

# INFLUENCE OF PREY MOVEMENT ON THE PERFORMANCE OF SIMPLE DETOURS BY JUMPING SPIDERS

by

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(With 6 Figures)

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## Summary

The influence of prey movement on the performance of simple detours by salticids was investigated. Seven species were studied. Two subject species, *Portia fimbriata* and *Portia labiata*, are specialized web-invading species that eat other spiders. The other five species investigated (*Euryattus* sp., *Euophrys parvula*, *Marpissa marina*, *Trite auricoma* and *Trite planiceps*) are more typical cursorial hunters of insects. We provide evidence that: 1) salticids will initiate detours toward motionless prey; 2) salticids are more inclined to initiate detours toward moving than toward motionless prey; 3) salticids tend to complete detours even when prey that had been moving at the start remains stationary during the detour; 4) prey movement makes the salticid more likely to stalk and attack when prey is only a few centimetres away and in a position from which it can be reached by a straightline pursuit; 5) *Portia* is more inclined than the other salticids to initiate detours to motionless prey, then to stalk and attack motionless prey when close, than the other salticids are. Mechanisms that might account for *Portia* being different from the other salticids are discussed.

## Introduction

Jumping spiders (Salticidae) have acute vision and unique, complex eyes (BLEST, 1985), and most species of jumping spiders seem to prey primarily on insects which they catch by actively hunting instead of by building webs (FORSTER, 1982). The salticid visual system consists of four pairs of eyes. These are the anterior median, or "principal", eyes and three pairs

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of "secondary" eyes, the anterior lateral, posterior lateral and posterior median (LAND, 1985a). The principal eyes are responsible for high resolution form vision when images are cast on the foveas of their retinae, the fovea being an area in the principal eye retina in which the photoreceptors are very tightly packed. Secondary eyes lack foveas, and they function primarily as motion detectors (LAND, 1971).

Taken together, the fields of view of the salticid's secondary eyes cover nearly 360° around the spider (LAND, 1985b), but the field of view of the principal eye fovea is only 2° (LAND, 1985a). However, by moving the eye tubes of their principal eyes, while keeping their cuticular lenses stationary, salticids can cover a field of view of *c.* 60° by 60° with their principal eye foveas. In typical predatory sequences, when a salticid detects prey movement with its secondary eyes, it turns to face the prey, thereby bringing the image of the prey into the visual ambit of the foveas of its principal eyes (LAND, 1972). Having identified the prey by using the high resolution system of its principal eyes, the salticid begins stalking the prey.

In most experimental studies on salticid predatory behaviour, the spider has had a direct route to its prey (*e.g.* FORSTER, 1977). However, for salticids in nature, straight-line approaches may not always be practicable, and some salticids are known to take indirect routes (*i.e.* detours) to reach prey (HEIL, 1936; CROME, 1957; HILL, 1979; JACKSON & WILCOX, in press). Detours are interesting because, if a salticid can not keep an image of the prey on the foveas of its principal eyes while detouring, then an ability to remember the prey's location is important (see HILL, 1979). Also, initiating a detour suggests that the salticids may plan ahead how to reach the prey before initiating the predation sequence.

Prey movement is known to be an especially effective stimulus for eliciting prey-stalking by salticids (*e.g.* DILL, 1975), but some salticids are also known to initiate straight-line stalking even when prey is completely motionless (JACKSON & TARSITANO, in press). Apparently, whether salticids will initiate detours when prey is motionless has not been investigated before. Also, whether a salticid that begins a detour in pursuit of a moving prey will complete the detour if the prey subsequently remains motionless has not been investigated.

In a previous study (JACKSON & TARSITANO, in press), 11 salticid species were tested and all sometimes stalked and attacked motionless prey. However, species tested from the genus *Portia* (*P. fimbriata*, *P. labiata* & *P. schultzei*) were more inclined to stalk and attack motionless prey than were the other eight species which belonged to other genera. The species of *Portia* tested are unusual salticids because each is known to invade alien

webs, practise aggressive mimicry and prey on the resident spiders (JACKSON, 1992).

