

DRAGLINE-MEDIATED MATE-SEARCHING IN *TRITE PLANICEPS* (ARANEAE, SALTICIDAE)

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ABSTRACT. *Trite planiceps* Simon 1899, a common New Zealand jumping spider (Salticidae), lives in the cavities formed by rolled-up leaves of New Zealand flax (*Phormium tenax*) and similar plants. This study presents evidence that *T. planiceps* males use cues from females' draglines deposited on the outside of these rolled-up leaves when searching for females hidden from view inside.

In choice tests, *T. planiceps* males preferentially associated with draglines deposited by conspecific females rather than areas lacking draglines. In contrast, females did not discriminate between areas with and without males' draglines and neither males nor females discriminated between areas with and without same-sex conspecifics' draglines. Additionally, *T. planiceps* males found openings and entered the cavities within rolled-up leaves occupied by females in nature sooner when leaves were tested within 24 hours of collecting (dragline cues deposited on leaves in nature) than after the same leaves had been cleaned and aged for seven days (dragline cues removed). Shorter latency to finding of leaf openings was restored after the same leaves were subsequently occupied by females in the laboratory (dragline cues replaced). The specific cues detected by *T. planiceps* males are probably pheromones loosely bound to females' draglines.

Jumping spiders (Salticidae) differ from other spiders by having remarkably acute vision (Blest et al. 1990) and are well-known for their elaborate use of vision when hunting, navigating, and communicating (Crane 1949; Hill 1979; Clark 1994; Jackson & Pollard 1996; Li & Jackson 1996). Although salticids depend on their acute vision for many tasks, evidence from laboratory studies suggests that chemical cues associated with females' draglines are important to male salticids searching for mates. Species and sex-specific pheromones appear to be loosely bound to the draglines of female salticids, eliciting courtship or associative behavior in males of some species (Oden 1981 in Pollard et al. 1987; Jackson 1987; Clark & Jackson 1995). Additionally, males of one species, *Carrhotus xanthogramma* (Latreille 1819), have been shown to walk more slowly and recognize dummy females as prospective mates more frequently when females' draglines are present (Yoshida & Suzuki 1981).

Females of *Trite planiceps* Simon 1899, a common New Zealand salticid, build their nests in the cavities formed by rolled-up

leaves of New Zealand flax (*Phormium tenax*) and similar plants (Forster & Forster 1973; Taylor 1997). Usually there is only a single small opening to these cavities (Fig. 1); males seeking females hidden from view inside rolled-up leaves face the challenge of finding these openings in a habitat containing many similar leaves that do not contain females. This study presents evidence that *T. planiceps* males use cues from draglines left by females on their 'home leaves' to identify occupied leaves and facilitate mate-searching.

METHODS

Substrate preferences.—This experiment was designed to investigate the tendencies of *T. planiceps* males and females to associate with or avoid areas containing draglines deposited by male and female conspecifics. Fifty three subadult females (penultimate molt) were collected near Christchurch, New Zealand, 2–8 weeks prior to testing and those that molted to adult were used in experiments as virgin females. Sixty eight adult males and 121 mated adult females (most females were collected from nests containing juveniles and all had distinctive white mating plugs in genital pores) were also collected from the same site 2–4 weeks prior to testing. All spiders

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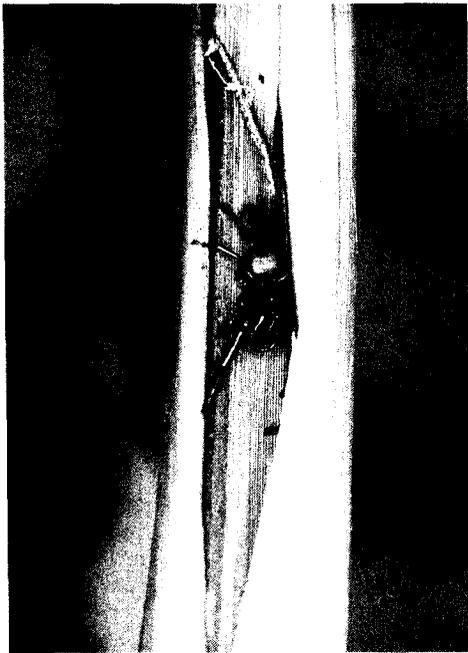


Figure 1.—*Trite planiceps* male entering the cavity formed by a rolled-up leaf of New Zealand flax (*Phormium tenax*). Spider's body length = 11 mm.

were maintained using standard methods (Jackson & Hallas 1986). Voucher specimens of *T. planiceps* have been deposited by Robert Jackson at the Florida State Collection of Arthropods (Gainesville).

