

## **SPIDER FLEXIBLY CHOOSES AGGRESSIVE MIMICRY SIGNALS FOR DIFFERENT PREY BY TRIAL AND ERROR**

by

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(With 3 Figures)

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### **Summary**

*Portia* is a jumping spider that invades other spiders' webs, makes vibratory signals that deceive the resident spider (aggressive mimicry), then attacks and eats the spider. *Portia* exploits a wide range of prey-spider species. Evidence is provided from observation and experimentation that *Portia* uses a trial-and-error method as part of its strategy for deriving appropriate signals for different prey. To use this method, *Portia* first broadcasts an array of different signals, then narrows to particular signals as a consequence of feedback from the prey spider. Feedback can be web vibration or seeing spiders move, or both. This appears to be an example of deception involving at least a limited form of learning, an uncommon phenomenon in invertebrates.

### **Introduction**

Aggressive mimicry is a game of deceit in which a mimic, a predator, broadcasts misinformation interspecifically to potential prey. There are formal similarities between these predator-prey interactions and intra-specific communication: a sender (here, a mimic) produces a signal which manipulates a receiver (a prey). However, aggressive mimicry is a communication system wherein the sender clearly increases its own fitness at the receiver's expense.

We use "aggressive mimicry" for behaviour by which predators deceive prey, because this expression currently enjoys wide usage. We recognize that the term "aggression" is sometimes restricted to discussion of active competitive interactions (threat displays and fighting) and that

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predator-prey interactions fall into a different category of behaviour. However, the term “aggressive mimicry” is currently a familiar term, unlike potential alternatives such as “Peckhamian mimicry” (WICKLER, 1968) and, for this reason, we choose not to break with tradition.

We studied three species of *Portia*, jumping spiders that invade webs, practise aggressive mimicry and eat other spiders (JACKSON & BLEST, 1982; JACKSON, 1985, 1992; JACKSON & HALLAS, 1986a), unlike most other salticids which are insectivorous hunting spiders (FORSTER, 1982). However, like other salticids, *Portia* has complex eyes and acute vision (BLEST, 1985; LAND, 1985).

Some web-invading aggressive mimics are known from families other than the Salticidae, but they appear to specialize at feeding on only a few types of web spiders (JACKSON, 1992). Specialization is not surprising because different kinds of web spiders seem to be vulnerable to exploitation by different aggressive mimicry signals (JACKSON & WILCOX, unpubl. data). *Portia* is distinctive because it successfully exploits a wide range of web spiders (JACKSON & HALLAS, 1986b).

How is it that *Portia* is able to derive effective tactics for catching its diverse victims? The answer appears complex, but our central hypothesis is that *Portia* combines two ploys: 1) use of specific signals when it receives cues from certain prey species; and 2) adjustment of signals in a flexible fashion to different prey species, as a consequence of feedback from the victims. The present paper provides evidence that *Portia* uses the second ploy, which we call the “trial and error method”. The first ploy will be considered elsewhere (JACKSON & WILCOX, unpubl. data; also see JACKSON & WILCOX, 1990).

When first going onto a web, it often appears that *Portia* presents its ‘victim’, a resident spider, with a kaleidoscope of different vibratory signals. Eventually, one of these signals elicits a response from the victim. We provide evidence that when a response is elicited, *Portia* will cease to vary its signals and continue to produce the signal that elicited the response.

### Materials and methods

Standard terminology, conventions for describing behaviour, and procedures for maintenance and testing were used (JACKSON & HALLAS, 1986a) except for details noted here. Prey spiders were maintained and tested in wooden-frame cages with removable glass sides (Fig.

