

JUMPING SPIDERS MAKE PREDATORY DETOURS REQUIRING MOVEMENT AWAY FROM PREY

by

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(With 2 Figures)
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Summary

The terms “reversed-route detours” and “forward-route detours” are introduced to distinguish between detours that require moving away from a goal and those that do not. We provide the first evidence under controlled laboratory conditions that salticids can perform reversed-route detours. Two species were tested: 1) *Portia fimbriata*, a web-invading salticid from Queensland, Australia, that normally preys on web-building spiders; 2) *Trile planiceps*, an insectivorous cursorial salticid from New Zealand. Although both of these species completed reversed-route detours, *Trile planiceps* was much more dependent on prey movement than *Portia fimbriata*. Interspecific differences appear to be related to the different predatory styles of these two salticids.

Introduction

Salticids, or jumping spiders, have unique, complex eyes and acute vision (LAND, 1985; BLEST, 1985). Considering their sophisticated visual system, it is not surprising that most salticid species are hunting spiders which, instead of building webs to ensnare their prey, rely on vision during predatory sequences in which they stalk, chase and leap on active insects (DREES, 1952; FORSTER, 1982). The salticid visual system consists of a pair of forward-facing principal, or antero-median (AM), eyes and three pairs of secondary eyes - the antero-lateral (AL), postero-medial (PM) and

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postero-lateral (PL) (HOMANN, 1928). The secondary eyes function as motion detectors (DUELLI, 1978), whereas the principal eyes are responsible for acute vision. In a typical prey-capture sequence, a salticid detects a moving object with its secondary eyes, turns to fixate on the object with its AM eyes, then behaves appropriately depending on whether the moving object is a prey, conspecific or potential predator (HOMANN, 1928; HEIL, 1936).

The retina of the AM eye has a unique boomerang shape, with a central fovea-like region (LAND, 1969a). The cuticular lenses of all eight eyes are fixed, but the AM eye tubes, which are unusually long, have six pairs of muscles attached to them (LAND, 1969b). Using these muscles, the salticid coordinates precise, complex rotational and side-to-side movements of the eye tube which are important in tracking moving prey and also probably in recognizing shapes (LAND, 1969b). The AM eye is a miniature telephoto system because of the large focal length resulting from the long eye tube and because there is a second (diffracting) lens at the rear of the eye tube, just in front of the retina (WILLIAMS & MCINTYRE, 1980). The AM eye's lens system and retina combine to provide extraordinary resolving power and let the salticid perform phenomenal feats of visual discrimination (see JACKSON & BLEST, 1982, JACKSON & TARSITANO, 1993). The resolving power of the AM eyes is achieved by sacrificing a wide field of view, but this is compensated for by the moveable AM eye tubes.

Because salticids can recognize a prey, on the basis of visual cues, from as far as 30 cm away (JACKSON & BLEST, 1982), a hunting salticid must often need to close the distance between itself and the prey before initiating prey-capture. In a flat, 2-dimensional world, this might be easy enough, but many salticids live in complex, 3-dimensional habitats of stones and vegetation where direct access to the prey is frequently unavailable. In a recent study, we (TARSITANO & JACKSON, 1993) showed that eight species of salticids - *Portia fimbriata*, *Portia labiata*, *Euryattus* sp., *Euophrys parvula*, *Marpissa marina*, *Trite auricomis* and *Trite planiceps* - will follow indirect routes to reach prey, extending the earlier work of HILL (1979) who showed that salticids from the genus *Phidippus* will re-orient towards prey after losing visual contact during a pursuit.

However, the detours required of the salticids in these experimental studies (HILL, 1979; TARSITANO & JACKSON, 1993) were simple and short.

