally being more active than females, and they were prone to precluding interaction either by walking off the platform without seeing the female or by running quickly across the platform causing the female to flee. Virgin females tended to orient toward males before males oriented toward them: female oriented first in 28 tests, male first in 12 tests ( $P < 0.05$ ). However, which spider oriented first had no apparent effect on the likelihood that an interaction would follow: interaction followed spectation in 75 % of tests in which females oriented first and in 92 % of the tests in which males oriented first ( $G_{adj} = 1.53, P > 0.2$ ). Previously mated females and males appeared to orient first about equally often: female first in 20 tests, male first in 17 tests ( $P > 0.7$ ). Also, which spider oriented first had no apparent influence on whether an interaction followed: interaction followed spectation in 80 % of tests in

which females oriented first and in 94 % of the tests in which males oriented first ( $G_{adj} = 1.49, P > 0.3$ ).

When a male was facing away, females either stood still and watched the male move about or else approached the male. Approach was by stalking, by charging with cephalothorax raised or by waving, gesturing or stamping while walking forward. Males, upon seeing the female, usually displayed immediately and approached. Virgin, but not previously-mated, females usually stopped approaching as soon as males oriented toward them.

Males zig-zag danced toward females while waving. Usually they leaned and tilted sideways at the end of each bout of veering in the dance. When a male was more than c. 80 mm away from a female, he usually postured with legs in the type 2 semi-erect position after each bout of waving. When closer to a female, however, males usually postured with legs in the type 2 or type 3 erect position. Palps were held downward throughout the approach. Also, males usually twitched their abdomens immediately before each bout of waving or walking. While approaching females, males occasionally stamped or gestured.

When males approached, females sometimes de-camped around the edge of the platform to the opposite surface. Next, with females out of view, males sometimes postured with Legs I in the type 2 erect position, intermittently stamping and pivoting about. These male behaviour sometimes continued for as long as 30 s after females moved out of sight. Alternatively, males followed females to the opposite surface of the platform and then pivoted about. While

**Table 1** Durations of intraspecific interactions of *Trite planiceps* in laboratory. Male-female interaction durations do not include copulation.

	Male-female (female receptive)	Male-female (female unreceptive)	Male-male	Female-female
<i>i) In the light</i>				
Number of tests	—	—	67	79
Number of spectations	—	—	10	20
Number of interactions	17	47	54	57
Maximum interaction duration	5 min	33 min	1 min	74 min
Minimum interaction duration	70 s	1 s	1 s	1 s
Median interaction duration	142s	49 s	18 s	34 s
<i>ii) In the dark (simulated rolled-up leaves)</i>				
Number of tests*	45	11	20	20
Maximum interaction duration	92 min	60 min	30 min	47 min
Minimum interaction duration	4 s	57 s	9 s	1 s
Median interaction duration	82 s	276 s	107 s	24s

\* Interaction occurred in all tests



pivoting about, males were apparently searching for departed females. Males began courting again whenever they regained orientation toward females. However, if a male failed to find the departed female, then, over a period of several minutes, he sometimes moved repeatedly from the upper to the lower surface and pivoted about.

Spiders appeared to detect each other's movements when on opposite sides of the platform. Females sometimes ran away immediately after males passed by on the opposite side. Alternatively, when one spider while still on the other side, walked near the other, one or both spiders sometimes reacted by raising the cephalothorax and then standing still.

When approached by males, previously mated females usually charged with cephalothoraces raised and abdomens bent, and then ran away from or made long leaps at the males. Previously mated females occasionally stamped and waved as they charged. Although virgin females sometimes charged with cephalothoraces raised, only one of 32 virgin females made a long leap at a courting male; in contrast, 10 of 32 previously-mated females made long leaps ( $G_{adj} = 9.63$ ,  $P < 0.01$ ). When females charged or made long leaps, males sometimes raised Legs I to the type 4 erect position and leaned backwards with cephalothoraces tilted upward. Occasionally males decamped when females charged or made long leaps.

When within c. 15 mm of a female, males, with Legs I in the type 1 erect position, stepped forward to mount (Fig. 12). Previously mated females never allowed males to mount; instead they decamped, struck at the male or fended him off, all the while keeping their cephalothoraces raised and their abdomens bent. Previously mated females usually kept their chelicerae open and fangs extended while facing males were attempting to mount.

In one instance, a type 1 embrace was observed when a male attempted to mount a previously mated female. After embracing for c. 5 min, the female stepped backwards, while fending off the male and striking at him. The male persisted with his mounting attempts, and eventually the female jumped off the platform, ending the interaction.

Virgin females either fended off males that attempted to mount or else decamped. When females decamped, males usually followed and continued courting. Sometimes virgin females eventually stopped fending males off and lowered their cephalothoraces, after which males immediately mounted. While mounting, males sometimes spun, depositing silk over the female's Legs I. Once posi-

tioned with their palps resting near the female's pedicel and with the tarsi of their highly flexed Legs I resting on either side of the female's abdomen, males usually paused for 10–20 s before initiating post-mount courtship.