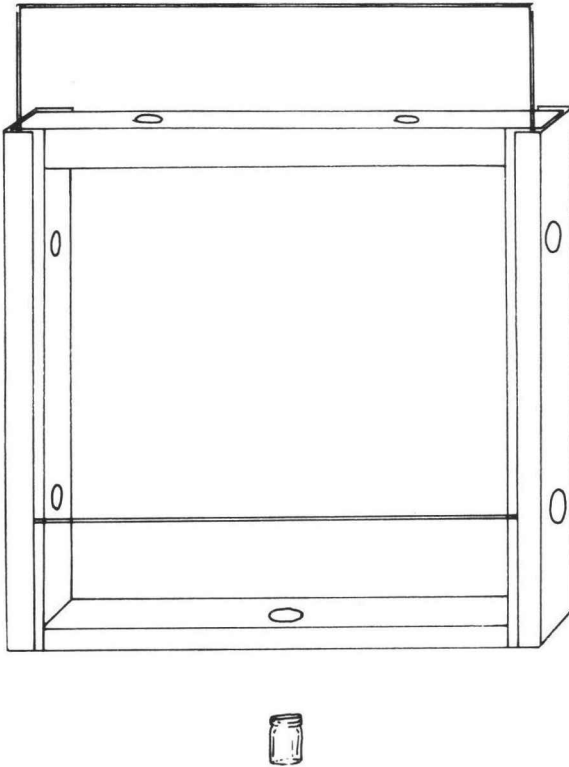


Fig. 1. Cage: wooden frame (200 mm×200 mm×30 mm interior dimensions), with seven cork holes (corks not shown), and removable glass sides on front and back. Glass fits in grooves in frame (front glass shown partly raised). *Portia* held in vial (below cage) before test. To start test, open vial connected to open hole at bottom of cage so that *Portia* can walk out into cage.

1). Before testing, each *Portia* was kept without food for 24-48 hr. We used three species of *Portia* and two species of prey (Table 1). All *Portia* that we used were reared from eggs in the laboratory and had no prior experience with the prey species used. Cultures of *Portia* and prey originated from established study sites (JACKSON & HALLAS, 1986a), and *Portia* is known to feed in nature on the prey species used (JACKSON, unpubl. data). Details concerning movement of appendages came from analysis of video tapes.

After moving onto webs, *Portia* performs a wide variety of vibratory behaviours, including twitching its abdomen and plucking, striking and fluttering movements using virtually any combination of legs and pedipalps in varied phase relationships and at varied rates and amplitudes (JACKSON & HALLAS, 1986a). During the course of the experiments described here, 119 distinct patterns ("signals") were recognized. The variety of signals *Portia* makes appears virtually unlimited, and additional signals would no doubt have been observed had additional experiments been carried out.

We used individuals of Australian *P. fimbriata* from Queensland (*P. fimbriata* (Q)) and the Northern Territory (*P. fimbriata* (NT)); *P. labiata* from Sri Lanka; and *P. schultzi* from Kenya.

TABLE 1. Spiders used in experiments

Species	Collection site	Adult female body length
<i>Portia fimbriata</i> (NT) Doleschall	Northern Territory, Australia	8 mm
<i>Portia fimbriata</i> (Q) Doleschall	Queensland, Australia	8 mm
<i>Portia labiata</i> (Thorell)	Sri Lanka	8 mm
<i>Portia schultzi</i> Karsch	Kenya	6 mm
<i>Philoponella variabilis</i> Rainbow	Queensland, Australia	4 mm
<i>Stegodyphus sarasinorum</i> Karsch	Sri Lanka	10 mm

*Unmanipulated interactions between Portia fimbriata and Philoponella variabilis.*

Numerous examples of apparent trial and error behaviour have been observed during the course of other studies on *Portia*. As examples, we provide data from representative instances of *Portia fimbriata* (Doleschall) from Queensland interacting with a common sympatric prey species, *Philoponella variabilis* (Keyserling). In these instances, there was no experimental manipulation of variables.

*Philoponella variabilis* is an orb-weaving uloborid spider which frequently lives in complexes of interconnected orbs, each orb being the resident spider's defended territory (JACKSON, unpubl. data). Data from unmanipulated interactions came from colonies of 10 individuals. At the start of each test, all *P. variabilis* were quiescent at the hubs of their webs. In each test, all *P. variabilis* were mature females and all *Portia* were juveniles of about the same size.