HILL (1979) emphasized that detouring required no great insight on the salticid's part because, if no straight route towards a prey was available, the salticid detoured merely by heading towards objects ("secondary goals") that would tend to bring them closer to the intended prey. However, *Portia fimbriata*, a salticid from Queensland, Australia, has been reported to take long, complicated detours in the field (JACKSON & WILCOX, 1993), including detours in which the salticid first moved away from the prey before heading towards it. Although most salticids, including *Phidippus*, *Euryattus* sp., *Euophrys parvula*, *Marpissa marina*, *Trite auricoma* and *Trite planiceps*, are cursorial insectivores, *Portia fimbriata* is an araneophagic web-invader (JACKSON, 1992). It has been argued that *Portia fimbriata*'s unusual style of predation makes long, complex detours especially advantageous for this unusual genus of salticid (TARSITANO & JACKSON, 1993; JACKSON & WILCOX, 1993).

We use the terms "reversed-route detours" and "forward-route detours" to distinguish between detours that require moving away from a goal and those that do not. Only forward-route detours have previously been investigated under controlled conditions in the laboratory (HILL, 1979; TARSITANO & JACKSON, 1993). In the present paper, we corroborate, under controlled laboratory conditions, the earlier report, from an observational study in the field (JACKSON & WILCOX, 1993), that *Portia fimbriata* undertakes reversed-route detours. Determining whether *Portia fimbriata*'s unusual style of predation has encouraged the evolution of ability at reversed-route detouring will require comparative data on a wide range of species. As a first step toward this goal, we investigate not only *P. fimbriata* but also an additional species, *Trite planiceps*. *Trite planiceps*, an insectivorous cursorial salticid from New Zealand, is of special interest because it has been reported (FORSTER, 1982) that this species was unable to detour.

Materials and methods

Standard housing and maintenance procedures were used (JACKSON & HALLAS, 1986), and basics of the testing procedures were as in TARSITANO & JACKSON (1993). Therefore, only the details of testing methods specific to the present study are described below.

Test apparatus consisted of a rectangular wood frame (the "mount": 250 mm high & 200 mm across), supported by two 300-mm rampways leading diagonally away from each bottom corner of the mount (Fig. 1). The angle between the rampways and the mount was 120°. Each rampway led to a support leg which was 200 mm high and 20 mm in diameter. To begin each test, a salticid was placed on top of a "starting platform" (150 mm high and