In the present paper, we investigate the influence of prey movement on the performance of simple detours by salticids. We consider six questions. 1) Do salticids initiate detours toward motionless prey? 2) Does prey movement make a salticid more inclined to initiate a detour? 3) Does prey movement after the salticid re-orient toward the prey make the salticid more inclined to continue a detour to the prey? 4) Does prey movement after the salticid gets "close" (*i.e.* when it is only a few centimetres away from the prey and in a position from which a straight-line pursuit will take it to the prey) make the salticid more inclined to stalk and attack the prey? 5) Is *Portia* more inclined than other salticids to initiate detours to reach motionless prey? 6) Is *Portia* more inclined than other salticids to stalk and attack motionless prey after getting close to the prey at the end of a detour? We also discuss mechanisms that might account for interspecific differences in predatory behaviours.

### Materials and methods

#### *General methodology.*

Seven species were tested (Table 1), each of these species having also been used in a previous study of straight-line pursuit of motionless prey (JACKSON & TARSITANO, in press). Maintenance procedures and terminology were as in numerous other studies of salticids (see JACKSON & HALLAS, 1986). This included the convention that the expressions "usually", "sometimes" and "infrequently" indicate frequencies of occurrence of >80%, 20-80% or <20%, respectively. The laboratory light regime was 12L:12D, with the light period beginning at 0800 hours. All testing was conducted between 0800 hours and 1700 hours.

The test apparatus was made of wood and consisted of three 150 mm high poles, that were 20 mm in diameter, at one end of a 300 mm x 300 mm base (Fig. 1). There was a 50 mm high cylinder that was 50 mm in diameter ("the starting platform") at the other end of the base. The centre of each pole was 80 mm from its nearest neighbour and 150 mm from the centre of the starting platform so that, from the centre of the starting platform, each pole was 30° from its neighbour.

The entire apparatus was painted with two coats of water-resistant polyurethane. Between each test, the apparatus was wiped with 80% ethanol, then allowed to dry for at least 30 min, thereby removing possible chemical traces of previous salticids.

Before the test, the salticid was placed in a pit (32 mm in diameter & 32 mm deep) centred at the top of the starting platform. The pit was covered with a piece of clear plastic until the salticid became quiescent. The cover was removed to start the test. In a "successful" test, the salticid walked slowly out of the pit and onto the platform, then "scanned" its surroundings. A salticid "scanned" by standing in place while pivoting about and repeatedly fixating its principal eyes on objects in its environment. ("Scanning", as defined here, should not be confused with LAND's (1969) use of this word for a specific movement pattern of the principal eye retinac). The test was aborted if the salticid stayed in the pit for 30 min or if it left the starting platform without first scanning. When tests were aborted, the salticid was re-tested repeatedly, up to four times per day, until a successful test was completed or four days of unsuccessful testing elapsed.

TABLE 1. Salticid species tested, and spiders and insects used as lures

Species	Description	Use	Origin
<i>Portia fimbriata</i> (Doleschall)	Spider-eating salticid	Test spider	Australia (Queensland)
<i>Portia labiata</i> (Thorell)	Spider-eating salticid	Test spider	Sri Lanka
<i>Euophrys parvula</i> Bryant	Salticid	Test spider	New Zealand
<i>Euryattus</i> sp.	Salticid	Test spider	Australia (Queensland)
<i>Marfissa marina</i> Goyen	Salticid	Test spider	New Zealand
<i>Trite auricoma</i> Urquhart	Salticid	Test spider	New Zealand
<i>Trite planiceps</i> Simon	Salticid	Test spider	New Zealand
<i>Eriophora pustulosa</i> (Walckenaer)	Web-building araneid spider	Lure	New Zealand
<i>Musca domestica</i> L.	House fly	Lure	Laboratory culture

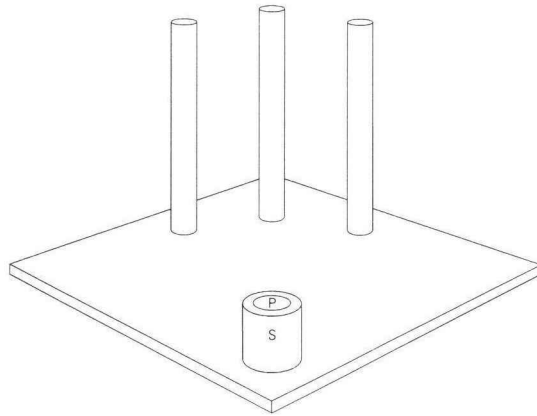


Fig. 1. Test apparatus. Lure suspended from one of three poles (which pole decided randomly). Salticid placed in pit (P) at top of starting platform (S) at start of test.