Example No. 1.

A *Portia* moved slowly onto the edge of a web, fixated its antero-medial eyes on *P. variabilis* c. 120 mm away, and moved its legs and palps to make a variety of vibratory signals. After c. 10 min, the *P. variabilis* oriented and moved a few millimetres toward *Portia* just after *Portia* had plucked slowly (c. 2/s) with its left palp for 1-2 s. From this time until *P. variabilis* was captured c. 8 min later, *Portia* plucked repeatedly (22 successive bouts) with its palp at c. 2/s for 1-2 s, but did not perform any other vibratory behaviours. *P. variabilis* usually approached a few millimetres each time *Portia* plucked. When the *P. variabilis* was less than the *Portia*'s body length (c. 4 mm) away, *Portia* lunged and grabbed it.

Example No. 2.

A *Portia* moved slowly onto the edge of a web and used its legs and palps to perform a variety of vibratory behaviours, but *Portia* did not have its antero-medial eyes fixated on the *P. variabilis*. After c. 5 min, *Portia* shook the web violently by forcefully plucking on the web with all eight legs, after which the *P. variabilis* performed pull-ups on the web. A resident *P. variabilis* typically performs pull-ups in response to a conspecific trespassing onto its web: the spider moves its body rhythmically forward and backward at c. 2/s by repeatedly flexing and extending its forelegs.

While still facing away from the *P. variabilis*, *Portia* plucked the same way four more times, with an intersignal interval of c. 30 s. *P. variabilis* performed pull-ups again each time *Portia* plucked. *Portia* then oriented toward the *P. variabilis*, which was c. 140 mm away, and plucked again in the same way. *P. variabilis* continued to perform pull-ups each time *Portia* plucked and *Portia* began approaching the *P. variabilis* a few steps at a time, plucking the same way each time it stepped.

When *Portia* was 80 mm from the *P. variabilis*, having plucked 16 successive times in the same way, the *P. variabilis* moved away. This was *c.* 20 min after *Portia*'s initial orientation toward the *P. variabilis*. For the next 8 min, the *P. variabilis* remained quiescent and *Portia* varied its vibratory signals, then the *P. variabilis* suddenly returned to the hub of the web during an interval when *Portia* was quiescent.

*Portia* continued to vary its vibratory behaviour for the next 15 min, then the *P. variabilis* moved a few millimetres toward *Portia* while *Portia* was fluttering its two palps up and down rapidly (*c.* 10/s) on the web for *c.* 1 s. During the next 6 min, *Portia* intermittently fluttered its palps again in the same way and did not perform any other vibratory behaviour. The *P. variabilis* usually approached another few millimetres each time *Portia* fluttered. At the end of this 6-min period, the *P. variabilis* was less than the *Portia*'s body length (*c.* 4 mm) away and *Portia* lunged and grabbed it.

#### Example No. 3.

A *Portia* moved slowly onto the edge of a web, fixated its antero-medial eyes on *P. variabilis* *c.* 100 mm away and performed a variety of vibratory behaviours using its legs and palps. When *Portia* plucked with its two palps in alternating phase for 2 s at 4 s, the *P. variabilis* performed pull-ups. During the next 27 min, *Portia* continued to pluck intermittently in the same manner and never performed any other vibratory behaviour. The *P. variabilis* often performed more pull-ups when *Portia* plucked. *Portia* moved slowly across the web to *P. variabilis*, usually plucking while taking each step. At the end of this 27-min period, *Portia* reached the hub, where it lunged and grabbed hold of the *P. variabilis*.

#### Summary

These and numerous similar observations suggest that *Portia* uses a tactic of repeating signals that immediately beforehand elicited localized movement of a victim on the web. Within predatory bouts, *Portia* appears to continue, and perhaps increase, performance of signals that elicit response from prey. Web movement alone, visual stimuli from seeing prey approach or both may be cues for signal repetition. We designed experiments to investigate both of these apparent effects of prey behaviour on *Portia*'s signalling.