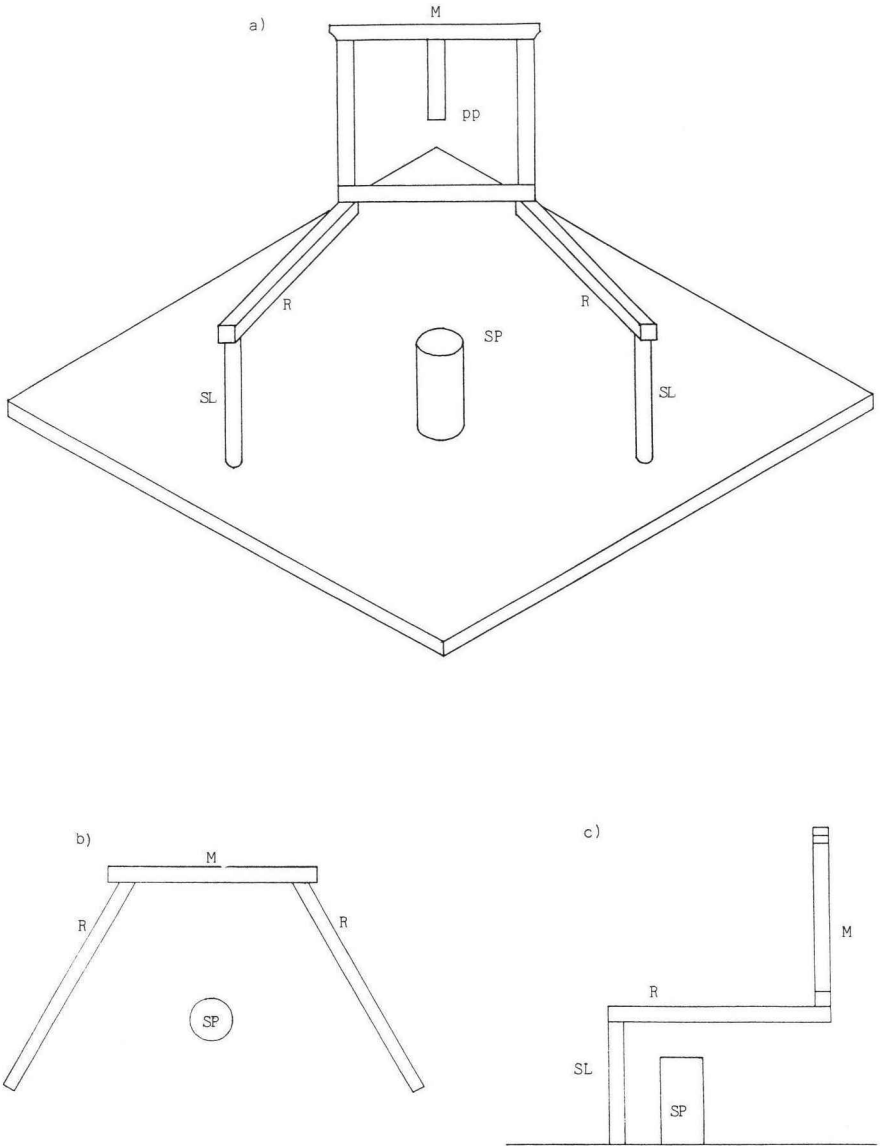


Fig. 1. Test apparatus for reversed-route detours as viewed from experimenter's perspective (a), top (b) and side (c). Lure (see Fig. 2) suspended from prey pole (PP). Salticid placed in pit (not shown) on top of starting platform (SP) before starting test. Two support legs (SL) connect to rampways (R) leading to prey pole.

50 mm in diameter). The starting platform was positioned equidistant from each support leg and 150 mm from the mount. Extending down from the top horizontal piece of the mount was a pole (the "prey pole": 100 mm long & 20 mm in diameter) from which a lure was dangled on the end of a human hair. The bottom of the lure was 10 mm from the bottom of the pole. The dimensions of the detouring apparatus were such that the salticid could reach the lure only by initially going away from the lure, climbing a support leg, then following a rampway to the prey pole.

The lures were dried, dead prey items, prepared as described elsewhere (TARSITANO & JACKSON, 1993). In each test, the lure was about $0.25 \times$ the size of the spider being tested. We used lures that corresponded to the preferred prey of the salticids - a spider, *Eriophora pustulosa* for *Portia fimbriata* and a fly, *Musca domestica*, for *Trite planiceps*.

The lure's movement was controlled by a function generator which regulated the amplitude and oscillation frequency of a magnetic field generated by a coil of wire placed behind a cardboard screen behind the prey mount. The magnetic field moved a magnet glued to the back of the lure. In this way, the lure's movement was standardized: bursts of movement 1 s in duration and 3-5 mm in amplitude at intervals of every 5 s.

Tests were concluded when: a) the salticid reached the lure or b) the salticid walked completely off the apparatus. If the salticid remained motionless on the starting platform for 30 min, the test was aborted. We recorded instances of "stalking", using FORSTER's (1982) definition of this behaviour: the salticid, with its body low to the ground and legs taut, faces a prey and advances by making slow, short steps. Because salticids are known to have dragline-associated pheromones (POLLARD *et al.*, 1987), the apparatus was wiped with acetone between tests.

We were interested in whether a salticid would go "correctly" from the starting platform to a support leg, and from there to the prey mount, or whether it would "erroneously" head from the starting platform directly towards the lure. We also recorded whether the salticids went to a support leg directly from the starting platform, because we wanted to distinguish between those salticids that seemed just to be wandering aimlessly about after leaving the starting platform and those that seemed to be purposefully heading somewhere. "Directly", therefore, meant that the salticid arrived at a support leg after leaving the starting platform without: 1) changing directions, 2) orienting towards anything else, 3) walking past the support leg or 4) pointing its body axis more than 30° from the support leg without immediately re-orienting towards it. Point 4 allows for the tendency of salticids to deviate slightly from a strictly straight route when walking towards a goal (TARSITANO & JACKSON, 1993).