Illumination was provided by a 200 W incandescent lamp, positioned c. 600 mm above the entire apparatus; fluorescent ceiling lamps provided additional, ambient, lighting. The apparatus was surrounded by a white cardboard screen on three sides, the open side being for the observer. The apparatus was oriented so that, during the test, the salticid moved away from the observer at the open end.

Before each test, a lure was placed on one of the three poles (called the "prey pole") 85 mm above the base. Which of the three poles would be the prey pole was determined randomly for each test. The lure was positioned on the side of the pole that faced the starting platform. At this height, the lure was  $30^\circ$  up from the base of the starting platform (Fig. 2). Because of the restricted fields of view of salticid principal eyes (LAND, 1985a), a salticid on the base between the starting platform and the prey should not have been able to fixate an image of the lure on the foveas of its principal eyes unless it lifted its cephalothorax and oriented its cephalothorax toward the lure. That is, to obtain a high resolution image of a motionless lure, a salticid would have to orient its cephalothorax toward the lure.

The lure was either a dead spider or a dead house fly (Table 1), made by killing the spider or fly by  $\text{CO}_2$  asphyxiation, then placing it in alcohol for 1 hr. After mounting the lure on one side of a disk-shaped piece of cork (c. 1.25 times the body length of the lure in diameter), the lure and the cork base were sprayed with an aerosol plastic adhesive for preservation and to eliminate the possibility of olfactory cues from the dead spider or insect. In each instance, the lure was about half as large as the salticid. The lure was held in place on the pole by a thin transparent thread glued at one end to the back of the cork disk and at the other end to the top of the pole. To control the lure's movement, a magnet was glued to the side of the cork opposite the dead spider or fly. A magnetic field generated by a wire coil placed behind the cardboard screen and connected to a function generator was used to move the magnet (and lure). By controlling the amplitude and frequency of the signal from the function generator, lure movement was standardized at 3-5 mm at c. 5/s for 1 s.

All salticids used were reared from eggs in the laboratory. Salticids were chosen for tests at random from the laboratory cultures, and no individual salticid was tested more than once (*i.e.* no individual salticid was used in more than one procedure or in more than one repetition of a given procedure). Each test ended when the salticid did one of the following: 1) walked off the base without having reached a pole, 2) contacted a pole other than the

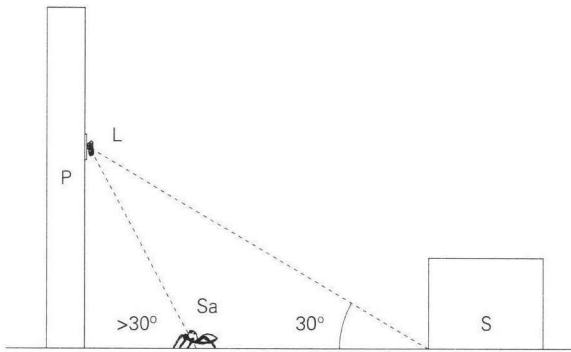


Fig. 2. Salticid (Sa) approaching prey pole (P). Vertical angle from base of starting platform (S) to lure (L) is  $30^\circ$ . Salticid on the base of apparatus anywhere between S and P cannot see lure with its principal eyes unless it re-orientates towards it.

prey pole, 3) began to walk back up the starting platform, 4) arrived at the prey pole, then left the prey pole without attacking the lure, or 5) arrived at the prey pole, then stalked and attacked the lure.

Only results 4 & 5 were taken as evidence of detouring. When a salticid failed to detour to the prey or failed to attack it, we needed to ascertain that this was not simply because the spider was disinterested in prey. Therefore, to ensure that spiders were hungry, all subjects were deprived of food for 10-14 days prior to testing. Also, immediately after each test in which the salticid failed to detour, or detoured (*i.e.* reached the prey pole) but failed to attack the lure, the salticid was given access to a live prey of the salticid's preferred type (spiders for *Portia*; flies for all other salticids). Most salticids attacked the live prey. However, whenever a salticid that failed to detour (or detoured but then failed to attack the lure) also failed to attack live prey, the test for this salticid was eliminated from the data set.