Procedures closely resemble those used by Clark & Jackson (1994). The arena was constructed from a 90 mm-diameter plastic petri dish (Fig. 2). The petri dish (base and lid) was cut in half, and an opaque plastic screen was glued into each half-base midway between the cut edge and the point of greatest distance to the cut edge. A 10 mm-diameter half-circle hole was melted into the cut edge of each half petri dish immediately adjacent to the wall at the end to which the screen was fixed.

One 'half-arena' was selected at random to be 'draglined'. The half-circle hole and open side of this half-arena were taped over and a 'source spider' was introduced. The source spider was left for 2 h to deposit draglines. After removing the source spider, the draglined half-arena was used in a test within the following 2 h.

To begin a test, the draglined half-arena was matched up with a clean half-arena so that the half-circle holes on the edge of the half-arenas

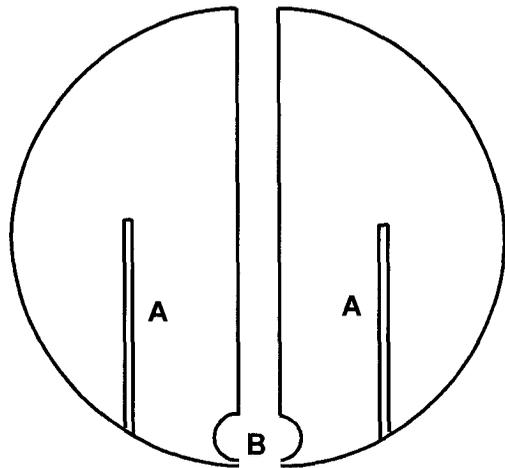


Figure 2.—Diagram showing the arena used to test substrate preferences (viewed from above with the two 'half arenas' separated). (A) Opaque plastic screens. (B) 10 mm diameter hole for insertion of the transfer tube.

formed a single 10 mm-diameter hole in the floor. The 'test spider' was placed in a clear plastic 'transfer tube' (40 mm × 10 mm external diameter) which was then corked at both ends. The transfer tube was inserted into the hole in the arena floor so that the tube protruded 1–2 mm into the arena and was held in place by the two half-arenas pressing together. The cork protruding into the arena was then removed and the two half lids were slid into place. The test spider climbed up out of the transfer tube into the arena, and the test began when the spider's palps were above the arena surface. The amount of time that the test spider spent on each side of the arena was recorded for 10 min, using the palps as the point of reference for location. If a spider stood with one palp on each side of the arena, it was counted as still being on the side previously occupied by both palps (i.e., failing to move to the other side). Each spider was used only once as a test spider or source spider for any particular treatment (e.g., male on male draglines).

Mate-searching on rolled-up leaves.—This experiment was designed to investigate whether mate-searching by *T. planiceps* males is facilitated by draglines left by conspecific females on leaf surfaces in the laboratory, and whether similar cues are present in nature.