#### Basic experimental methods.

All tests were carried out as paired comparisons, where each individual *Portia* was used in an experimental test one day and a control test either the previous or the next day (decided using a random numbers table); however, when a test had to be aborted, another attempt was made the next day until successful. If testing was still unsuccessful after 5 days, the test pair was aborted.

In all experiments, *Portia* were juveniles of about the same size as the victim spider. Adult *P. variabilis* females (body length: *c.* 4 mm) and *Stegodyphus sarasinorum* Karsch juveniles (*c.* 7 mm) were used. *S. sarasinorum* is a social crested spider from Sri Lanka and India which builds a communal sheet web shared freely by as many as several hundred individuals (BRADDOO, 1980). House flies, *Musca domestica* L., and fruit flies, *Drosophila melanogaster* Meigen, were used as prey for *S. sarasinorum* and *P. variabilis* respectively. Colonies of ten *S. sarasinorum* per cage were set up for experiments. *P. variabilis*, however, was set up one per cage to obtain solitary spiders in isolated webs.

*P. variabilis* and *S. sarasinorum* were set up in the test cage with excess prey for 20-40 days before testing began. The day before a test, all prey and prey remains were removed from the cage, keeping damage to the web minimal. *P. variabilis* was always at the hub of its web when testing began.

Lights came on in the laboratory at 0800 hrs, and testing began at about 0900 hrs. Before each test, a *Portia* was taken from its cage and kept in a vial for *c.* 10 min. The vial was then

connected to a hole in the bottom of the cage. If *Portia* did not go onto the web in the cage within 60 min after the vial was connected, the test was aborted. Tests were also aborted if, at any time, *Portia* got closer than 50 mm from the victim spider (at which distance *Portia* was likely to stop signalling and, instead, attack) or if *Portia* failed to make signals within 60 min after going onto the web.

In each experiment we waited 5 min after *Portia*'s first signal, then randomly chose one of *Portia*'s next five signals for reinforcement or for a control. Reinforcement was always provided *c.* 1 s after *Portia* performed the chosen behaviour by using a coil and magnet (see WILCOX, 1979) to make either a *P. variabilis* or a 4×4 mm square of cork move on the web: a 1×1×1 mm samarium cobalt magnet was glued to the dorsal abdomen of a spider or to a cork and driven by a 5 Hz sine wave from a function generator; amplitude was set so that the cork or spider moved 2-4 mm. The test was aborted if the victim spider moved at any time during a test other than the time chosen for reinforcing *Portia*'s signals. *P. variabilis* with magnets on their abdomens were habituated by playing the magnets repeatedly for at least 10 min before starting tests. If, after we chose a signal for reinforcement, *Portia* performed another signal in the 1-s interval before experimental reinforcement was applied, the test was aborted. Also, if *Portia* did not perform another vibratory behaviour within 10 s after reinforcement, the test was aborted.

## Experiments

### Experiment 1.

Does localized movement by *Philoponella variabilis* encourage *Portia* to repeat signals?

#### *Methods.*

Only *Portia fimbriata* (Q) was used in this experiment. For reinforcement, we made a quiescent *Philoponella variabilis* shake for 1 s. There was only one reinforcement in each test and the test ended as soon as *Portia* performed its next behaviour following reinforcement. In control tests, we chose at random a signal made by *Portia* and, as in the experimental tests, recorded whether that signal was the next behaviour performed by *Portia*. In control tests there was no reinforcement: the magnet on the prey spider was not turned on.

#### *Results.*

*Portia* often repeated signals we chose randomly and reinforced by making the *P. variabilis* move and only infrequently repeated signals we chose randomly but did not reinforce in this way ( $p < 0.001$ ) (Table 2).

### Experiment 2.

Does web movement encourage *Portia* to repeat signals if no spider is in the web, but a spider is visible in another web?

#### *Methods.*

Two cages were set up side by side (Fig. 2). Cage A contained a vacant web built by ten *Stegodyphus sarasinorum*. These *S. sarasinorum* were removed the day before the test. Ten *S.*

TABLE 2. Results from experiments with single reinforcement.