Comparisons between tests and between species were made using tests of independence, with Bonferroni adjustments for repeated testing of the same data sets (see RICE, 1989).

To simplify presentation, data from tests using the two species of *Portia* were pooled and data from tests using the seven species of salticids other than *Portia* ("non-*Portia*") were pooled. In all instances, for data were pooled,  $p > 0.01$ .

#### *Test procedures.*

Four test procedures were used.

*Procedure 1.* The lure remained motionless throughout the test.

*Procedure 2.* At the start of the test, after the salticid walked out onto the platform, but before it fixated its principal eyes on the lure, the lure was moved every 5 s. When the salticid fixated its principal eyes on the lure the first time, lure movement was stopped until the salticid oriented away from the lure. However, the lure was moved again whenever the salticid re-oriented toward it and whenever the salticid started to climb the prey pole.

*Procedure 3.* This procedure began like procedure 2. However, once the salticid on the starting platform fixated its principal eyes on the lure, the lure was kept stationary for the rest of the test.

*Procedure 4.* No lure was present on any of the three poles (control).

## Results

Salticids initiated detours toward motionless prey.

Some individuals of each salticid species tested provided evidence of detouring to the prey pole in tests in which procedure 1 (motionless lure) was used (Fig. 3). However, no salticids contacted any of the poles in tests using procedure 4 (control: no lure present) ( $N=12$  for each species). Salticids only rarely (7 instances) contacted any pole other than the prey pole in tests in which procedures 1-3 were used (pooling data for all species, 3 instances for procedure 1, none for procedure 2, & 4 for procedure 3).

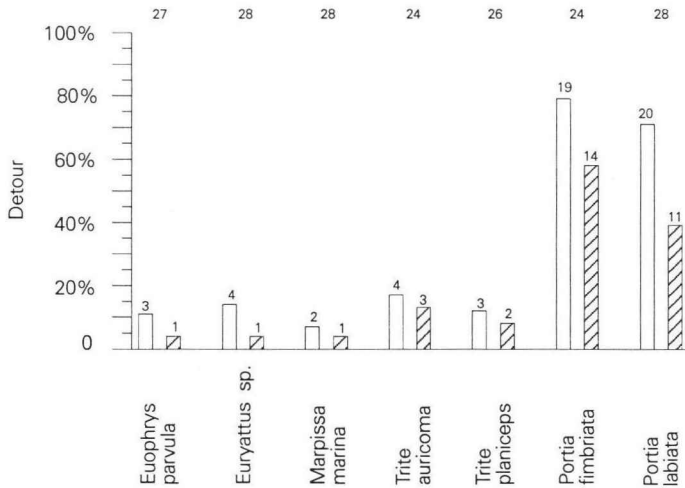


Fig. 3. Results from tests using procedure 1 (lure motionless throughout test). Arrival at prey pole (plain bars) and attacked lure (striped bars): No. above bar and percentage of tests on vertical axis. No. of tests above pair of bars of each species.

Prey movement made salticids more inclined to initiate detours.

The salticids tested took detours to the prey pole more often in tests using procedure 2 (lure movement until initial orientation, then after each re-orientation) (non-*Portia*,  $p < 0.001$ ; *Portia*,  $p < 0.005$ ) and procedure 3 (lure movement until initial orientation but not afterwards) (non-*Portia*,  $p < 0.001$ ; *Portia*,  $p < 0.001$ ) than in tests using procedure 1 (no lure movement) (Fig. 3-5).

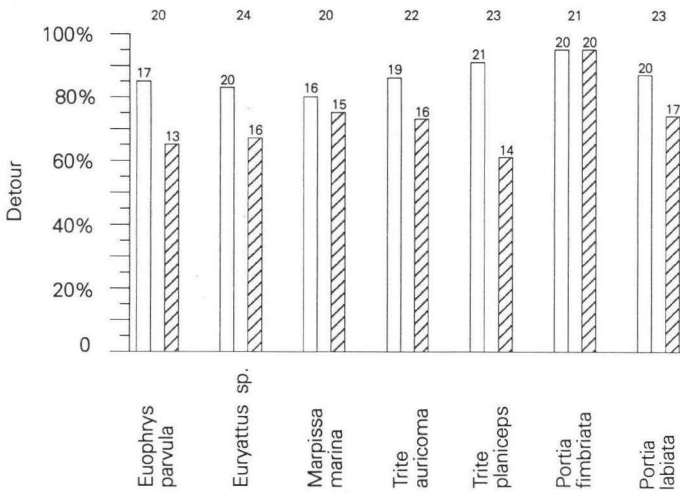


Fig. 4. Results from tests using procedure 2 (lure movement up until initial orientation, then after each re-orientation). Arrival at prey pole (plain bars) and attacked lure (striped bars): No. above bar and percentage of tests on vertical axis. No. of tests above pair of bars for each species.

