Cues for web invasion and aggressive mimicry signalling in *Portia* (Araneae, Salticidae)

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(With 2 figures in the text)

Portia is a web-invading araneophagic spider that uses aggressive mimicry to deceive its prey. The present paper is a first step toward clarifying experimentally the cues that govern *Portia*'s decisions of whether to enter a web, whether to make signals once in a web, and whether to persist at signalling once started. The following conclusions are supported: cues from seeing a web elicit web entry, but volatile chemical cues from webs of prey spiders are not important; seeing a spider in a web increases *Portia*'s inclination to enter the web; after web entry, cues from webs of prey spiders are sufficient to elicit signalling behaviour, even in the absence of other cues coming directly from the prey spider; seeing a prey spider or detecting vibrations on the web make Portia more prone to signal, but volatile chemical cues from prey spiders are not important; once *Portia* is on a web and signalling, seeing a moving spider and detecting vibrations on the web encourage *Portia* to persist in signalling; on the basis of visual cues alone, *Portia* can distinguish between quiescent spiders, insects and eggsacs.

Contents

Introduction

Spiders generally have poorly developed eyes (Homann, 1971; Land, 1985*a*). Web-building spiders recognize and locate prey and predators primarily by interpreting vibrations coming across silk, and cursorial spiders may sense substratum-borne vibrations or rely on touch (Foelix, 1982). Salticids, or jumping spiders, are exceptional. They have complex eyes (Homann, 1928; Blest & Carter, 1987) which enable these spiders to be efficient cursorial predators on motile insects (Heil, 1936; Drees, 1952; Forster, 1977, 1982).

Three pairs of 'secondary' eyes—the antero-lateral (AL), postero-medial (PM) and postero-lateral (PL) eyes—are primarily movement detectors (Land, 1972), except that the PM eyes in most salticid species are apparently degenerate (Eakin & Brandenburger, 1971). It is the salticid antero-medial (AM), or 'principal', eyes, however, that are especially noteworthy because it is

these eyes that provide for acute vision (Land, 1969a, b; Williams & McIntyre, 1980; Blest, 1985). As might seem befitting of predators with acute vision, most salticids do not frequent webs.

However, some salticids are atypical (Richman & Jackson, 1992), the species in the genus *Portia* being the most thoroughly studied (Wanless, 1978; Jackson, 1992). *Portia* builds its own prey-catching web and, also, *Portia* is a web-invading araneophagic spider that uses aggressive mimicry to deceive its prey (Jackson & Blest, 1982a; Jackson, 1992). After entering an alien web, *Portia* makes vibratory signals by performing specialized leg, palp and abdomen movements. These signals either lure the victim spider to within attack range or keep the victim spider pacified while *Portia* stalks across the web. *Portia* also takes insects and the victim spider's eggs while in the alien web.

Yet, like all salticids, *Portia* has acute vision (Jackson & Blest, 1982b) which allows for visually-mediated cursorial predation on motile insects. *Portia*'s secondary eyes (AL, PM and PL) detect movement and control orientation by the predator toward objects in its field of vision (Land, 1985b). Discrimination between classes of objects (e.g. prey, mate and conspecific of same sex) are then mediated through the principal eyes. This is essentially the same way that all salticids use their eight eyes, except that the PM eyes of most salticids are degenerate.

Portia is a predator with an unusually complex conditional strategy (*sensu* Dominey, 1984), each individual having a repertoire of predatory tactics, the particular tactic used in any instance depending on local circumstances. That is, an individual *Portia* behaves differently depending on whether it is in a web (its own or alien) or away from webs, and also depending on the type of prey encountered. *Portia* is also known sometimes to use prey-specific prey-catching behaviour against particular prey species (Jackson & Wilcox, 1990, unpubl. data). So complex a strategy raises questions about cues: how does *Portia* know when to do what? In the present paper, as a first step in addressing questions about cues, I investigate the cues for web invasion and aggressive mimicry signalling.

General methods

Standard spider laboratory maintenance procedures, cage design and terminology were adopted (Jackson & Hallas, 1986). Four previously studied species of *Portia*, and 2 previously studied populations of *P. fimbriata* (Doleschall), were used: *P. africana* (Simon) and *P. schultzi* Karsch from Kenya, *P. labiata* (Thorell) from Sri Lanka, *P. fimbriata* from the Northern Territory (NT) in Australia and *P. fimbriata* from Queensland (Q), Australia. Pooled data were used whenever there was no evidence of differences among species or populations of *Portia*. Sample sizes were always about equal for the different data sets pooled. All