	Repeat in experimental test only	Repeat in control only	Repeat in both	Repeat in neither	McNemar Test*
<i>Portia fimbriata</i> (Q) with localized movement of <i>Philoponella variabilis</i> (Experiment No. 1)	39	5	8	34	p<0.001
<i>Portia fimbriata</i> (NT) in shaking web with quiescent <i>Stegodyphus sarasinorum</i> (Experiment No. 2)	14	2	0	11	p<0.01
<i>Portia fimbriata</i> (Q) in shaking web with quiescent <i>Stegodyphus sarasinorum</i> (Experiment No. 2)	20	5	0	18	p<0.01
<i>Portia labiata</i> in shaking web with quiescent <i>Stegodyphus sarasinorum</i> (Experiment No. 2)	11	1	3	17	p<0.01
<i>Portia schultzi</i> in shaking web with quiescent <i>Stegodyphus sarasinorum</i> (Experiment No. 2)	12	2	2	19	p<0.05
<i>Portia fimbriata</i> (Q) in shaking web with quiescent <i>Stegodyphus sarasinorum</i> . Same signal in experimental and control (Experiment No. 3)	7	0	0	5	p<0.01
<i>Portia fimbriata</i> (Q) with approaching <i>Stegodyphus</i> <i>sarasinorum</i> (Experiment No. 4)	17	3	6	14	p<0.005

See text for details.

\* For this test, data in first two columns only are used (SOKAL &amp; ROHLF, 1981)

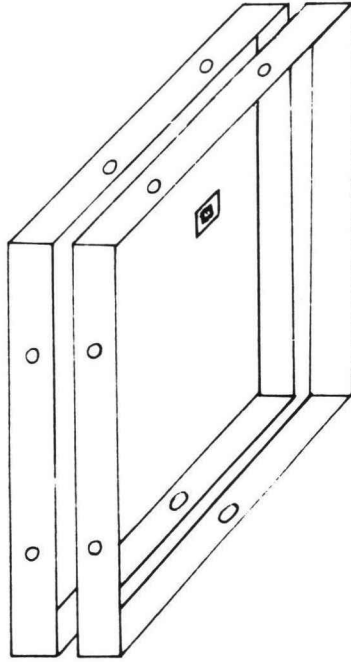


Fig. 2. Set-up used in Experiment 3. Two cages side by side. Cage A (in front) has magnet glued to cork sitting near top of vacant web (now shown) built by 10 *Stegodyphus sarasinorum*. *Portia fimbriata* put into this web. Cage B (behind) contains 10 *S. sarasinorum* in web (not shown).

*sarasinorum* were left in an equivalent web in cage B. *Portia* was allowed to enter cage A to start a test, and testing methods were basically the same as in Experiment 1 except that a magnet on a cork square centred near the top of the web in cage A was played to provide reinforcement. In successful tests, *Portia* entered a web in cage A, fixated on quiescent spiders in cage B, and made signals. A test was aborted if spiders in cage B were active or if *Portia* was not fixated on a *S. sarasinorum*. Because this experiment was easier to carry out than Experiments 1, 3, 4, and 5, data were obtained for three species of *Portia* and two populations of *P. fimbriata*.

### Results.

*Portia fimbriata* (NT), *Portia fimbriata* (Q), *Portia labiata* and *Portia schultzi* each often repeated signals we randomly chose to reinforce and only infrequently repeated signals we randomly chose but did not reinforce ( $p < 0.05$  for each, Table 2).



### Experiment 3.

Does web movement encourage *Portia* to repeat particular signals?

#### *Methods.*

In all other tests, the signal we chose randomly for reinforcement was never the same as the signal we chose randomly for the control. This means that these tests did not allow us to test whether *Portia* would more often have repeated the particular signal we chose for the control if that signal had been reinforced. Experiment 3 was designed to test whether *Portia* would do this.

Methods were as for Experiment 2 except that a signal chosen randomly for the first test in a test pair was used for the second test in the test pair.