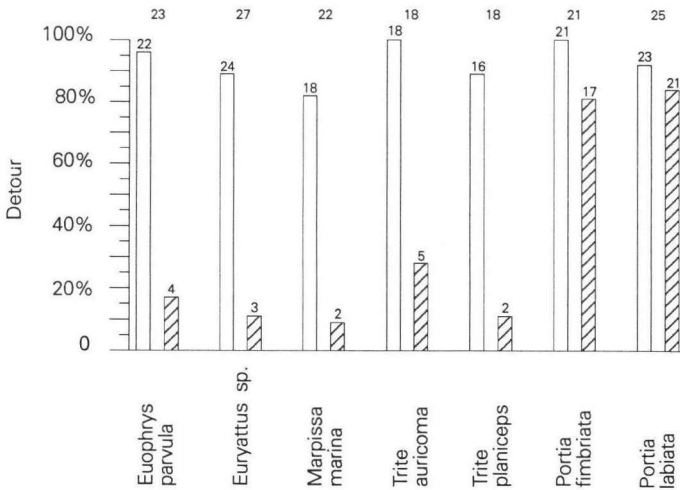


Fig. 5. Results from tests using procedure 3 (lure movement up until initial orientation but not afterwards). Arrival at prey pole (plain bars) and attacked lure (striped bars): No. above bar and percentage of tests on vertical axis. No. of tests above pair of bars for each species.



Prey movement after salticids re-oriented appeared not to change the number of detours completed by salticids.

For the salticid species tested, results from procedure 2 and 3 were similar (tests of independence, NS) (Fig. 4-5).

Prey movement after salticids got close to prey made salticids more inclined to stalk and attack prey.

Only data from those salticids that reached the prey pole was used for this analysis because "close" was defined as "on the prey pole". For the salticid species tested, more individuals attacked the lure in tests using procedure 2 (Fig. 4) than in tests using procedure 1 or 3 (Fig. 3 & 5) (non-*Portia*,  $p < 0.001$ ; *Portia*,  $p < 0.001$ ).

*Portia* was more inclined than other salticid to initiate detours to reach motionless prey.

In tests using procedure 1, *Portia* detoured more often than did the other salticids (Fig. 3) ( $p < 0.001$ ).

*Portia* was more inclined than other salticids to stalk and attack motionless prey after reaching the prey pole at the end of detours.

Only those salticids that reached the prey pole were used in this analysis. In tests using procedure 1, *Portia* stalked and attacked the lure more often than the other salticids did ( $p < 0.001$ ) (Fig. 3).

Details of the behaviour of salticids during the tests.

Salticids other than *Portia* scanned in an irregular fashion during the tests, pausing 1-10 s while facing in any one direction, then rotating  $20^\circ$ - $120^\circ$  to face in a new direction. *Portia*, however, tended to scan by pausing only 2-3 s while facing in any one direction and by rotating only  $30^\circ$ - $40^\circ$  during each turn.

Similar interspecific differences were seen whenever a salticid that had left the starting platform re-oriented to face the lure. Salticids other than *Portia* turned in a single smooth movement toward the prey pole. If the salticid's principal eyes were not centred on the prey pole after a re-orienting turn, the salticid tended to make additional turns in the same erratic way as when it was on the starting platform. *Portia*, however, turned in a series of arcs, each of  $30^\circ$ - $40^\circ$ , paused only 2-3 s between turns, and continued to turn and pause until oriented toward the lure.