Fresh leaf tests: Twenty rolled-up flax

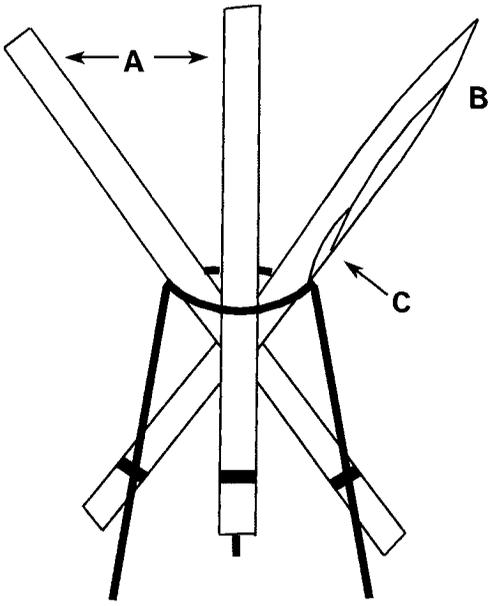


Figure 3.—Diagram showing the arena used to test the effects of dragline cues on mate-searching efficiency. (A) Arrows indicating two dried leaves that are not rolled-up. (B) Rolled-up leaf. (C) Arrow indicating the opening of the cavity within the rolled-up leaf. The same spatial arrangement of leaves was adopted for all tests.

leaves containing *T. planiceps* nests and maternal females were collected on the evening prior to testing. Fresh leaves would typically be covered by draglines deposited by resident females in nature. Because many salticid pheromones are water-soluble (Jackson 1987), and therefore susceptible to being depleted by rain, leaves were collected at least 5 days after the most recent rainfall. Residents were removed, and the rolled-up leaves were cut to 500–550 mm long with the opening near the middle.

On the day of testing, each rolled-up leaf was mounted (using plastic insulating tape) on a tripod with two other dried leaves (500–550 mm long) that were not rolled up (Fig. 3). The tripod and attached leaves were placed in a clean glass tank (300 mm × 300 mm floor, 600 mm high). The opened cage of a *T. planiceps* male was placed on the tank floor and the tank was sealed with a glass lid. All experiments were started in the middle 2 h of the laboratory light phase (12L:12D). After the male left his cage I recorded, at 5 min intervals for a maximum period of 5 h, wheth-

er the male had entered the cavity within the rolled-up leaf. If the male could not be seen in the tank, the rolled-up leaf was carefully unrolled to confirm that the male was inside (end of test). Each leaf was used only once (i.e., 20 tests in total).

Cleaned leaf tests: After fresh leaf tests ended, the glass tanks, tripods and leaves (each of the 20 tripod and leaf setups were kept intact) were thoroughly washed with distilled water and then ethanol to remove draglines and pheromones. They were then left for 7 days, so that remaining pheromones could dissipate, and the testing procedure was repeated. This treatment's title 'cleaned leaves' was justified because, in other salticids, aging and washing with polar solvents such as water is known to eliminate the effectiveness of draglines at eliciting associative behavior and courtship of males (Jackson 1987; Clark & Jackson 1995).

Lab-draglined leaf tests: After cleaned leaf tests the 20 tanks, tripods and leaves (tripod and leaf setups still intact) were washed again and allowed to dry for 24 h. The adult female that was in the leaf in nature was then replaced in the leaf, left for 7 days in the closed tank, and testing was repeated again. On the day before testing a lab-draglined leaf, the resident was removed and the whole arena (tank, tripod, leaves), except the rolled-up leaf, was washed.

The same group of 20 males was used for the 20 tests using fresh, cleaned, and lab-draglined leaves, but each male was used only once per treatment and the same male was not used for more than one treatment of a particular leaf. To ensure that results were not confounded by shrinkage of the openings of rolled-up leaves during the interval between treatments, maximum width and length of openings were measured to the nearest millimeter following the first and third treatments, and compared.

RESULTS

Substrate preferences.—Males spent more time on the side of the arena containing draglines of conspecific females than on the clean side but there was no evidence that females (mated or virgin) either associated with or avoided draglines deposited by males (Table 1). Also, neither males nor females showed

Table 1.—Proportions of total time spent on the draglined half-arena vs. clean half-arena. Comparisons are by Wilcoxon signed ranks test.

Test spider	Source spider	<i>n</i>	median	Upper quartile	Lower quartile	<i>P</i>
Male	Mated female	47	0.78	0.91	0.52	<0.001
Mated female	Male	37	0.48	0.77	0.30	>0.3
Virgin female	Male	37	0.47	0.63	0.34	>0.5
Male	Male	56	0.51	0.68	0.34	>0.4
Mated female	Mated female	92	0.56	0.69	0.36	>0.5

any tendency to associate with or avoid draglines of same-sex conspecifics (Table 1).