TABLE I

Spiders used as stimuli and sources of webs when testing **Portia**

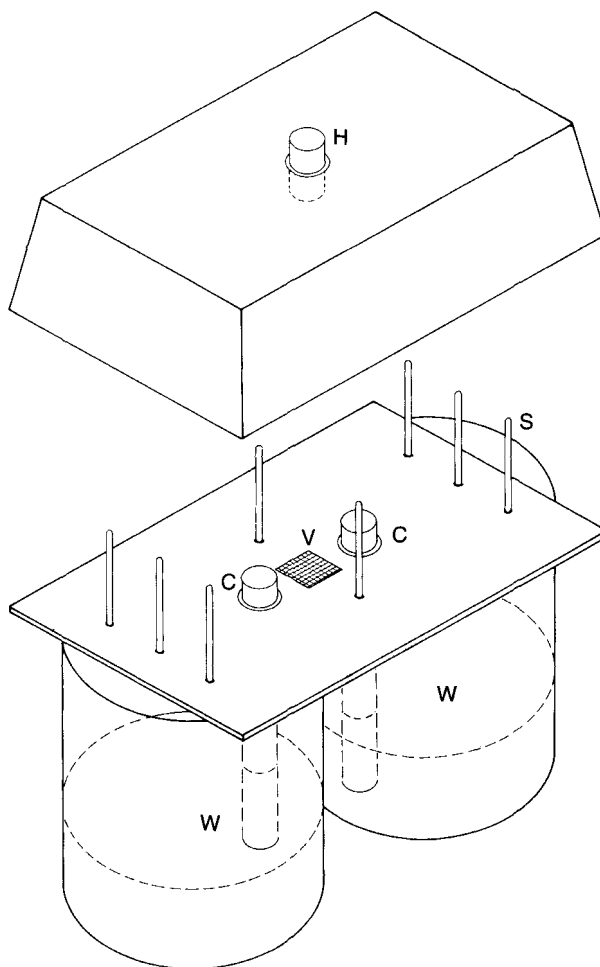| Species	Family	Type of web	Collection site
Achaearanea sp.	Theridiidae	Ecribellate sticky space web	New Zealand
Badumna longinqua (L. Koch)	Amaurobiidae	Cribellate sheet web	New Zealand
Eriophora pustulosa (Walckenaer)	Araneidae	Ecribellate sticky orb web	New Zealand
Inola subtilis Davies	Pisauridae	Non-sticky sheet web	Australia
Pholcus phalangioides (Fuesslin)	Pholcidae	Non-sticky dome web	New Zealand
Stegodyphus sarasinorum Karsch	Eresidae	Communal cribellate sheet web	Sri Lanka
Zosis geniculatus (Olivier)	Uloboridae	Cribellate orb web	Australia

FIG. 1. 'Stick cage.' Made from $151 \times 123 \times 70$ mm transparent plastic lunch box. All holes in cage 9 mm in diameter, except for holes for sticks (1 mm). H: hole plugged with cork. V: ventilation hole covered with brass screen. C: cotton roll ('dental wad') projecting through hole in bottom of cage and resting in 79×58 mm plastic cup filled with water (W). S: Stick (68 mm long) inserted into hole and extending upright into cage. Spider fastens web primarily to sticks. Top of cage can be lifted (as in drawing) without extensive damage to web.

Portia tested were reared from eggs in the laboratory. A variety of spider and insect species were used as prey, all of which have been used in previous studies (Table I).

Unless stated otherwise, experiments were carried out as 'paired comparisons' by testing each individual *Portia* on alternate days, one day with one condition and the other day with a different condition (order decided randomly). The tests on alternate days were always at about the same time of day. All testing was carried out between 14:00 and 19:00 h (lights on in the laboratory 08:00 h, off at 20:00 h). No individual *Portia* was used more than once in any one type of experiment, although it might be used in more than one type of experiment. No individual *Portia* was tested more than once per day.

All webs used in tests were built by spiders in the laboratory in 1 of 2 types of cages: 'stick cages' (Fig. 1) or 'glass cages' (Fig. 2). These cages could usually be opened with only minimal damage to the webs. Spiders in

stick cages fastened their silk primarily to the sticks that were anchored to the bottom of the cage. By removing the bottom of the cage, the web could be extracted intact. Spiders in glass cages fastened their silk primarily to the wooden sides of the cage and sticks within the cage, instead of to the glass sides. These webs could be exposed intact by removing the sides of the cage. For details about construction of spider cages, see Jackson (1974) and Phibbs & Jackson (1981).

Except when stated otherwise, webs were always exposed during tests. Vacant webs were obtained by removing the host spiders and all large pieces of detritus (e.g. prey remains). Damage to the webs was minimized by using a heated wire to sever threads that adhered to detritus. 'Recently vacated' webs were obtained by removing spiders 5–10 min before tests began; '7-day vacant' webs were obtained by removing the spiders 7 days before tests began and leaving the webs exposed during this 7-day period. 'Empty' webs refers to 'recently vacated' webs except when stated otherwise.

Some experiments were carried out using a species of social spiders, *Stegodyphus sarasinorum* Karsch (Sri Lanka); these are eresids that spin communal sheet webs (Bradoo, 1980) with no spacing into individual territories ('communal & non-territorial'; terminology from Jackson, 1978). All webs of *S. sarasinorum* that were used were built by colonies of spiders. A 'colony' was established each time by putting 10 juveniles of similar size together in a cage.

Adult males and females are referred to simply as 'males' and 'females'. Two size classes of juveniles are recognized: small (2–4 mm) and large (6–8 mm). The performance by *Portia* of vibratory aggressive mimicry signals is referred to simply as 'signalling'. Data generally not being normally distributed are given as medians followed by range in parentheses. Except when noted otherwise, the *Portia* and any other spider, or an insect or eggsac, used in a test were about the same size.