During post-mount courtship, males initially post-mount tapped the female's abdomen with their palps, shuddered and intermittently twitched their abdomens while slowly leaning to one side of the female's abdomen (Fig. 13). Males sometimes paused for 10–30s during post-mount courtship. While males paused, females sometimes began flexing and extending all their legs slightly. Whenever this happened, males began post-mount courting again.

The female eventually raised Leg IV on the side to which the male was leaning and the male leaned further over, reaching his closer Leg I under the female's abdomen. The male then continued post-mount tapping with palps and shuddering with the other Leg I for 10–30 s, by which time both of his Legs I had reached around the female's abdomen, which was now rotated. Once the female's abdomen was rotated, the male switched from post-mount tapping with palps to scraping. Eventually he applied his closer palp (i.e., initiated copulation) (Fig. 14).

While copulating, the spiders' bodies rocked gently 1–2 mm from side to side in phase with pulsation of the male's haematodocha. Pulses tended to be 2–6 s apart early on, but often became irregular and less frequent near to the end of a palp application. Between palp applications, males usually returned to the female's midline and paused in the same position as during the pause following mounting. They then leaned to the other side, post-mount tapped with palps and shuddered again, and eventually applied the second palp.

Mating ended either when males withdrew their palps and dismounted or when females became active and dislodged the male. Once males had dismounted or been dislodged, females usually opened their chelicerae, extended their fangs, and held their Legs I in the type 4 erect position. Sometimes, females raised their cephalothoraces, bent their abdomens and then charged at and struck the male. If both palps had been applied, males usually decamped readily. However, males that had applied only one palp usually began courting again.

#### Male-male interactions in the light

Smaller males tended to orient first: smaller oriented first in 42 tests; larger in 20 tests ( $P < 0.01$ ). Interaction followed expectation in 90% of tests in which smaller spiders oriented first and in 81% of tests in

which larger spiders oriented first ( $G_{\text{adj}} = 0.83$ ,  $P > 0.3$ ). A male that saw another male that was facing away usually arched its palps and then, while charging or veering toward the other spider, waved or stamped. The other spider usually responded by orienting more or less immediately. Males only rarely stalked or made long leaps at other males.

Once interaction began, the two males charged or veered toward each other, usually with chelicerae opened and fangs extended. Spiders usually stamped or gestured while charging and veering. Instead of approaching, males sometimes stepped sideways in place. Stepping in place was usually accompanied by posturing (type 2 or type 3 erect), gesturing or stamping. After veering or stepping in place, spiders usually leaned and tilted in the direction of movement. Males often twitched their abdomens immediately before walking. Between bouts of walking, spiders usually postured with legs in the type 2 or type 3 erect or semi-erect position.

When facing each other and less than two body lengths apart, the spiders sometimes initiated an embrace (type 1 or type 2) by stepping forward until their chelicerae touched (palps raised and overlapping). Embracing spiders usually duelled and then hooked and pushed down legs. While type 2 embracing, spiders usually hooked and pulled, and occasionally they lunged and attempted to bite each other. Smaller males were more likely than larger spiders to decamp: first to decamp was the smaller male in 44 of 53 interactions in which a size difference was detected ( $P < 0.001$ ). When one male decamped, the other male sometimes ran or leaped after it, but no injuries were evident during encounters between males.

#### Female-female interactions in the light

Size had no apparent effect on which spider oriented first: the smaller female oriented first in 41 tests, and the larger female oriented first in 30 tests ( $P > 0.2$ ). Nor did which spider oriented first appear to influence whether interaction followed: interaction followed expectation in 80% of tests in which smaller spiders oriented first and in 67% of tests in which larger spiders oriented first ( $G_{\text{adj}} = 1.68$ ,  $P > 0.1$ ). Upon seeing another female that was facing away, females either stood still and watched the other spider or they approached the other spider by stalking, by making long leaps, or by charging with cephalothorax raised and abdomen bent. Charging spiders sometimes waved, gestured or stamped. Two instances of cannibalism (both times by the larger female) were observed immediately following

expectations. In one instance, a female stalked and then made a long leap, grasping the other spider as she oriented to face her attacker. In the other instance, a spectator stood still, apparently undetected, as a smaller spider approached. When the approaching spider got close, the quiescent spider made an attack by lunging and grabbing.

During interactions, the two females sometimes adopted distinctly different tactics, with one female arching her palps, posturing (usually type 2 or type 3 erect or semi-erect, rarely hunched), waving and stamping while the other spider lowered her cephalothorax (palps frontal) or raised her cephalothorax and bent her abdomen (palps arched). Next, while the other spider stood still, one spider approached by charging or stalking or less often by making long leaps. Spiders sometimes responded to charges and long leaps directed at them by raising Legs I to the type 4 erect position, by leaning backwards and tilting upwards, or by decamping. Sometimes, after a long leap, the spiders grasped each other with Legs I and rolled off the platform while struggling and attempting to bite each other. Embraces between females were rare. However, when females did embrace, they tended to do so for much longer than males (males  $n = 7$ , range 1–29 s; females  $n = 3$ , range 21–73 min;  $P < 0.05$ ). When one female decamped, the other female usually followed by chasing, and occasionally by making long leaps or strikes. Smaller females were more inclined than larger females to decamp first: in 43 of 54 interactions in which a size difference was detected, it was the smaller female that decamped first ( $P < 0.001$ ).