When a *Portia* failed to use the chosen signal as one of its initial five signals at the start of the second test of a test pair, the second test was aborted. If a second test in a pair of tests had to be aborted, another attempt was made to complete the second test the next day until successful. If testing was still unsuccessful after 5 days, we waited 7 days, then continued testing *Portia* daily until *Portia* used the chosen signal. If 5 days elapsed again without *Portia* using the chosen signal, we waited another 7 days, then continued as before. If *Portia* did not use the chosen signal after four such repeated testing sessions, the test pair was aborted.

#### *Results.*

*Portia* tended to repeat chosen signals when reinforced but never repeated the same chosen signal in controls ( $p < 0.05$ ) (Table 2).

### Experiment 4.

Does seeing spiders in another web approach, in the absence of web movement in the occupied web, encourage *Portia* to repeat signals?

#### *Methods.*

Only *Portia fimbriata* (Q) was used in this experiment. The set-up was as in Experiment 3 except the cork and magnet were near the bottom of the web in cage B and the ten *S. sarasinorum* in cage B were kept without prey for 7 days prior to testing. In successful tests, one or more *S. sarasinorum* approached the moving cork. Because *Portia* was in the bottom of the web in cage A, when spiders in cage B approached the cork they also approached *Portia*. A strip of black paper across the bottom third of cage B (Fig. 3) kept the cork and magnet out of *Portia's* view.

#### *Results.*

*Portia* often repeated signals we chose randomly to reinforce and only infrequently repeated signals we chose randomly but did not reinforce ( $p < 0.005$ ) (Table 2). Therefore, seeing spiders approach, while not “hearing” them (*i.e.* while not perceiving web vibration), reinforces *Portia's* tendency to use a particular signal.

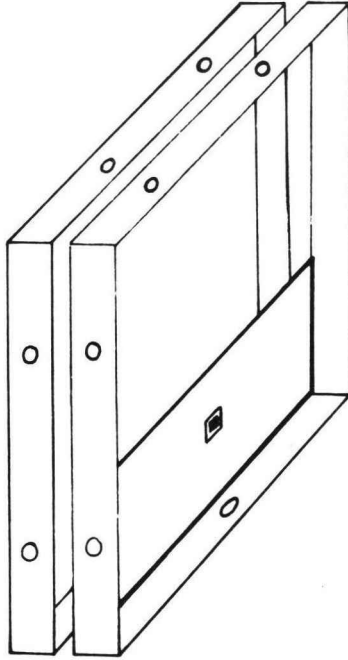


Fig. 3. Set-up used in Experiment 4. Two cages side by side. Cage A (behind) contains vacant web (not shown) built by 10 *Stegodyphus sarasinorum*. *Portia fimbriata* put in this web. Cage B (in front) contains 10 *S. sarasinorum* in web (not shown) and a magnet glued to cork sitting near bottom of web. Black cardboard between cages hides cork and magnet from *P. fimbriata*'s view.

### Experiment 5.

Does repeated localized movement by *Philoponella variabilis* increase how often *Portia* uses a signal?

#### *Methods.*

Only *Portia fimbriata* (Q) was used in this experiment. After we randomly chose a signal, we reinforced it (using the same methods as in Experiment 1) each time *Portia* used it during a 20-min test period. The number of times the chosen signal was used by *Portia* in each of 10 successive 2-min periods was recorded, and a least squares linear regression was carried out for each test to see if signals were used by *Portia* more frequently over successive intervals (indicated by a regression coefficient larger than zero). We also recorded how often the initially performed but not reinforced signals were used by *Portia* over successive 2-min periods. Tests were aborted if *Portia* left the web or stopped signalling for longer than 2 min. Controls were like experimental tests except that the playing of a magnet was not paired with performance of a particular signal during the 20-min test period. Instead, we simply played a magnet at random intervals during a test (using a random numbers table, each successive "reinforcement" could be 20 s, 40 s, 60 s, 80 s, or 100 s after the previous reinforcement).