Only adult females were tested. To avoid effects of prior experience with the apparatus, each spider was tested only once. To avoid bias, salticids were chosen at random from available cultures. The *P. fimbriata* tested were reared from eggs in the laboratory; the *T. planiceps* were collected from the field, in New Zealand, a few weeks before testing. All tests were conducted between 0900 and 1700 hours in a laboratory with a 12:12 LD regime with lights coming on at 0800 hours.

Results, being frequency data, were analyzed using Fisher's exact test of independence (HAYS, 1963). From previous work, *Portia* is known to respond readily to motionless prey, whereas *Trite planiceps* usually requires a moving prey (JACKSON & TARSITANO, 1993). This interspecific difference was taken into account when designing the test procedures.

Two different procedures were used for testing *Portia fimbriata*: P1, *Portia* was tested in the presence of a motionless lure; P2, *Portia* was tested with no lure present.

Three different procedures were used when testing *Trite planiceps*: T1, *Trite* was tested with a motionless lure; T2, the lure was moved at the start of the test every 5 s until *Trite* oriented towards it (see LAND, 1972) and again whenever *Trite* re-oriented towards it; T3, the lure was moved, as in T2, at the start of the test, but not when *Trite* re-oriented.

Results

All *Portia* in P1 appeared to fixate on the lure, the mount, the rampways and the support legs before leaving the starting platform. The *Portia* in P2 also appeared to fixate on the different parts of the detour apparatus. The presence of a lure significantly increased the number of *Portia* that arrived at the prey pole (7 out of 10 in P1 when tested with a lure, but 0 out of 10 in P2 when tested without a lure; $p < 0.005$).

The presence of a lure significantly influenced the number of *Portia* that went directly from the starting platform to a support leg. Five of the seven *Portia* that arrived at the prey pole when tested with a lure (P1) went directly from the starting platform to a support leg, but no *Portia* tested without a lure (P2) went towards a support leg ($p < 0.05$). All *Portia* that completed detours re-oriented towards the lure after climbing to the top of a support leg (Fig. 2).

The other two *Portia* that arrived at the prey pole in P1 first went directly towards the lure and arrived at a position directly underneath it. Next, they re-oriented towards the lure, then towards a support leg. The three *Portia* that did not complete the detour also went directly towards the lure and re-oriented towards it. However, they did not re-orient towards a support leg. Eventually they wandered under the mount and off the apparatus.

While on the starting platform, all *Trite* in each group appeared to fixate on the various parts of the apparatus. However, *Trite* tested with a motionless lure (T1) did not appear to fixate on the lure. Lure movement at the start of a test increased the number of *Trite* that arrived at a support leg (2 out of 10 when tested in T1 without lure movement; 16 out of 20 when tested in T2 & T3 with lure movement; $p < 0.005$). All *Trite* that arrived at a support leg went there directly from the starting platform.

Fifteen out of the 16 *Trite* that arrived at a support leg, when presented with a moving lure at the start of the test (T2 & T3), re-oriented towards the lure after climbing to the top of the support leg. However, of the *Trite* that re-oriented, only those that re-oriented towards a moving lure (T2) completed the detour (8 out of 8 in T2, but 0 out of 7 in T3; $p < 0.001$).

The numbers of *Portia* that arrived at the prey pole when tested with a motionless lure in P1 (7 out of 10) and the numbers of *Trite* in T2 that arrived at the prey pole when tested with a lure that moved whenever