Methods specific to different questions and hypotheses will be given in the appropriate sections of the paper (see below). *Portia*'s decision to start signalling while on a web will be considered before *Portia*'s
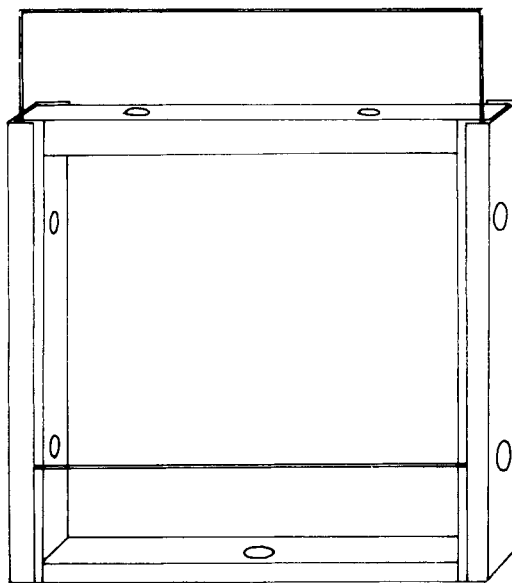

Fig. 2. 'Glass cage.' Wooden frame (200 × 200 × 30 mm interior dimensions), with seven cork holes (corks not shown), and removable glass sides on front and back. Glass fits in grooves in frame (front glass shown partly raised). *Portia* held in vial (below cage) before test. To start test, open vial connected to open hole at bottom of cage so that *Portia* can walk out into cage. Spider fastens web primarily to wooden frame. Glass sides can be lifted (as in drawing) without extensive damage to web.

decision to enter a web because the methods for the latter are easier to explain after the methods for the former have been given.

Deciding to start signalling

A *Portia* on an alien web makes a decision of whether to signal or not. A series of experiments was carried out to examine the cues on which *Portia* bases this decision.

Methods

Unless stated otherwise, a test began by placing a *Portia* on a web and observing its behaviour continuously for the next 30 min (Experiment 1) or 10 min (all other experiments). If the *Portia* left the web before the time period (30 min or 10 min) elapsed, the test was aborted and attempted again each successive day until a successful test was obtained or 4 days elapsed (i.e. as many as 5 days could intervene between the 2 tests in a test pair). If a successful test was not obtained after 4 attempts, the test pair was aborted.

Experiment 1
*How does **Portia** respond to contact with recently vacated webs?*

Portia normally approaches a web occupied by another spider, goes slowly on to the alien web, then begins making vibratory signals. The web resident may stay quiescent until after *Portia* starts signalling, and *Portia* might not be oriented directly toward the resident spider until after starting to signal. These observations suggest that there are cues for starting aggressive mimicry behaviour that *Portia* receives from contacting webs, independent of any cues that might come directly from the spider in the web.

Tests were carried out to examine this hypothesis. These tests were not, strictly speaking, an experiment (there was no control), but will be referred to as Experiment 1 for consistency of terms. These tests provided baseline information out of which subsequent experiments were designed.

Methods

A series of tests was carried out using empty webs of a variety of spider species. These webs varied considerably in geometry and design (Table I). All webs were in open glass cages. Tests using webs of *Badumna longinqua* (L. Koch) were carried out on all available species, populations and sex-size classes of *Portia*. Tests using the other types of webs were carried out on only small juveniles of *P. fimbriata* (Q) and *P. labiata*.

Results and discussion

At least three individuals of each sex-size class of each species and population of *Portia* signalled on empty webs of *Badumna longinqua* (Table II); using pooled data, 68% signalled. On the other kinds of empty webs, similar response rates were obtained (Table III); using pooled data, 56% signalled. Apparently, cues received from contacting empty webs of a variety of types elicit signalling by all species, populations and sex-size classes of *Portia* tested.

TABLE II

Species and sex-age classes of **Portia** *tested on vacant webs of* **Badumna longinqua.** *Note that all types of* **Portia** *signalled*

		No. of tests	No. of tests in which *Portia* signalled
P. africana	Male	10	3
	Female	13	10
	Large juvenile	11	7
	Small juvenile	10	5
P. fimbriata (NT)	Male	12	7
	Female	12	9
	Large juvenile	10	8
	Small juvenile	10	5
P. fimbriata (Q)	Male	11	8
	Female	18	14
	Large juvenile	19	14
	Small juvenile	20	15
P. labiata	Male	12	8
	Female	15	14
	Large juvenile	20	17
	Small juvenile	10	8
P. schultzi	Male	16	8
	Female	17	11
	Large juvenile	14	9
	Small juvenile	10	3

Experiment 2

How does **Portia** *respond to contact with webs that have been empty for a week?*

Are there volatile chemical cues on empty webs that make *Portia* more often signal after contact with recently vacated webs than after contact with webs that have been vacant for a long time? An experiment was carried out to examine this question.

TABLE III

Small juveniles of **Portia fimbriata** *and* **P. labiata** *tested on vacant web. Note that both species of* **Portia** *signalled on each type of web*

Type of web	*Portia* tested	No. of tests	No. of tests in which *Portia* signalled
Achaearanea sp.	*P. fimbriata* (Q)	12	8
	P. labiata	14	11
Eriophora pustulosa	*P. fimbriata* (Q)	11	4
	P. labiata	10	6
Inola subtilis	*P. fimbriata* (Q)	12	5
	P. labiata	10	6
Pholcus phalangioides	*P. fimbriata* (Q)	15	9
	P. labiata	15	5
Zosis geniculatus	*P. fimbriata* (Q)	28	16
	P. labiata	22	14

Methods

Tests were paired: *Portia* tested one day on a recently vacated *Badumna longinqua* web (as in Experiment 1) and on the other day with a 7-day vacant *B. longinqua* web. There were 27 test pairs, all using large juveniles of *P. fimbriata* (Q).