*Results.*

Signals we chose randomly were used more often by *Portia* in tests with reinforcement than in controls (Table 3; Wilcoxon test,  $p < 0.005$ ). The frequency with which *Portia* used signals we chose randomly steadily increased during the course of 7 of 16 tests, as indicated by regression coefficients significantly greater than zero. However, there were no control tests in which *Portia* appeared to increase the frequency of use of randomly chosen, but not reinforced, signals (regression coefficients always NS). Using a McNemar test for significance of changes, there was a significant trend ( $p < 0.05$ ) to obtain regression coefficients significantly greater than zero more often in experimental than in control tests.

None of the regression coefficients in Table 3 were negative. To obtain a negative regression coefficient, *Portia* would have had to have initially used the randomly chosen signal frequently, then diminished how often it used the signal. This never happened. Instead, *Portia* always started off using the signal infrequently, ruling out the possibility of diminishing use over time.

*Repetition of non-chosen signals during experimental tests.*

In each experiment, *Portia* tended to repeat the signals we chose randomly and reinforced, consistent with our hypothesis that *Portia* uses a trial-and-error method. An alternative hypothesis, that *Portia* is simply more inclined to make signals of all sorts after the reinforcement stimulus, can be ruled out.

In each experimental test, we chose one out of a set of up to five signals randomly for reinforcement. If the alternative hypothesis were true, then the non-chosen signals should have been repeated about as often as the chosen (and reinforced) signals.

This prediction was examined by, first, excluding all experimental tests in which the first signal, from the set of 1-5, was chosen randomly for reinforcement. This left a set of tests in which *Portia* made a known signal that was reinforced plus 1-4 preceding known signals that were not chosen for reinforcement. Signals before this were not recorded (*i.e.* were not "known").

Next we kept only those tests in which the signal *Portia* made after the reinforcement stimulus was either the chosen (reinforced) signal or one of the 1-4 known non-chosen signals. This left us with a set of data from

TABLE 3. Results from experiment with repeated reinforcement (Experiment No. 5)

<i>Portia</i>	Total No. of repeats of randomly chosen & reinforced signal in experimental test	Total No. of repeats of non- chosen signal in experimental test	Total No. of repeats of randomly chosen signal in control test	Regression coefficient for repeats of reinforced signal in experimental test	Regression coefficient for repeats of chosen signal in control test	Regression coefficient for repeats of non- chosen signal in experimental test
1	30	0	9	0.06	0.00	+
2	25	2	7	0.72***	0.04	0.01
3	36	0	1	0.11	0.03	+
4	69	2	3	0.80***	0.11	0.19
5	101	3	4	0.10	0.04	0.21
6	8	0	5	0.09	0.19	+
7	28	1	2	0.34	0.01	0.17
8	3	2	6	0.01	0.14	0.12
9	0	0	4	+	0.08	+
10	42	3	3	0.46*	0.04	0.04
11	60	2	0	0.77***	+	0.08
12	74	1	1	0.77***	0.08	0.27
13	83	0	0	0.74***	+	+
14	51	0	0	0.84***	+	+
15	1	-	0	+	+	-
16	0	-	1	+	+	-

See text for details.

\*  $p < 0.05$ , \*\*\*  $p < 0.001$ , + Repeats too infrequent for regression, - First signal was chosen randomly for reinforcement in experimental test.

TABLE 4. Results from experiments with single reinforcement

	No. of tests	Repeated chosen signal	Repeated non-chosen signal	Test of goodness of fit*
<i>Portia fimbriata</i> (Q) with localized movement of <i>Philoponella variabilis</i> (Experiment No. 1)	41	39	2	p<0.001
<i>Portia fimbriata</i> (NT) in shaking web with quiescent <i>Stegodyphus sarasinorum</i> (Experiment No. 2)	14	14	0	p<0.001
<i>Portia fimbriata</i> (Q) in shaking web with quiescent <i>Stegodyphus sarasinorum</i> (Experiment No. 2)	15	15	0	p<0.001
<i>Portia labiata</i> in shaking web with quiescent <i>Stegodyphus sarasinorum</i> (Experiment No. 2)	13	13	0	p<0.001
<i>Portia schultzei</i> in shaking web with quiescent <i>Stegodyphus sarasinorum</i> (Experiment No. 2)	13	11	2	p<0.05
<i>Portia fimbriata</i> with approaching <i>Stegodyphus sarasinorum</i> (Experiment No. 4)	18	18	0	p<0.001