While scanning or re-orienting, all salticid species tended to pause for 3-4 s whenever a turn ended with the principal eyes fixated on one of the poles. Also, the salticid usually oriented its principal eyes to the top of the pole by tilting its cephalothorax upwards from the pedicel. If the lure was moving, salticids usually next fixated their principal eyes on the lure, but they usually failed to do so if the lure was motionless. Unlike the other salticids, *Portia* usually fixated on the lure even if the lure was motionless. After fixating on the lure, salticids (both *Portia* and non-*Portia*) usually headed towards the prey pole.

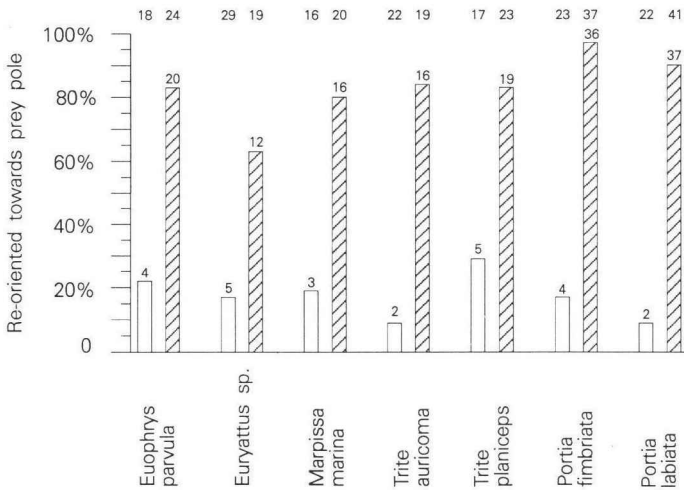


Fig. 6. Percentages of salticids that re-oriented toward prey pole, according to whether or not they faced away from prey pole at an angle greater (plain bars) or less than  $30^\circ$  (striped bars). No. above bar and percentage of tests on vertical axis. No. of tests above bars.

After scanning from the starting platform, salticids tested without a lure (procedure 4) left the starting platform in apparently random directions and eventually wandered off the base of the apparatus without having contacted a pole. In about half of these tests for each species, the salticid scanned one or more times after leaving the starting platform and often changed its direction of walking, but still never contacted a pole. For tests using salticids other than *Portia*, most of the results from tests with lures that never moved (procedure 1) were similar to results from tests in the absence of lures (procedure 4): only a few individuals of each species contacted the prey pole and those individuals that failed to contact the prey pole behaved more or less the same as in tests without lures.

When a salticid headed toward the prey pole after descending from the starting platform, it usually did not follow a completely straight path. About half of the individuals of each species eventually stopped and made distinct re-orienting turns, then headed in a nearly straight line towards the prey pole during detours. Most of the other individuals followed curvilinear paths and corrected deviations from a straight path to the prey pole in a gradual and continuous manner.

Each species sometimes deviated more than  $30^\circ$  from a straight path to the prey pole (*i.e.* the angle between the sagittal plane of the salticid's cephalothorax and a straight line drawn from the centre of the salticid's cephalothorax to the prey pole was greater than  $30^\circ$ ). Those individual salticids that deviated by more than  $30^\circ$  *en route* to the prey pole more often made a distinct re-orientation turn toward the lure than did those salticids that did not deviate by as much as  $30^\circ$  (Fig. 6) (non-*Portia*,  $p < 0.001$ ; *Portia*,  $p < 0.001$ ). For this analysis, data were taken from only those tests in which the salticid contacted the prey pole.

## Discussion

From this study of seven salticid species, we can attempt to answer the questions raised in the Introduction:

1. Salticids do initiate detours toward motionless prey: in our tests, each species at least sometimes undertook a detour to a motionless lure.
2. Prey movement does seem to make salticids more inclined to initiate detours: each species made detours and contacted the prey pole more often in tests in which the lure moved than in tests in which the lure remained motionless.
3. Prey movement after the salticid reaches the prey pole does make the salticid more inclined to stalk and attack prey: after contacting the prey pole, each species stalked and attacked more often when the lure moved and less often when the lure remained motionless.
4. There was no evidence that prey movement after a salticid re-orientates makes the salticid more inclined to continue a detour route to prey: each species continued detours and contacted the prey pole about as often when the lure remained motionless after re-orientation as when the lure moved after the salticid re-orientated.
5. *Portia* is also more inclined than other salticids to stalk and attack motionless prey after getting close (*i.e.* contacting the prey pole) at the end of a detour: the two species of *Portia* more often stalked and attacked a

motionless lure after contacting the prey pole than did the other five salticid species.