#### Interactions between males and subadult females in the light

Subadult females were more inclined to be the first to orient: subadults first in 22 tests, males first in 6 tests ( $P < 0.005$ ). Interaction more often followed expectation when the male oriented first: interaction followed in only 45% of tests in which subadult females oriented first but in all tests in which males oriented first ( $G_{\text{adj}} = 7.27$ ,  $P < 0.01$ ). Subadult females occasionally charged and waved at males that were facing away, but more frequently remained still while the male was distant and ran away when the male came close. After seeing subadult females, males usually displayed more or less the same as when courting adult females. Subadult females sometimes raised their cephalothoraces and charged at courting males. They only rarely made long leaps at males. When they did, they always ran away immediately afterwards. When subadult females failed

to decamp, males always tried to mount. Their attempts failed because subadult females fended them off and tilted their cephalothoraces upward. Although subadult females sometimes decamped while males were trying to mount, they rarely moved more than 50 mm away before stopping. Males usually followed them, courting and attempting to mount several times, but eventually the subadult females walked or jumped off the platform or the males desisted.

#### **Interactions between adult and subadult females in the light**

Subadults tended to orient before adult females: subadult first in 21 tests, adult first in 7 tests ( $P < 0.05$ ). Interaction followed spectation more often when the adult oriented first: 48% of tests in which subadult females oriented first and in all tests in which adult females oriented first ( $G_{\text{adj}} = 7.81$ ,  $P < 0.01$ ). After orienting toward adult females, subadults tended to lower their cephalothoraces and remain still, or else they decamped. Interactions between subadult and adult females were generally similar to interactions between two adult females. One spider, usually the adult, charged or veered toward the other spider while posturing (type 2 or type 3 erect or semi-erect), gesturing, stamping or waving, while the other spider watched, stalked, or charged with cephalothorax raised and abdomen bent. Adult and subadult females sometimes made long leaps at each other. It was most often the subadult that decamped first: in 16 of 20 interactions, the subadult female decamped first ( $P < 0.001$ ). Adult females that decamped first were always smaller than the subadult female. No injuries were evident during interactions between adult and subadult females.

#### **Juvenile-juvenile interactions in the light**

Size had no apparent influence on which spider oriented first: smaller juveniles first in 19 tests and larger first in 14 tests ( $P > 0.4$ ). Interaction followed spectation more often when the spider that oriented first was the larger of the pair: interaction followed in 79% of tests in which larger spiders oriented first versus 32% of tests in which smaller spiders oriented first ( $G_{\text{adj}} = 7.14$ ,  $P < 0.01$ ). Juveniles occasionally stalked and made long leaps at other juveniles that were facing away. In one instance, a larger juvenile captured and killed the other juvenile immediately after a long leap. Interactions between two juveniles were generally similar to interactions between two adult females: one juvenile usually postured (type 2

or type 3 erect or semi-erect), stamped, and waved, while the other raised its cephalothorax and bent its abdomen. Both juveniles usually arched their palps. One spider usually decamped immediately after the other spider charged and then made a long leap. Smaller juveniles decamped first in 22 of 26 interactions in which a size difference was detected ( $P < 0.001$ ).

#### **Male-juvenile interactions in the light**

Juveniles oriented first more often than males: juvenile first in 24 tests and male first in 12 tests ( $P < 0.001$ ). Interaction more often followed spectation when males oriented first: in 8% of tests in which juveniles oriented first and in 92% of tests in which males oriented first ( $G_{\text{adj}} = 25.09$ ,  $P < 0.001$ ). Juveniles rarely approached males, instead either lowering their cephalothoraces and standing still or immediately decamping. When they oriented toward juveniles, males behaved much the same as during interactions with adult or subadult females: zig-zag dancing, waving, gesturing and posturing with legs in the type 2 or type 3 erect or semi-erect position. Males held their palps downward while they approached. Juveniles usually ran away after standing still and watching males for less than 10 s, but they infrequently charged or made long leaps before running away. While charging, juveniles held their cephalothoraces raised.

#### **Female-juvenile interactions in the light**

Juveniles oriented first more often than females: juvenile first in 28 tests and female first in 10 tests ( $P < 0.01$ ). Interaction followed spectation more often when females oriented first: in 4% of tests in which juveniles oriented first and in 70% of tests in which females oriented first ( $G_{\text{adj}} = 16.74$ ,  $P < 0.001$ ). Juveniles appeared to avoid interactions with females by lowering their cephalothoraces and remaining still, and they usually decamped within 10 s after interactions began. During interactions, juveniles never displayed at females. Females sometimes charged, waved and made long leaps at juveniles regardless of whether the juvenile was oriented toward the female or facing away. In one instance, a female captured and killed a juvenile immediately after a long leap.

#### **Male-female interactions in the dark**

While walking along a tube toward a female, the male usually flicked his palps, twitched his abdomen and pounded. Sometimes he also spun. When the male touched an occupied nest, the female some-

times approached, even when the male was as far as 25 mm away. However, if the female remained quiescent, the male palpated (flicking, sliding, and up-and-down), chewed, tugged, pounded, pawed and probed on the nest.