Data from experimental tests only. All tests excluded in which the first signal out of five was chosen randomly for reinforcement and in which *Portia* failed to repeat either the reinforced (chosen) or one of the preceding (non-chosen) signals. See text for details.

\* Null hypothesis: signal that is repeated is equally often the chosen and a non-chosen signal.

experimental tests in which one of 2-5 known signals was repeated after an experimental stimulus was applied (Table 4). Conservative tests of goodness of fit were carried out on these data, letting repetition of any of the 1-4 non-chosen signals in a given test be an alternative to repetition of the chosen signal. Even with these conservative criteria, in Experiments 1-4 *Portia* clearly tended to repeat the chosen (reinforced) signal instead of non-chosen signals (Table 4). Also, there was no evidence that *Portia* increased the frequency of use of non-reinforced signals during the course of the experimental tests (regression coefficients always NS) of Experiments 5 (Table 3).

## Discussion

In all experiments, *Portia* frequently repeated signals we chose randomly and reinforced but only infrequently repeated signals we chose randomly but did not reinforce. This was true even when, for a given *Portia*, the same signal was singled out in both the experience and the control test (Experiment 3). Localized movement of a spider in the same web (Experiment 1), perceiving movement of a web with no victim spiders in it while watching quiescent spiders in another web (Experiment 2 & 3), and seeing spiders approaching but not perceiving web movement (Experiment 4) were all effective reinforcements. Repeated reinforcement tended to result in steadily increasing use of signals we chose randomly (Experiment 5).

Apparently, these results are a consequence of *Portia* using a trial-and-error method in which it decides to repeat signals that are reinforced. An alternative explanation for these results was considered, but not supported. That is, it does not appear that the effect of each stimulus used for reinforcement is simply to make *Portia* more inclined to make signals of all sorts.

In each part of its distribution – tropical Africa, Asia and Australasia (WANLESS, 1984) – *Portia* efficiently exploits a large array of different species of web-building of spiders. *Portia* apparently responds to some of its victims in an appropriate (pre-set) way from the beginning (JACKSON & WILCOX, 1990, unpubl. data), but is unlikely that *Portia* has evolved a separate (pre-set) means of deception for *each* of its many different victim species. From the present study, it appears that *Portia* uses a trial-and-

error method to derive signals appropriate for victim spiders. The rules of the trial-and-error tactic appears to be:

1. begin by broadcasting a general-purpose array of signals;
2. when there is feedback from a victim after making a particular signal, narrow broadcast to this signal for as long as it continues to elicit feedback (*i.e.* *Portia* continues doing what works).

Trial and error allows for flexible narrowing in on particular signals in response to feedback. Using this tactic, *Portia* may be able to derive appropriate responses to a wide range of the diverse types of victim spiders it encounters.

MITCHELL (1986) has categorized animal deception into four levels: Level 1, simply mimicry in which deception is effected by appearance (*e.g.* Batesian mimics); Level 2, deception effected by coordinated perception followed by action (*e.g.* firefly femmes fatales: LLOYD, 1986); Level 3, deception effected by learning (*e.g.* stomatopods learn to associate with greater fighting ability the posture used by bluffing opponents: CALDWELL, 1986); and Level 4, planned deception (*e.g.* many instances of deceit in humans). *Portia's* use of trial and error implies at least short-term memory (memory of the last signal performed), and *Portia's* trial and error tactic appears to be an example of MITCHELL's (1986) third level deception, apparently a rare ability to find in invertebrates. We do not know yet for how long these behaviour changes persist.

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