Results and discussion

There was no evidence that *Portia* was any less prone to signal on seven-day vacant webs than on recently vacated webs: eight *Portia* signalled on recently vacated but not seven-day vacant webs, and five signalled on seven-day vacant but not recently vacated webs (McNemar test for significance of changes, NS); eight signalled on both webs and six failed to signal on either web. Apparently, the cues from empty webs that elicit signalling from *Portia* are something other than volatile chemical cues.

Experiment 3
How does a **Portia** respond to contact with vacant webs if it can see quiescent spiders?

Experiments 1 & 2 illustrated that *Portia* need not see a spider before signalling. However, the possibility remains that seeing a quiescent spider on a web might stimulate *Portia* to signal more often than it signals when no victim spider is in view. Therefore, an experiment was carried out to examine the hypothesis that seeing a quiescent spider makes a *Portia* on a web more prone to signal than it would be when no spider is visible. It would appear reasonable to suppose that seeing a quiescent spider affects *Portia*'s signalling behaviour because the web spiders on which *Portia* preys in nature are often quiescent when *Portia* starts signalling (Jackson & Hallas, 1986), and *Portia* is known to stalk motionless prey under controlled conditions in the laboratory (Tarsitano & Jackson, 1992; Jackson & Tarsitano, 1993).

Methods

During each test, 2 empty *Stegodyphus sarasinorum* webs, in separate glass cages, were used. Before the test, 10 dead *Stegodyphus sarasinorum* were evenly spaced about on 1 of the 2 webs and the glass sides were returned to the cage containing this web (Cage B). The silk of *S. sarasinorum* is very sticky and, although living *S. sarasinorum* do not normally get stuck to their own webs, dead *S. sarasinorum* adhere firmly.

One glass side was returned to the other cage (Cage A). Cage A was placed with this side next to and aligned with the cage containing the *S. sarasinorum* (Cage B) so that adjacent glass sides of the 2 cages were only *c.* 5 mm apart. The *S. sarasinorum* in Cage B were all positioned so that their dorsal sides were oriented toward Cage A. To start a test, a *Portia* was dropped on the web in Cage A and the remaining glass side replaced.

Tests were carried out using large juveniles of *P. fimbriata* (Q), *P. labiata* and *P. schultzi*. Each test was paired with a control. In the control test, Cage B was kept empty (i.e. there were no dead spiders present), but otherwise control tests were the same as experimental tests.

Results and discussion

More *Portia* (pooled data) signalled when they could see quiescent spiders in an adjacent web

than when they could not (Table IV): 61 signalled in experimental tests only and 36 signalled in control tests only (McNemar test, $P < 0.05$); 53 signalled in both tests and 44 signalled in neither test. Apparently, seeing a quiescent spider is a cue that makes *Portia* more prone to signal.

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Experiment 4
*How does **Portia** respond to contact with vacant webs if it can see moving spiders?*

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Experiment 3 showed that cues from seeing spiders make *Portia* more prone to signal when on a web and it is not necessary that the spiders *Portia* sees move. However, the possibility remains that, when seeing the spider move, *Portia* is more prone to signal than when seeing a quiescent spider? An experiment was carried out to examine this question.

Methods

Methods were, in basic respects, like those for Experiment 3. Large juveniles of *P. fimbriata* (Q), *P. labiata* and *P. schultzi* were used. In the experimental test, one of the *S. sarasinorum* (near the centre of the web) had a 2×2 mm samarium cobalt magnet glued to its ventral cephalothorax. During the experimental test, this spider was made to move by means of an electromagnetic field from a coil behind the case (see Jackson & Wilcox, 1994). Using a signal generator, the *S. sarasinorum* was made to jiggle 2–3 mm up and down on the web at *c.* 5 Hz. It was repeatedly jiggled for *c.* 5 s, then left quiescent for *c.* 10 s, then jiggled again for *c.* 5 s, and so forth. The control test was set up the same as the experimental, except that the coil was not activated (i.e. the magnet and *S. sarasinorum* in front of the coil did not move during the test).

Results and discussion

More *Portia* (pooled data) signalled when spiders in adjacent webs moved than when they stayed quiescent (Table V): 30 signalled in experimental tests only and eight signalled in control tests only (McNemar test, $P < 0.001$); 108 signalled in both tests and nine signalled in neither. Apparently, movement is a cue that makes *Portia* more prone to signal.

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Experiment 5
*How does **Portia** respond to contact with vacant webs if it can see insects?*

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Portia does not normally signal when stalking an insect, instead of a spider, on a web (Jackson & Hallas, 1986). This suggests that *Portia* can distinguish between insects and spiders by means of visual cues alone. An experiment was carried out to investigate this hypothesis.

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TABLE IV

*Large juveniles of **Portia** tested on vacant webs with quiescent spiders in view (experimental tests) and without quiescent spiders in view (controls). Webs of **Stegodyphus sarasinorum***

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	P. fimbriata (Q)	*P. labiata*	*P. schultzi*
Signalled in experimental test only	24	19	18
Signalled in control test only	13	11	12
Signalled in both tests	18	20	15
Signalled in neither test	13	17	14

Methods

Methods were, in basic respects, the same as those for Experiment 3. Large juveniles of *P. fimbriata* (Q), *P. labiata* and *P. schultzi* were used. In the experimental test, there were 10 dead adult *Musca domestica* L (house flies) or 10 dead noctuid moths (unknown genus and species) on an otherwise empty web of *Stegodyphus sarasinorum* in Cage B. In the control, there were 10 dead *S. sarasinorum* in Cage B, as in the experimental tests in Experiment 3.