When touched by males, females usually raised their palps, opened their chelicerae, raised legs into the type 3 or type 4 erect position, leaned backwards and tilted their cephalothoraces upwards. Females sometimes next lowered Tarsi I back down to the substrate, raised their cephalothoraces, twitched their abdomens and thrusted. Previously mated females not on nests sometimes lunged and grabbed, but previously mated females on nests and virgin females, whether on or off nests, only rarely lunged. On one occasion, a lunging female (previously mated, away from nest) caught and killed a male.

After touching females, males usually stepped forward and by pawing repeatedly touched the female again with Legs I. After fending males off for as long as 2 min, previously mated females at nests and virgin females, whether at or away from nests, tended to lower their cephalothoraces and allow the male to mount. When fended off by females, males pre-mount tapped with legs. Rather than standing their ground, females (especially if previously mated and not on a nest) sometimes retreated to the narrow space beside the cone at the end of the glass tube. At first, males followed and attempted to mount, but they soon switched to pre-mount tapping with legs and palps for as long as 40 min, after which females usually walked forward and out of the narrow space and the male immediately mounted. Details of mounting, post-mount courtship and copulation were similar to what was observed in the light. Previously mated females more frequently mated when nests were present (12 of 14 tests) than when nests were absent (6 of 15 tests) ( $G_{adj} = 6.46, P < 0.02$ ). Virgin females always mated when encountered by males inside dark tubes (10 at nests, 17 away from nests).

#### **Interactions between males and subadult females in the dark**

Males approached subadult and adult females in more or less the same manner. If the subadult female was at a nest and failed to approach the male when he touched the silk, the male up-and-down palpated, chewed, tugged and probed. Immediately after being touched by males, subadult females usually leaned backwards while either raising Legs I into the type 3 or type 4 erect position or raising the cephalothorax and sometimes opening chelicerae, extending fangs and swiping. When hit by swiping

subadult females, males usually leaned backwards and raised Legs I into the type 4 erect position.

Instead of mounting, males pounded, pawed, pre-mount tapped with their legs and palps, twitched their abdomens and then backed away after 20–60 s. Males usually next turned around to face the tube entrance and, while remaining in this position, groomed (drawing appendages through their chelicerae and rubbing their eyes with their palps) until the test ended 1 h later. Subadult females sometimes approached, swiping as they moved forward, and touched males. When touched, males turned away from the tube entrance and oriented toward the subadult female. Soon afterwards, either the male turned and faced away from the subadult or the subadult retreated back to her nest.

#### **Male-male interactions in the dark**

Intruders twitched their abdomens, flicked their palps, swiped and pounded as they walked toward residents. There was usually no evident response by residents until the spiders touched each other. Upon first contact, both spiders usually leaned backwards, tilted their cephalothoraces upwards, raised Legs I into the type 4 erect position, raised their palps, opened their chelicerae and extended their fangs.

Interactions sometimes appeared especially cautious. A spider twitched its abdomen, leaned forward and pawed or pounded until it touched either the other spider or the substrate, after which it leaned back again. Spiders responded to being touched, or to the other spider touching the substrate no more than 5 mm away, by raising Legs I into the type 4 erect position, tilting their cephalothoraces upwards and leaning backwards. Spiders sometimes remained quiescent for as long as 1 min facing one another and only 5–20 mm apart or even with Legs I draped loosely over each other's Legs I or carapaces. While in this position, spiders sometimes gently pulled at each other's appendages by flexing and extending Legs I. Palps were always held in the raised position during these exchanges.

While facing one another and 5–20 mm apart, males sometimes took turns (at intervals of 0.5–2 s) drumming and pounding. During these exchanges, one spider leaned, stepped or walked forward 1–2 paces, drummed or pounded especially forcefully and then leaned, stepped or walked back to its original position.

Residents sometimes retreated to the narrow space by the cone at the end of the tube. Intruders usually followed and pushed up against cornered residents. Resident usually kept Legs I in the type 4

erect position, and intruders usually draped Legs I loosely over residents. Sometimes intruders gently pulled at residents by flexing and extending Legs I. Cornered residents sometimes walked sideways until on the surface opposite the intruder and then walked past the intruder to the tube opening. The first spider to decamp tended to be the smaller of the pair (Table 2,  $P < 0.01$ ) or the intruder (Table 2,  $P = 0.06$ ). Males only rarely lunged at each other, and no injuries were evident during male-male interactions.

#### Female-female interactions in the dark

Intruding females palpated (flicking and sliding), swiped and pawed as they walked along inside tubes. Upon touching the resident's nest, intruders sometimes up-and-down palpated. Sometimes residents next walked quickly toward intruders from as far as 25 mm away. However, if no nest was present, residents did not appear to respond until touched.

When they touched, females usually leaned backwards immediately, tilted their cephalothoraces upwards, raised their palps, opened their chelicerae and raised Legs I into the type 3 or type 4 erect position. After a few seconds, spiders sometimes lowered Legs I back down to the substrate and raised their cephalothoraces. Females with raised cephalothoraces sometimes thrust and twitched their abdomens.