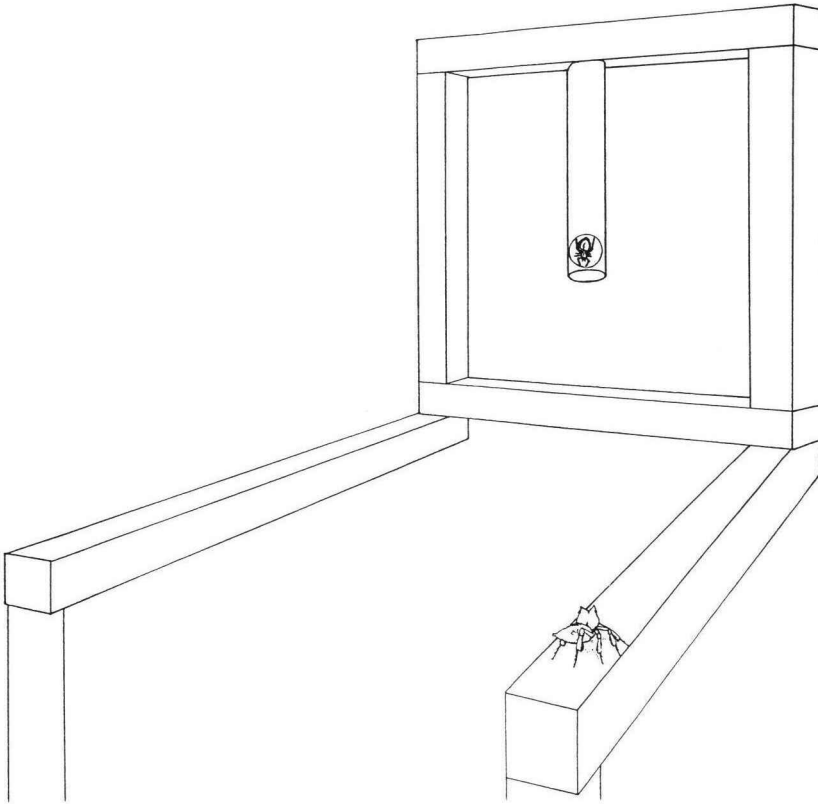


Fig. 2. *Portia fimbriata* re-orienting toward lure (on prey pole) from top of support leg on test apparatus for reversed-route detours (see Fig. 1). Typical response of spider after climbing support leg.

Trite re-oriented (8 out of 10) were virtually identical. However, there was a difference ($p < 0.005$) between the number of *Portia* that arrived at the prey pole when tested in P1 with a motionless prey (7 out of 10) and the number of *Trite* that arrived at the prey pole when tested in T3 with a lure that did not move whenever the *Trite* re-oriented (0 out of 10).

Discussion

The results from this study provide the first evidence under controlled laboratory conditions that salticids can perform reversed-route detours.

In conflict with HILL's (1979) conclusion that salticids must choose secondary goals that bring them closer to a primary goal, *Portia* and *Trite* routinely, in our laboratory tests, completed detours that included a secondary goal (the support leg) which took them further away from the primary goal (the lure). Furthermore, the total length of this detour (1250 mm) was virtually the same as the longest detour (1270 mm) *Portia* has been reported to make in the field (JACKSON & WILCOX, 1993), and 4-5 times the length of the detours reported for *Phidippus* by HILL (1979).

However, *Trite* was much more dependent on prey movement than *Portia*. While on the starting platform, *Trite* never oriented towards a motionless lure (T1); and all *Trite* that re-oriented from the top of a support leg towards a motionless lure (T3) abandoned the detour at this point. In contrast, 7 out of 10 *Portia* fixated on a motionless lure at the start of the test, and all seven continued their detour after re-orienting from the top of a support leg. Comparable differences between *Trite*'s and *Portia*'s responses to motionless lures have been noted before (JACKSON & TARSITANO, 1993) and probably stem from *Portia*'s preference for eating web-building spiders, which tend to remain motionless in their webs when not disturbed. As *Trite*'s dependence on prey movement while re-orienting was unknown at the time, FORSTER (1982) apparently did not take this factor into account in her testing procedures, and this probably accounts for our different findings for this species.

That the salticids frequently re-oriented towards the lure at positions on the detour route where turning back or leaping off the rampway would have led to failure (*i.e.* at the top of support legs) suggests that *Portia* and *Trite* re-oriented in order to obtain visually information about their position relative to the lure. This is consistent with HILL's (1979) conclusion that salticids complete detours as a series of steps. Furthermore, *Portia* and *Trite* headed directly towards one of the support legs after visually fixating, from the starting platform, on key features of the testing apparatus, including the position (top of support legs) from which they would later in the test re-orient towards the lure. This suggests that the salticid was planning ahead the route to be taken, an ability we are currently investigating in the laboratory.

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