Results and discussion

More *Portia* signalled (Tables VI & VII) when spiders, instead of insects, were in the adjacent cage (Cage B). When houseflies were used (pooled data): 40 signalled in experimental tests only and 70 signalled in control tests only (McNemar test, $P < 0.005$); 71 signalled in both tests and five signalled in neither test. When moths were used (pooled data): 13 signalled in experimental tests only and 29 signalled in control tests only ($P < 0.05$); 22 signalled in both tests and seven signalled in neither test. Apparently, *Portia* can distinguish between insects and spiders by means of visual cues.

Experiment 6
How does **Portia** respond to contact with vacant webs if it can see egg sacs?

Portia does not normally signal when stalking an egg sac, instead of a spider, on a web. This suggests that *Portia* can distinguish between egg sacs and spiders by means of visual cues alone. An experiment was carried out to investigate this hypothesis.

Methods

Methods were basically the same as for Experiment 5 except that webs of *Zosis geniculatus* (Olivier) were used and egg sacs were present in the experimental tests instead of insects. *Zosis geniculatus* builds an orb web and normally rests at the hub near the centre of the web. *Zosis geniculatus* places its egg sacs on the web near the hub. In the experimental test, the *Z. geniculatus* was removed from the web and there was one egg sac in the web near the hub. In the control test, there was a *Z. geniculatus* at the hub, but no egg sacs in the web. The *Z. geniculatus* was quiescent when the test began. If it moved during the test, the test was aborted. Large juveniles of *P. fimbriata* (Q), *P. labiata* and *P. schultzi* were used.

Results and discussion

More Portia signalled when a spider, instead of an egg sac, was in the adjacent cage (Table

TABLE V

*Large juveniles of **Portia** tested on vacant webs with dead spiders moved by magnets in view (experimental tests) and only quiescent dead spiders in view (controls). Webs of **Stegodyphus** sarasinorum*

	P. fimbriata (Q)	*P. labiata*	*P. schultzi*
Signalled in experimental test only	14	9	7
Signalled in control test only	4	4	0
Signalled in both tests	35	40	33
Signalled in neither test	0	4	5

TABLE VI

*Large juveniles of **Portia** tested on vacant webs with quiescent houseflies in view (experimental tests) and quiescent spiders in view (controls). Webs of **Stegodyphus sarasinorum***

	P. fimbriata (Q)	P. labiata	P. schultzi
Signalled in experimental test only	13	14	13
Signalled in control test only	22	27	21
Signalled in both tests	22	25	24
Signalled in neither test	0	3	2

VIII): 36 signalled in experimental tests only and 60 signalled in control tests only (McNemar test, $P < 0.05$); 82 signalled in both tests and eight signalled in neither test. Apparently, *Portia* can distinguish between an egg sac and a spider by means of visual cues.

*Is seeing insects or egg sacs a cue that affects how prone **Portia** is to signal when on an alien web?*

Comparing signalling rates in experimental vs. control tests from Experiments 5 & 6 provided evidence that *Portia* is more prone to signal if it sees a spider rather than an insect or egg sac. However, does *Portia* respond differently to seeing insects or egg sacs compared to how it responds to being on an empty web and not seeing spiders, insects or egg sacs?

To answer this question, the results from the tests in Experiment 1 in which empty webs of *Badumna longinqua* were used (Table II) were compared to the results from experimental tests in Experiment 5 (Tables VI & VII), and the results from the tests in Experiment 1 in which *Zosis geniculatus* were used (Table III) were compared to the results from the experimental tests in Experiment 6 (Table VIII). The webs in Experiment 5 were from *Stegodyphus sarasinorum*. *S. sarasinorum* and *B. longinqua* both build cribellate sheet webs. The webs in Experiment 6 were from *Z. geniculatus*.

Portia signalled in 183 (68%) of 270 tests on empty cribellate sheet webs with no spiders, insects or egg sacs in view and in 146 (57%) of 257 tests on empty cribellate sheet webs with insects in view (test of independence, $P < 0.01$). *Portia* signalled in 30 (60%) of 50 tests on empty webs of *Z. geniculatus* with no spiders, insects or egg sacs in view and in 118 (64%) of 184 tests on empty webs of *Z. geniculatus* with egg sacs in view (test of independence, NS).

There is no evidence that seeing an egg sac makes *Portia* more prone to signal than when it is on an empty web. In relation to deciding to signal or not, seeing egg sacs appears to be irrelevant

TABLE VII

*Large juveniles of **Portia** tested on vacant webs with quiescent moths in view (experimental tests) and quiescent spiders in view (controls). Webs of **Stegodyphus sarasinorum***

	P. fimbriata (Q)	P. labiata	P. schultzi
Signalled in experimental test only	5	4	4
Signalled in control test only	12	8	9
Signalled in both tests	8	6	8
Signalled in neither test	3	3	1

TABLE VIII

*Large juveniles of **Portia** tested on vacant webs with motionless egg sacs in view (experimental tests) and quiescent spiders in view (controls). Webs of **Zosis geniculatus***

	P. fimbriata (Q)	P. labiata	P. schultzi
Signalled in experimental tests only	12	12	12
Signalled in control test only	23	20	17
Signalled in both tests	29	25	28
Signalled in neither test	1	2	5

to *Portia*. Seeing insects, however, appears to make *Portia* somewhat less prone to signal. Why this might be so is not clear.