Residents sometimes lunged and grabbed at intruders, after which intruders sometimes immediately decamped from the tube. Alternatively, residents retreated to the narrow space by the cone at the end of the tube. Intruders usually followed and then stepped forward so that their Legs I extended over the resident. Usually the resident's Legs I were initially in the type 4 erect position, but later they were lowered onto the intruder so that the two spiders stood face to face with their Legs I loosely

draped over one another. Positioned face to face, with legs draped over each other, the two spiders might remain almost motionless for as long as 20 min, after which the intruder retreated and left the tube. When away from the narrow space at the end of the tube, spiders sometimes stood 5–20 mm apart while intermittently pawing and touching each other for as long as 5 min, after which the intruder decamped.

Females usually decamped by walking backwards until they reached the tube opening. They next stepped out of tube backwards, turned and walked away. Intruders tended to decamp first (Table 2,  $P < 0.005$ ), but there was no evidence that relative size influenced tendency to decamp first (Table 2,  $P > 0.5$ ). The only injury observed was when an intruder, after lunging and grabbing, killed a smaller resident almost immediately after contact.

#### Effects of reproductive state and interaction site on mating

The number of palp applications during copulation tended to be greater for previously mated (in the dark only) than virgin females (in the light or in the dark) (Table 3, for both comparisons  $P < 0.001$ ). Also, durations of individual palp applications were shorter when males copulated with previously mated (in the dark) rather than virgin females (in the light or in the dark) (Table 3, for both comparisons  $P < 0.001$ ). Males applied their palps for shorter durations each time when mating with virgins in the light rather than in the dark (Table 3,  $P < 0.001$ ).

With virgin females, total copulation duration (sum of the individual palp application durations) was shorter in the light than in the dark (Table 3,  $P < 0.001$ ), but total copulation duration was similar for previously mated and virgin females in the dark (Table 3,  $P > 0.3$ ). Distinctive white deposits were

**Table 2** Relationship between residence status, relative size and decamping in interactions between *Trite planiceps* adults in the dark (in simulated rolled-up leaves). Sample size: 20 male-male and 20 female-female interactions (for males and for females, intruders larger in 10 tests and smaller in other 10). End of interaction: one spider was killed by other spider (happened only once) or one spider decamped.

Spider that decamped	Male-Male	Female-Female
Smaller intruder	10	8+
Larger intruder	4	9
Smaller resident	6	1
Larger resident	0	1

always present on the female's genital pores after mating, and similar deposits were often observed on adult females collected from nature.

### Behaviour of spiders on rolled-up leaves occupied by females

Before orienting toward the openings, males moved frequently and rapidly in bursts lasting 0.1–0.5 s, broken by pauses of 1–15 s. Males palpated the leaf surface whenever they stopped (flicking and sliding palps), and occasionally they spun. After orienting toward openings, males sometimes postured with legs in the type 2 erect or semi-erect position, and then stamped and twitched their abdomens while walking towards the opening. Upon reaching the opening, males, while pounding, drumming and repeatedly twitching their abdomens, leaned forward into the cavity. Before walking further in, males usually turned 180° several times, drumming and pounding all the while. Soon after entry, scuffling sounds were sometimes heard, after which males retreated out of the cavity with Legs I in the type 4 erect position and continued decamping once outside. In each case, the female was seen at the opening immediately after the male departed. In one test, a female stepped out of the opening and onto the outside surface of the rolled-up leaf as a male approached the opening. The female made a long-leap at the male and then ran back inside, with the male

immediately following the female through the opening into the cavity within the rolled-up leaf.

Females never displayed while approaching openings of rolled-up leaves ( $n = 17$ ). However, while and immediately after entering cavities, females usually turned 180° several times, drummed and pounded repeatedly, and twitched their abdomens.

## DISCUSSION

### Condition-dependent signaling strategies

With more than 4000 described species (Coddington & Levi 1991), Salticidae is the largest spider family and, in morphology and predatory behaviour, these spiders are highly diverse (Richman & Jackson 1992; Pollard 1994; Jackson & Pollard 1996). Yet all salticids are distinctly different from the rest of the Araneae because of their complex eyes and acute vision. Consistent with their exceptionally good eyesight, all salticids appear to make use of vision-based communication during interactions with conspecifics to a degree that is unknown in other spiders (Crane 1949; Richman 1982). However, no salticid species that have been studied in detail are limited to vision-based communication. Conditional signaling strategies, including courtship versatility, appear to be prevalent, if not universal, this family: the salticid relies especially on vision-based communication

**Table 3** Number of palp applications, duration of palp applications and total copulation durations during matings involving virgin and previously mated *Trite planiceps* females in the light and in the dark (simulated rolled-up leaves). No copulations observed for previously mated females in the light.