The two *Portia* species we tested are known to prey readily on quiescent web-building spiders in nature and in the laboratory (JACKSON & HALLAS, 1986). The other salticids we tested probably prey primarily on active insects. Therefore, a possible explanation of interspecific differences obtained in the present study is that all salticids readily detect motionless objects the size of prey, but only *Portia* is motivated to pursue motionless (quiescent) prey.

However, details of how the seven salticid species behaved during tests suggest, instead, that *Portia* detects and recognizes motionless prey more readily than other salticids, and this may largely account for the observed interspecific differences in the results of tests using motionless lures. When scanning from the starting platform, and when re-orienting toward the lure after leaving the starting platform, *Portia* made small-angle turns (30°-40°) and paused between each successive turn. In contrast, the other salticids tended to scan by taking more variable, and often larger, turns (20°-120°), and they tended to re-orient by making smooth, continuous turns.

The short, stepwise turns *Portia* made when scanning and re-orienting would give *Portia* slow stepwise coverage of its surroundings with its principal eyes. The different styles of scanning and re-orienting adopted by the other salticids would result in these salticids' principal eyes sweeping rapidly over large surrounding areas and, therefore, probably moving past small motionless objects too quickly to detect them.

It would appear that *Portia* relies, to an unusually large extent, on the acute vision of its principal eyes for prey detection. Other salticids appear to rely primarily on their secondary eyes (movement detectors) for prey detection. It is probable that most salticids, and not just *Portia*, tend to respond in a predatory fashion when they detect motionless prey with their principal eyes, but the behaviour of salticids other than *Portia* appears to be such that these species would only rarely succeed in having images of motionless prey fall directly onto the 2° field of view of the principal eye foveas.

If the way they scan and re-orient makes most salticids less efficient than *Portia* at detecting motionless prey, then it might be reasonable to say that *Portia* spends more of its time "looking for" motionless prey than other salticids do. Because *Portia* routinely feeds on quiescent web-building spiders, efficiency at detecting motionless prey may be more relevant to *Portia* than to most salticids. This suggests that *Portia's* scanning and re-

orientation methods may have been shaped by a natural selection regime benefitting individuals with greater efficiency at detecting motionless prey.

The abilities of salticids to detect motionless objects must surely vary with the size of objects. All salticids tested appear to have detected the poles on the test apparatus, and salticids must generally be able to examine the terrain around them accurately. However, when a salticid was on the test apparatus, the angle subtended by the poles was always greater than the width of the salticid's fovea. This means that the entire fovea would have been occluded by the image of a pole when the salticid was facing the pole.

In a study of *Salticus scenicus*, DILL (1975) demonstrated that, once this salticid has begun to take a straight-line route to a prey that had been moving, it will continue toward, then attack, the prey even if the prey does not move again. DILL's observation can be accounted for readily: the salticid, having oriented toward a moving prey, and identified it by using its principal eyes, only has to maintain its initial orientation toward the prey as it approaches. However, salticids undertaking the simple detours required in the present study could not have been doing this because, during the detour, the salticid always had to orient away from the lure. However, DILL's observation does suggest a conceivable mechanism by which salticids might have completed the simple detours with which they were presented in our tests. Conceivably, the salticid's behaviour could have been simply to begin walking away from the starting platform in the general direction of the lure, without navigating toward the prey pole, then to climb the prey pole it encountered along this path and to re-locate the lure from there. However, this does not appear to be the mechanism used by the salticids tested. Instead, the salticids appeared to navigate towards the prey pole by using their principal eyes to keep track of the prey pole's position: while approaching the prey pole, each salticid species tested tended to wander off from an exactly direct route towards the prey pole and, whenever deviation exceeded *c.* 30°, each salticid species tested tended to re-orient towards the prey pole.

It is known that *c.* 30° is the maximum angle by which a small object can deviate to either side of the mid-line of the salticid's cephalothorax and still be tracked ("tracked": eye tubes moved so that an image of the object remains on the principal eye fovea (LAND, 1969)). This suggests that salticids in our tests usually re-oriented towards the lure only when the lure's image moved out of the range of the principal eye foveas.