Mate-searching on rolled-up leaves.—Males found the openings and entered the cavities within rolled-up leaves during the 5 h testing period in all tests using fresh ($n = 20$) or lab-draglined leaves ($n = 20$), and in 18 of 20 tests using cleaned leaves (Fisher exact test, $P > 0.3$). However, latency until entering cleaned rolled-up leaves (median 83 min; quartiles 33–136 min) was greater than for fresh leaves (median 23 min; quartiles 12–42 min; Wilcoxon signed ranks test, $P < 0.005$) or lab-draglined leaves (median 18 min; quartiles 11–25 min; Wilcoxon signed ranks test, $P < 0.001$). There was no evidence that latency to entry of rolled-up leaves differed for fresh and lab-draglined leaves (Wilcoxon signed ranks test, $P > 0.2$). Also, there was no evidence that length or width of the openings to rolled-up leaves changed during the three week interval between tests (Wilcoxon signed ranks test, for both dimensions $P > 0.9$).

DISCUSSION

Males of some salticids begin courting when they come into contact with draglines deposited by conspecific females (Jackson 1987). Although females' draglines do not elicit courtship in *T. planiceps* males (Jackson 1987), the present study shows that females' draglines do elicit associative behavior in males of this species. In this respect, *T. planiceps* resembles *Portia fimbriata* (Doleschall 1859) and *P. labiata* (Thorell 1882), the only other salticids for which comparable data are available (Jackson 1987; Clark & Jackson 1995). Although other possibilities cannot be ruled out, related studies suggest the specific relevant cues eliciting association in *T. planiceps* males are pheromones loosely bound to

the nest and dragline silk of females (Jackson 1987, Oden 1981 in Pollard et al. 1987, Clark & Jackson 1994).

In addition to associating with females' draglines in choice tests, *T. planiceps* males found females' nesting sites sooner when females' draglines were present on rolled-up leaves. Although increased success at mate-searching may be explained by associative behavior alone, we should also consider the possibility that *T. planiceps* males actively searched for the openings of rolled-up leaves when they contacted the draglines. Female salticids typically build their nests in only a narrow range of easily identified microhabitats (Hallas & Jackson 1986) and commonly reside at a single nesting site with their developing young for many weeks (Jackson 1979; Taylor 1997). Brooding females deposit draglines as they move about near their nests, and this would be the most common natural context in which an area would be densely covered by draglines. Male salticids that encounter dragline-covered areas might next search visually both for females directly and for typical nesting microhabitats.

The present study of *T. planiceps* has an important feature that emulates nature more completely than previous studies using other salticids. In addition to using draglines deposited in the laboratory (all tests of association and 'lab-draglined leaves'), I also used leaves on which draglines had been deposited in nature ('fresh leaves'). Identifying a similar response to lab-draglined and fresh leaves strengthens the assertion that dragline cues are present and used by *T. planiceps* males searching for mates in nature. The need for such confirmation was highlighted by Persons & Uetz (1996) in the context of predation. These authors found that a lycosid spider,

Schizocosa ocreata (Hentz 1844), associates with areas recently occupied by large numbers of crickets but express doubt that adequate concentrations of the kairomones responsible would occur naturally. Similar doubts could be expressed about studies of how salticids use dragline-cues, as none have confirmed that similar cues are present in adequate density in nature. Results of this study provide some assurance that laboratory assays of salticid responses to dragline-cues produce results that are indeed relevant in nature.

ACKNOWLEDGMENTS

This research was carried out with support from a New Zealand Universities Postgraduate Scholarship. The manuscript was prepared with additional support from Binational Science Foundation grant 93-125 to Oren Hasson and David Clark. Allon Bear, Robert Clark, Robert Jackson and Mary Whitehouse provided useful discussions and comments on the manuscript.

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Manuscript received 1 April 1997, revised 15 May 1998.