Experiment 7
How does *Portia* respond to contact with a vacant web over which it is receiving vibratory stimuli?

If a spider is moving on a web, it will probably make vibratory stimuli perceptible to *Portia* even when *Portia* does not see the spider. This suggests that vibratory stimuli might be cues that make *Portia* more prone to signal. An experiment was carried out to examine this hypothesis.

Methods

Empty webs of *Stegodyphus sarasinorum* were used. A samarium cobalt magnet, as used in Experiment 4, was centred on and glued to a 4 × 4 mm square of cardboard. The cardboard square was placed on the web, and a coil was positioned behind the glass on one side. The other glass side was removed.

Throughout the experimental test, the cardboard was made to jiggle 2–5 mm up and down on the web at *c.* 5 Hz, as in Experiment 4, by repeatedly turning the coil on for 5 s, leaving it off for 10 s, then turning it on again for 5 s, and so forth. The control test was set up the same as the experimental, except that the coil was not activated. Therefore, the web vibrated intermittently during the experimental test but not during the control.

In each test, *Portia* was placed on the web at least 100 mm away from the magnet and facing away from it. Large juveniles of *P. fimbriata* (Q) and *P. labiata* were used.

Results and discussion

More *Portia* signalled when on a web with vibratory stimuli than when on a web without vibratory stimuli present (Table IX): 21 signalled in experimental tests only and five signalled in control tests only (McNemar tests, $P < 0.005$); 62 signalled in both tests and six signalled in neither test. Apparently, movement of the web is a cue that makes *Portia* more prone to signal. The only effect we discerned was increased incidence of signalling. That is, *Portia* did not tend to turn and face toward the magnet during the tests.

Deciding to enter a web

Portia does not appear just to walk on to webs inadvertently in most instances. Instead, it appears that, when near a web in nature, *Portia* makes a decision to enter or not to enter the web (Jackson & Wilcox, 1993). I carried out experiments to investigate the cues by which *Portia* decides whether or not to enter a web.

Methods

Tests were carried out by using 600 mm × 380 mm ×290 mm glass tanks and standard glass cages. Before each test, a glass cage was placed at one end of a tank. To start a test, a *Portia* was placed on the floor of the tank at the side opposite the glass cage and the lid was placed on the tank. *Portia* was watched until it 'responded' to the cage. The criteria for 'responded' were that *Portia* entered the cage (if the cage was open but did not contain a web), or entered the web (if there was a web in the cage and the cage was open), or went on to the glass of a closed cage. During tests in which cages were kept closed, the glass sides were in place and plastic tape was placed along the edge of the glass to make a tight seal, to rule out the possibility of cues from volatile chemicals.

Tests were paired and, in general respects, methods were similar to the methods used when testing *Portia*'s responses to contact with webs, only now the behaviour recorded was not whether *Portia* signalled but whether *Portia* responded to the cage.

Experiment 8
How does **Portia** respond to seeing an empty web in a closed cage?

In nature and the laboratory, *Portia* has often been seen to orient toward a web, then walk to the web and enter it (Jackson & Blest, 1982*a*; Jackson & Wilcox, 1993). These observations give the impression that cues for entering a web come from seeing the web. An experiment was carried out to examine this hypothesis.

Methods

Cages were kept closed. In the experimental test, there was an empty *Stegodyphus sarasinorum* web in the cage. In the control test, the cage was identical to the cage in the experimental test, except that there was no web present. These tests were carried out using males, females and large juveniles of all species and populations of *Portia*. A series of similar tests was carried out using empty webs of *Zosis geniculatus* and large juveniles of *Portia fimbriata* (Q) and *P. labiata*.

Results and discussion

All sex-size classes of all species and populations of *Portia* sometimes responded to cages containing empty *Stegodyphus sarasinorum* webs (Table X). More *Portia* (pooled data) responded to cages containing empty *S. sarasinorum* webs than responded to cages with no webs: 36 responded to the cage in experimental tests only and two responded to the cage in the control test only (McNemar test, $P < 0.001$); four responded to both cages and 73 responded to neither cage.

Also, more *P. fimbriata* (Q) and *P. labiata* (pooled data) responded to cages containing empty *Zosis geniculatus* webs than responded to cages with no webs (Table XI): 13 responded to cages in

TABLE IX

Large juveniles of Portia tested on vacant webs with vibratory stimuli present (experimental tests) and vibratory stimuli not present (controls). Webs of Stegodyphus sarasinorum

	P. fimbriata (Q)	P. labiata
Signalled in experimental test only	10	11
Signalled in control test only	2	3
Signalled in both tests	32	30
Signalled in neither test	2	4

experimental tests only and two responded to cages in control tests only (McNemar test, $P < 0.005$); one responded to both cages and 37 responded to neither cage.

Portia's latency to respond to cages (time elapsing from start of test until response) tended to be shorter for cages containing empty webs than for cages containing no webs: 81.5 s $(24-229$ s$)$ for cages containing empty *S. sarasinorum* webs vs. 268 s $(20-493$ s$)$ for controls (Mann-Whitney U test, $P < 0.05$); 78 s $(18-219$ s$)$ for cages containing empty *Zosis geniculatus* webs vs. 162 s $(107-235$ s$)$ for controls $(P < 0.05)$.

Apparently, *Portia* has a visual system capable of seeing empty webs, and seeing empty webs apparently provides cues for web entry.

Experiment 9
How does **Portia** respond to exposure to an unenclosed empty web?