HILL (1979) argued that salticids take indirect routes to prey by heading

towards successive "secondary goals", each of which brings the salticid closer to the prey. This hypothesis can readily account for our findings. For salticids in our tests, arriving at the prey pole and arriving at the lure occurred sequentially. Because the salticid appeared to navigate to the prey pole, reaching the prey pole appeared to be, for the salticid, a secondary goal or sub-goal towards achieving the primary goal of reaching the lure.

Our findings suggest that the process by which salticids completed the simple detours required by our tests was as follows:

- a. identify the lure as a potential prey item (the primary goal).
- b. associate the prey pole (a sub-goal) with the prey (the primary goal),
- c. navigate towards the prey pole by keeping the image of the prey pole on the foveas of the principal eyes,
- d. after reaching the prey pole (*i.e.* the sub-goal), climb the pole, thereby bringing the lure into view,
- e. stalk and attack the lure.

The interspecific differences we observed appear to be accounted for primarily by *Portia* being relatively more responsive to motionless prey than are other salticids. Differences between *Portia* and the other salticids tested in responsiveness to stationary prey appear to be accounted for by differences in scanning and re-orienting behaviours.

*Portia fimbriata* has been credited with taking longer, more complicated detours than investigated in the present study (JACKSON & WILCOX, in press), and we are currently studying mechanisms by which complex detours are completed.

## References

- BLEST, A. D. (1985). Fine structure of spider photoreceptors in relation to function. — In: Neurobiology of arachnids (F. G. BARTH, ed.). Springer Verlag, Berlin, pp. 79-102.
- CROME, W. (1957). Arachnida. — In: (E. STRESEMANN, ed.). Exkursionsfauna, Wirbellose. Volk & Wissen, Berlin, pp. 289-361.
- DILL, L. M. (1975). Predatory behaviour of the zebra spider, *Salticus scenicus* (Araneae: Salticidae). — Can. J. Zool. 53, p. 1284-1289.
- FORSTER, L. M. (1977). A qualitative analysis of hunting behaviour in jumping spiders (Araneae: Salticidae). — N. Zeal. J. Zool. 4, p. 51-62.
- (1982). Vision and prey-catching strategies in jumping spiders. — Am. Sci. 70, p. 165-175.
- HEIL, K. H. (1936). Beiträge zur Physiologie und Psychologie der Springspinnen. — Z. Vergl. Physiol., 23, p. 125-149.
- HILL, D. E. (1979). Orientation by jumping spiders of the genus *Phidippus* (Araneae: Salticidae) during the pursuit of prey. — Behav. Ecol. and Sociobiol. 6, p. 301-322.
- JACKSON, R. R. (1992). Eight-legged tricksters: spiders that specialize at catching other spiders. — BioSci. 42, p. 590-598.

- & HALLAS, S. E. A. (1986). Comparative biology of *Portia africana*, *Portia albimana*, *Portia fimbriata*, *Portia labiata*, and *Portia schultzi*, areneophagic, web-building jumping spiders (Araneae: Salticidae): utilisation of webs, predatory versatility and intra-specific interactions. — *N. Zeal. J. Zool.* 13, p. 423-489.
- & TARSITANO, M. S. (In press). Responses of jumping spiders to motionless prey. — *Bull. Br. Arachnological Society*.
- & WILCOX, R. S. (In press). Observations in nature of detouring behaviour by *Portia fimbriata*, a web-invading araneophagic jumping spider (Araneae, Salticidae) from Queensland. — *J. Zool., London*.
- LAND, M. F. (1969). Movements of the retinae of jumping spiders (Salticidae: Dendryphantinae) in response to visual stimuli. — *J. Exp. Biol.* 51, p. 471-493.
- (1971). Orientation of jumping spiders in the absence of visual feedback. — *J. Exp. Biol.* 54, p. 119-139.
- (1972). Stepping movements made by jumping spiders during turns mediated by the lateral eyes. — *J. Exp. Biol.* 57, p. 15-40.
- (1985a). The morphology and optics of spider eyes. — In: *Neurobiology of arachnids* (F. G. BARTH, ed.). Springer Verlag, Berlin, pp. 53-78.
- (1985b). Fields of view of the eyes of primitive jumping spiders. — *J. Exp. Biol.* 119, p. 381-384.
- RICE, (1989). Analyzing tables of statistical tests. — *Evolution* 43, p. 223-225.
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