	Virgin females		Mated females	
	In the light	In the dark	In the light	In the dark
<i>General</i>				
Number of interactions	32	27	29	32
Number of copulations	17	27	0	18
<i>Number of palp applications</i>				
Maximum	2	3	–	9
Minimum	2	2	–	1
Median	2	2	–	5.5
<i>Palp application duration (min)</i>				
Maximum	22	79	–	45
Minimum	1	5	–	1
Median	12	27	–	6
<i>Total copulation duration (min)</i>				
Maximum	38	119	–	92
Minimum	19	18	–	5
Median	23	61	–	39

when in the light, vibratory signals when communicating at nests, and tactile signals when touching conspecifics (Jackson 1992; Richman & Jackson 1992). All salticids studied in detail also practise cohabitation (Jackson 1986b), a mating tactic in which a male resides with a subadult female and mates with her after she moults and matures. *Trite planiceps*, in broad terms, appears to be a typical salticid in that it uses vision-based signals when in the light, has a condition-dependent signaling strategy and practises cohabitation.

Even in the details of elements of behaviour during interactions with conspecifics, there are some remarkable similarities between *T. planiceps* and other salticids. This allowed us to retain many previously used terms in the present study. When interacting with distant conspecifics in the light, the behaviour of *T. planiceps* included holding chelicerae open and fangs extended, a bent-abdomen posture, displays with legs erect, semi-erect or hunched, stamping, gesturing, waving, stalking, flickering, charging, long-leaping, stepping in place, veering, zig-zag dancing, four types of posturing with Legs I, and three palp postures, as well as raising, lowering, leaning and tilting of the cephalothorax. When interacting with conspecifics at nests, *T. planiceps*' behaviour included thrusting, pawing, pounding, chewing, tugging, palpating, and probing. When in the light and touching a conspecific of the same sex, *T. planiceps*' behaviour included hooking and pulling, pushing, duelling and pushing down legs. When touching females, the behaviour of *T. planiceps* males included pre-mount and post-mount tapping with palps, pre-mount tapping with legs, shuddering and scraping. Behaviour resembling each of these elements from *T. planiceps*' repertoire have been described for one or more of the previously studied salticid species (Crane 1949; Richman 1982; Jackson 1992; Jackson & Willey 1995). However, *T. planiceps*' display repertoire also included atypical elements that appear to be especially adapted to the unusual habitat where this species' interactions take place.

### Displaying at openings of rolled-up leaves

*Trite planiceps* males sometimes displayed (erect and semi-erect legs, stamping, abdomen twitching) while walking toward openings of rolled-up leaves, even when no conspecific was visible. This is very unusual for a salticid. It is likely that displaying males were alerted to a resident female's presence and identity by sex pheromones left by the female on the leaf surface (Jackson 1987; Taylor 1998). In nature, females some-

times stood just inside the openings to rolled-up leaves. Our findings suggest that male's strategy is to display when openings to rolled-up leaves are seen just in case there is a watching female inside.

In the courtship of ctenid and lycosid spiders, vibratory signals are transmitted through leaves (Barth & Schmitt 1991; Schmitt et al. 1994; Scheffer et al. 1996). Stamping and abdomen twitching by *T. planiceps* males probably function as visual signals, but these same behaviours may also send vibratory signals across the leaf to females inside. In other salticids, similar behaviours have been shown to produce substrate vibrations and even audible sounds (Bristowe 1958; Edwards 1981; Gwynne & Dadour 1985; Maddison & Stratton 1988).

### Signaling in darkness within rolled-up leaves

Other salticids are known to communicate with conspecifics when in darkness only when nests are present. *Trite planiceps* resembles other salticids by using vibratory signals when interacting in darkness at nests, but this species differs by also having an additional display repertoire for use when in darkness but away from nests: swiping, pawing, pounding, drumming, thrusting and twitching abdomens.

*Trite planiceps* often pounded and swiped, and sometimes pawed, while walking about inside darkened glass tubes, even when no conspecific had been encountered. Forster (1982b) similarly noted that blinded *T. planiceps* walked about "with much foreleg tapping" and "foreleg waving", behaviour most likely analogous to pounding and pawing, and swiping, respectively. Forster (1982b) suggests that swiping (foreleg waving) functions in the detection of airborne vibrations. Another possible non-signaling function might be that these leg movements are the means by which *T. planiceps* feels its way about in the dark.

In addition to possible non-signaling functions, pounding was common during interactions in the dark and, along with drumming, appears to function in vibratory signaling. When one spider pounded or drummed, the other spider usually responded by raising its palps, leaning backwards and raising Legs I into the type 4 erect position, apparently a defensive posture elicited by substrate vibrations. When pounding or drumming, one spider sometimes hit the other spider, which raises the possibility that these are instances of tactile signaling. Pawing and pre-mount tapping with legs and palps have the appearance of tactile signals while abdomen twitching, commonly observed in all interactions, may be involved in vibratory signaling.



Thrusting is similar to 'holding lunging', a signal commonly used by females of *Cobanus mandibularis* and *Euophrys parvula* when inside nests communicating with males outside (Jackson 1989; Jackson & Willey 1995). Living inside rolled-up leaves, a substrate that readily transmits vibrations, appears to have allowed *T. planiceps* to adopt this signal for use in the absence of a nest.