Although the results from Experiment 2, in which we compared *Portia*'s responses to contact with recently vacated vs. seven-day vacant webs, provided no evidence that cues from volatile chemicals affect signalling, we do not know from Experiment 2 whether or not cues from volatile chemicals affect *Portia*'s decision to enter a web. An experiment was carried out to answer this question.

Methods

Large juveniles of *Portia labiata* were used in tests with empty *Stegodyphus sarasinorum* webs and large juveniles of *P. fimbriata* (Q) were used in tests with empty *Zosis geniculatus* webs. There was an empty web in the cage in both the experimental and the control test. In the experimental test the cage was open, but in the control the cage was closed.

Results and discussion

There was no evidence that *Portia* responded to open cages containing webs any more frequently than it responded to closed cages containing webs. In tests using *Stegodyphus sarasinorum* webs, two *P. labiata* responded to the cage in experimental tests only and four responded to the cage in controls only (NS); four responded to the cage in both tests and 22 responded to the cage in neither test. In tests using *Zosis geniculatus* webs, two *P. fimbriata* (Q) responded to the cage in experimental tests only and two responded to the cage in control tests only (NS); eight responded to the cage in both tests and 18 responded to the cage in neither test.

Latencies to respond to cages were similar for open and closed cages: 79.5 s $(22-183$ s$)$ for open

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TABLE X

Portia tested with closed cage containing empty **Stegodyphus sarasinorum** web (experimental tests) and closed cage with no web (controls)

		Entry in experimental test only	Entry in control test only	Entry in both tests	Entry in neither test	N
P. africana	Male	1	0	1	5	7
	Female	3	1	0	4	8
	Large juvenile	3	0	1	3	7
P. fimbriata (NT)	Male	1	1	0	4	6
	Female	3	0	0	5	8
	Large juvenile	2	0	0	7	9
P. fimbriata (Q)	Male	1	0	0	7	8
	Female	3	0	0	6	9
	Large juvenile	4	0	1	5	10
P. labiata	Male	2	0	0	6	8
	Female	5	0	0	2	7
	Large juvenile	2	0	0	4	6
P. schultzi	Male	1	0	0	5	6
	Female	3	0	1	4	8
	Large juvenile	2	0	0	6	8

cages containing empty *S. sarasinorum* webs vs. 65·5 s (20–207 s) for closed cages (NS); 75 s (11–213 s) for open cages containing empty *Z. geniculatus* webs vs. 73 s (39–140 s) for closed cages (NS).

There is, from these tests, no evidence that volatile chemical cues influence *Portia*'s decision to enter a web.

Experiment 10
How does **Portia** respond to seeing a spider in a web in a closed cage?

Although the results from Experiments 8 and 9 imply that *Portia* need not see a spider in a web before deciding to enter the web, it still might be that seeing a spider in a web is a cue that makes *Portia* more prone to enter a web than it would be if no spider was seen. An experiment was carried out to examine this hypothesis.

TABLE XI

Large juveniles of **Portia** *tested with closed cage containing empty* **Zosis geniculatus** *web (experimental tests) and closed cage with no web (controls)*

	P. fimbriata (Q)	*P. labiata*
Entry in experimental test only	8	5
Entry in control test only	2	0
Entry in both tests	0	1
Entry in neither test	17	20

TABLE XII

Large juveniles of **Portia** *tested with closed cage containing spiders in web (experimental tests)
and closed cage containing empty web (controls)*

	P. fimbriata (Q)	P. labiata	P. schultzi
Entry in experimental test only	4	4	3
Entry in control test only	0	1	0
Entry in both tests	9	9	10
Entry in neither test	7	4	5

Methods

Large juveniles of *P. fimbriata* (Q), *P. labiata* and *P. schultzi* were tested using webs of *Stegodyphus sarasinorum*. The web in the cage in the experimental test had 10 dead *S. sarasinorum* spaced about on the silk, as in Experiment 3. The web in the cage in the control test was empty. Cages were kept closed during the tests.

Results and discussion

More *Portia* (pooled data) responded to cages containing webs on which there were spiders than responded to cages containing webs on which there were no spiders (Table XII): 11 responded to the cage in the experimental test only and one responded to the cage in the control test only (McNemar test, $P < 0.005$); 28 responded to both cages and 16 responded to neither cage. Also, *Portia*'s latency to respond to cages tended to be shorter if the web contained spiders: 55 s (14–216 s) to respond to experimental cages containing spiders vs. 93 s (26–210 s) to respond to control cages ($P < 0.005$). Apparently, seeing spiders in webs makes *Portia* more prone to enter webs.

Deciding to persist

After entering an apparently empty web and signalling, *Portia* must decide whether to: (1) remain in the web and (2) continue to signal. Experiments were carried out to clarify what cues influence these two decisions. The rationale for these experiments is that, in nature, spiders in webs are often quiescent and out of view when *Portia* arrives (Jackson & Hallas, 1986). Whether a web is truly vacant may not be immediately evident to *Portia*. By entering, and signalling in, a web that appears to be empty, *Portia* may be able to obtain additional information about whether a spider is present. That is, signalling may elicit a response from a hidden resident spider, and this response may be important in informing *Portia* that the web is occupied.

Methods

In each test, *Portia* was put in an empty web in an open cage and allowed 30 min in which to start signalling. Tests were aborted if *Portia* left the web before signalling or if *Portia* stayed on the web for 30 min but failed to signal. A potential cue was provided 5 s after *Portia* signalled for the first time in each experimental test, after which *Portia*'s behaviour was recorded for the next 10 min or until *Portia* left the web.

Experiment 11
How does a **Portia** *that has begun signalling on an empty web respond to
seeing a moving spider?*

In nature, a *Portia* might go on a web and start signalling without first perceiving the presence of a resident spider (Jackson & Wilcox, 1994). A hidden resident spider might respond to *Portia*'s signalling by moving and thereby becoming visible to *Portia*. Does seeing a moving spider, after signalling, provide a cue for remaining on the web and continuing to signal?

Methods

As in Experiment 4, there were 2 cages. One cage contained an empty web of *Stegodyphus sarasinorum* and the other contained 10 dead *S. sarasinorum* spaced evenly about in the web, with a magnet on one of the *S. sarasinorum*, as in Experiment 4. At the start of the test, there was an opaque cardboard partition between the 2 cages. To start a test, an adult female *P. labiata* was placed on the empty web. Immediately after the *Portia* signalled the first time, the partition was lifted and the magnet activated by a coil so that the dead *S. sarasinorum* moved for 60 s. Control tests were carried out in the same way as experimental tests except that the web in the second cage was, like the web into which *Portia* was placed, empty: when the partition was lifted, *Portia* could see only another empty web.

Results and discussion

Portia tended to signal longer if spiders were visible after starting to signal: signalling duration in experimental tests was 183 s (8–506 s) but only 13 s (3–318 s) in control tests (Wilcoxon test, $P < 0.001$). *Portia* also tended to stay in webs longer if spiders were visible after starting to signal: stayed in web 545·5 s (96–600 s) in experimental tests vs. 294 s (45–600 s) in control tests ($P < 0.05$). Apparently, seeing a spider provides cues for *Portia* to stay on a web and continue signalling.

Experiment 12
How does a **Portia** *that has begun signalling on an empty web
respond to web movement?*

In nature, a *Portia* might go on a web containing a quiescent spider and start signalling without first perceiving the presence of the spider (Jackson & Wilcox, 1994). After *Portia* signals, a resident spider might start moving, but still not come into *Portia*'s view. Perhaps detection of something moving on the web is enough to encourage *Portia* to stay on the web and continue signalling. That is, *Portia* may not have to see the moving spider. An experiment was carried out to examine this hypothesis.

Methods

To start a test, an adult female *P. labiata* was put on an empty *Stegodyphus sarasinorum* web on which there was a magnet, as in Experiment 7. After *Portia* signalled the first time, the magnet was made to move (as in Experiment 7) for 60 s. Control tests were carried out in the same way except that the magnet was not made to move.

Results and discussion

Portia tended to signal longer if there was movement on the web after it started: signalling duration in experimental tests was 49 s (14–493 s), but only 15 s (3–151 s) in controls (Wilcoxon test, $P < 0.05$). *Portia* also tended to stay on webs longer if there was web movement: stayed on web 600 s (178–600 s) in experimental tests, but only 322 s (49–600 s) in control tests ($P < 0.05$). Apparently, web movement provides *Portia* with cues for staying on webs and continuing to signal. Seeing a moving spider is not necessary. Although *Portia* can see the magnet, *Portia*'s visual acuity is known to be sufficient to enable it to distinguish spiders from insects (Experiments 4 & 5). Therefore, it is unlikely that *Portia* mistook the moving magnet for a spider. Also, although *Portia* sometimes oriented toward the magnet briefly during these tests, the *Portia* never persisted in facing the magnet.

Conclusions

The present study has been a first step toward understanding the decision rules that govern *Portia*'s complex predatory strategy. Among *Portia*'s most basic decisions are whether to enter a web, whether to signal when on a web, and whether to persist once signalling has begun. Some of the cues of these decisions were investigated, and some conclusions can be offered.

Cues from seeing a web elicit web entry. However, there is no evidence that volatile chemical cues from webs of prey spiders influence *Portia*'s decision to enter webs. Seeing a spider in a web makes *Portia* more prone to enter the web.

After web entry, cues from webs of prey spiders are sufficient to elicit signalling behaviour by *Portia*, even in the absence of other cues coming directly from the prey spider. However, seeing a quiescent prey spider or detecting vibrations on the web make *Portia* more prone to signal. For increasing *Portia*'s inclination to signal, seeing a moving spider is more effective than seeing a quiescent spider. There was no evidence that seeing an egg sac influenced *Portia*'s decision to signal, but seeing an insect apparently made *Portia* less prone to signal.

From another study (Willey & Jackson, 1993), it is known that volatile chemical cues from other conspecific *Portia* inhibit aggressive mimicry signalling. However, there was no evidence from the present study that volatile chemical cues from prey spiders affect *Portia*'s decision to signal or not.

Once *Portia* is on a web and signalling, seeing a moving spider or detecting vibrations on the web encourage *Portia* to persist in signalling.

Some of the capabilities of *Portia*'s visual system have been highlighted by this study. On the basis of visual cues alone, *Portia* can distinguish a web from an empty cage. Also, *Portia*'s visual system permits distinguishing between quiescent spiders, insects and egg sacs. Although salticid eyes are large and complex for a spider, this is no primate (Land, 1974). The principal eye lens is only a few millimetres in diameter. There are only a limited number of receptors in the salticid eye and neurones in the salticid brain. How so small a visual system, with so few components, is able to perform these perceptual feats is currently a mystery.

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