### Use of vibratory signaling by leaf-dwelling salticids

Habitat-adapted display behaviour has also been reported in *Euryattus* sp., a salticid from Queensland, Australia. *Euryattus* females live inside dry, rolled-up, leaves that they suspend by heavy silk guy-lines from foliage and rock ledges (Jackson 1985). After seeing a suspended leaf, even if no female is present, *Euryattus* males climb down onto the leaf and then display by abruptly flexing their legs to make the leaf rock to and fro (Jackson et al. 1997). The female responds to the male's signal by coming out of the cavity within the rolled-up leaf and either mating with or driving away the male. *Trite planiceps* and *Euryattus* sp. are the most dramatic examples of habitat-adapted signaling in salticids, each of these species using forms of vibratory signaling that have not been reported in other salticids. However, we might expect every salticid's communication system to be more or less adapted to make optimal use of signaling opportunities provided by habitat features. In many salticids, such adaptation will be more subtle than in *T. planiceps* and *Euryattus* sp.

Many vision-based displays used by salticids involve forceful movement of the abdomen, legs, palps or entire body. Forceful movement during display appears to be especially pronounced in salticids that live on leaves, suggesting a function in substrate-vibration signaling, perhaps concurrent with these same behaviours functioning as vision-based signals. For example, *Epeus* sp. and three lyssomanines (*Asemonea tenuipes*, *Goleba puella* and *Lyssomanes viridis*), all of which live on broad waxy leaves that should readily transmit vibrations, have courtship displays that include up-and-down jerking of the whole body accompanied by forceable abdomen twitching (Jackson 1988; Jackson & MacNab 1991). These displays of *Epeus* and the lyssomanines, along with the leg-waving, stamping and abdomen twitching behaviour of *T. planiceps*, might make vibratory cues that pass through the leaves and supplement or complement the role of the visual cues made available by these same behaviours. Similar multichannel

communication may be common in the animal kingdom (see Johnstone 1997).

For *T. planiceps* and *Asemonea tenuipes* (Jackson & MacNab 1991), even when interacting in the light, substrate-vibration appears to function as an alternative to visual signaling. When females moved to the opposite side of the simulated leaf during interactions in the light, *T. planiceps* males sometimes pivoted about while stamping and twitching their abdomens. Males of *A. tenuipes*, when on the opposite side of the leaf from a female, twitch their abdomens and jerk their bodies just before moving around to the leaf surface on which the female is standing. These appear to be instances where males of these salticid species signal to prospective mates by substrate vibration.

Other observations suggest that *T. planiceps* and *A. tenuipes* can readily detect substrate vibrations through leaf surfaces and use these for surveillance as well as signaling. When conspecific walked on an opposite leaf surface, *T. planiceps* often raised its body and remained still, or sometimes it ran away. These appear to have been responses to substrate vibrations. *Asemonea tenuipes* males go a step further. While on the opposite side of a leaf, *A. tenuipes* often takes a path parallel to an unseen female, apparently tracking the movements of the female (Jackson & McNab 1991).

Living on leaves, a substrate especially suitable for transmission of vibratory signals, may broaden the range of channels through which a salticid can both communicate with and monitor conspecifics. In future studies, more attention should be given to how habitat, by defining the challenges and opportunities for signaling, influences the evolution of communication systems and signal form in salticids.

### Sex and site differences in mating behavior

*Trite planiceps* males appear to be more or less continuously receptive to mating. In our study, they invariably courted whenever they encountered females, regardless of whether in the light or in the dark. In contrast, females varied in receptivity depending on: 1) whether they were in the light or in the dark, 2) whether a nest was present and 3) whether they were virgin or previously mated. Similar sex and site differences in receptivity to mating are known from studies of behaviourally, geographically and taxonomically diverse salticids (Jackson 1980b; Jackson 1982; Jackson & Harding 1982).

Greater receptivity of *Phidippus johnsoni* females in nests, as opposed to out in the open, may be explained by diminished exposure to predators while

mating in nests (Jackson 1976). A similar explanation may underlie site differences in receptivity of *T. planiceps* females. *Trite planiceps* shares its habitat with diurnal predators, including birds, pompilid wasps, vespid wasps, dragonflies, lizards, and other spiders (PWT, unpublished data). Mating in the open might put *T. planiceps* at a high risk of being attacked by these predators, whereas mating while concealed inside rolled-up leaves would appear to provide safety from these predators. In a study of a congeneric species, *Trite auricoma*, Forster (1982a) took this idea even further, suggesting that, after encountering males in the open, females may lead courting males home to the secluded safety of their nests before mating.

In our laboratory study, previously mated females were never receptive to courting males in the light. However, virgin females sometimes mated in the light. This suggests: 1) for virgin females, the cost of not accepting the male is likely to override the risk of being preyed upon; 2) for reproductively-secure (non-virgin) females, not accepting a male tends to be less costly (Jackson 1981). Females of some salticids can, over a period ranging from a few months to over a year, fertilize multiple egg batches using sperm gained in a single mating (Jackson 1980b). This is also true of *T. planiceps* (PWT, unpublished data). A consequence is that a previously mated female may be able to reproduce whether or not she accepts her current suitor, but a virgin female may be unable to afford the luxury of such choosiness in the face of pressures imposed by a limited reproductive season and a short life span.

Mating plugs may be another factor influencing how virgin and previously mated females respond to courting males in the light. After mating, deposits were left over the genital pores of *T. planiceps* females. In other spiders (Austad 1984), including other salticids (Jackson 1980b), similar deposits are known to function in sperm competition (see Birkhead & Parker 1997). During copulation, a mating plug left by a previous mate hinders the current male's attempts to deposit sperm (Jackson 1980b; Austad 1984). In the present study, when previously mated females accepted males in the dark, the frequency and rate of palp applications were highly variable when compared with copulations in the dark involving virgin females (Table 3), suggesting that plugs were interfering with palp engagement and sperm transfer. Also, copulations involving previously mated females were considerably prolonged when compared with copulations involving virgins. The apparent need for prolonged copulation, and

associated exposure to danger, may make copulation in the light too risky for previously mated females.

### Male-female differences in agonistic behavior

*Trite planiceps* females tended to be more aggressive than males in all types of interaction. When interacting in the light, females stalked and often made long leaps at conspecifics, including subadult females, juveniles and other adult females. Previously mated females especially often made long leaps at males. In contrast, males never stalked or leapt at females, subadult females or juveniles, and they only rarely stalked or leapt at other males. When interacting in the dark in simulated rolled-up leaves, females often lunged and grabbed at males and at other females, in some cases catching and killing the other spider. Males, on the other hand, only rarely lunged at other males or at females, and they never injured the other spiders.

There was another intersexual difference: the display repertoire of females, both in the light and in the dark, contained fewer elements and appeared less stereotyped than that of males. Similar tendencies for females to be more aggressive and possess smaller, less stereotyped display repertoires than males have been reported in many other salticids (Jackson & Hallas 1986a,b; Jackson & MacNab 1989a; Jackson et al. 1990).

### Predictors of contest outcome

When two males, two females, two juveniles or a subadult and an adult female interact, the behaviour of each salticid appears directed toward repelling the other spider and in the literature, these interactions are usually interpreted as contests (Forster 1982a; Wells 1988; Jackson & Cooper 1991; Faber & Baylis 1993). Size difference between rivals tends to be a reliable predictor of the outcome of animal contests (Huntingford & Turner 1987). Previous studies have reported an advantage for larger rivals in contests between juveniles of *T. planiceps* (Forster 1982a) and in contests between same-sex conspecific adults of other salticids (*Phidippus johnsoni*, Jackson 1980c; *Euophrys parvula*, Wells 1988; *Marpissa marina*, Jackson & Cooper 1991; *Zygoballus rufipes*, Faber & Baylis 1993; but see Jacques & Dill 1980 for an exception in *Salticus scenicus*). Our findings for *T. planiceps* in the light were consistent. Across all types of intraspecific contests, larger rivals tended to have a considerable advantage.

In addition to size differences, residency status is also a powerful predictor of contest outcome in many animals (Huntingford & Turner 1987), including

some spiders (Agelenidae, Riechert 1984; Linyphiidae, Hodge 1987; Lycosidae, Fernandez-Montraveta & Ortega 1991). In the only previous study to have addressed this issue in salticids, resident *Marpissa marina* males tended to win contests at nests irrespective of size (Jackson & Cooper 1991). In the present study, residency was an important predictor of the outcome of contests between same-sex *T. planiceps* adults in the dark. Residents, especially if they were females, took advantage of the opportunity to retreat into a narrow space and wait out the seige until the intruder gave up. Having this option means that residents can avoid dangerous passage past an intruder. For males, residency was not as important as it was for females, a sex-difference that may arise from sex differences in tendency to attack conspecifics. A smaller male resident, unlike a smaller female resident, could safely move past a larger intruder with little risk of attack. Another factor may be, for females, a tendency to defend oviposition sites, which would not be a factor for males.

#### Decisions made before interaction

In some interaction types, one class of individual was more likely to see the other first. For example, virgin females and juveniles were more likely to see males first. This tendency may be partly explained by size differences, and associated apparency, but may also reflect differences in vigilance. A spider that sees a conspecific may respond with behaviour that serves to promote interaction. However, the spectator may instead avoid interaction by adopting behaviour that diminishes the likelihood of detection. In *T. planiceps*, there was a tendency for different size and sex classes to choose different options. Juveniles and subadult females, after seeing adults, more often appeared to avoid detection by remaining still or decamping. In contrast, adult females were prone to stalking, and then making long leaps at the other spider, thereby bringing attention to themselves. Males tended to display immediately, irrespective of the sex or age of the conspecific they saw.

Salticids vary considerably in the ease with which interactions can be induced in the laboratory (Crane 1949). For example, males of *Epeus* sp. are especially reluctant to interact (Jackson 1988) whereas males of *Cobanus mandibularis* interact very readily (Jackson 1989). Sex differences within a species are also common. For example, in a study of *Corythalia canosa* (Jackson & MacNab 1989b), interactions began within 30 min of release into a testing arena in 30 of 44 (68%) male-male tests, but in

only 14 of 86 (16%) female-female tests. Similar sex differences have been found in *Cobanus mandibularis* (Jackson 1989), *Euophrys parvula* (Jackson & Willey 1995) and *Marpissa marina* (Jackson et al. 1990). Species and sex differences in the tendency of spectators to avoid or promote detection, and thereby interaction, may explain many of these species and sex differences.

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