

# TRIAL-AND-ERROR SOLVING OF A CONFINEMENT PROBLEM BY A JUMPING SPIDER, *PORTIA FIMBRIATA*

by

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(Acc. 27-VII-2001)

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## Summary

*Portia* is a genus of web-invading araneophagic jumping spiders known from earlier studies to derive aggressive-mimicry signals by using a generate-and-test algorithm (trial-and-error tactic). Here *P. fimbriata*'s use of trial-and-error to solve a confinement problem (how to escape from an island surrounded by water) is investigated. Spiders choose between two potential escape tactics (leap or swim), one of which will fail (bring spider no closer to edge of tray) and the other of which will partially succeed (bring spider closer to edge of tray). The particular choice that will partially succeed is unknown to the spider. Using trial-and-error, *P. fimbriata* solves the confinement problem both when correct choices are rewarded (*i.e.* when the spider is moved closer to edge of tray) and when incorrect choices are punished (*i.e.* when the spider gets no closer to edge of tray).

## Introduction

Convergence of behavioural ecology and cognitive psychology has generated considerable interest in how the cognitive capacities of animals influence

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<sup>3</sup>) For valuable discussion and for reading and commenting on the manuscript, we thank Simon Pollard, Duane Harland, Richard Andrew and Allen Rodrigo. Tracey Robinson, Helen Spinks and Lyn de Groot are gratefully acknowledged for help in preparing the manuscript. The research that went into this paper was initiated by MST as part of a MSc thesis, then developed further by the other authors. All authors were involved in the writing. This work was supported by grants from the Marsden Fund of the New Zealand Royal Society (UOC512) and the U.S. National Science Foundation (BNS 8617078).

behaviour (Yoerg, 1991; Belisle & Cresswell, 1997; Dukas, 1998a; Kamil, 1998). Important questions remain unresolved concerning the extent to which an animal's various cognitive abilities are single-purpose adaptations tailored for specific functions (Stephens, 1991; McFarland & Boser, 1993). How often and under what circumstances does evolution of cognitive skills push animals across a threshold, enabling them to respond flexibly and adaptively to problems outside the context in which these skills originally evolved (see Dennett, 1996)? These questions may be especially tractable in an unusual group of predatory arthropods, the araneophagic jumping spiders (Wilcox & Jackson, 1998; Harland & Jackson, 2000).

The eyes of most spiders lack the structural complexity required for acute vision (Homann, 1971; Land, 1985), but the unique, complex eyes of jumping spiders (Salticidae) support resolution ability that has no known parallels in other animals of comparable size (Land, 1969a, b, 1974; Blest *et al.*, 1990). Most salticids are cursorial hunters of insects and make no use of webs in their intricate vision-controlled predatory behaviour (Richman & Jackson, 1992; Jackson & Pollard, 1996), but there are exceptions, the most striking of which are tropical African, Asian and Australian salticids from the genus *Portia* (Wanless, 1978). Besides capturing prey away from webs, these species also spin prey-capture webs (Jackson, 1985), and they routinely invade alien webs (Jackson & Wilcox, 1998) where they take their preferred prey, other spiders (Li & Jackson, 1996, 1997; Li *et al.*, 1997).

*Portia*'s prey, web-building spiders, have only rudimentary eyesight and use interpretation of web signals (tension and movement patterns conveyed through the silk lines of the web) as a primary sensory modality (Foelix, 1996). The web is an integral part of the typical web-building spider's sensory system (Witt, 1975). After entering another spider's web, *Portia* does not simply stalk or chase down its victim but instead generates aggressive-mimicry web signals (Jackson & Pollard, 1996; Tarsitano *et al.*, 2000) by using any combination of its eight legs, two palps and abdomen. Ability to alter sequences, and to vary the speed, amplitude, and timing of the movement of each appendage independently (Jackson & Blest, 1982; Jackson & Hallas, 1986a; Jackson, 1992), gives *Portia* an almost unlimited repertoire of signals (Jackson & Wilcox, 1993a).

*Portia* is effective at capturing a very wide range of web-building spiders (Jackson & Hallas, 1986b) despite considerable variation among spider species in how they respond to different types of signals. Two basic signal-generation tactics appear to be critical (Jackson & Wilcox, 1998): 1) use

of prey-specific pre-programmed signals when cues from certain common prey are detected; 2) flexible adjustment of signals in response to feedback from the intended victim. The second tactic, trial-and-error derivation of the appropriate web signals, is a generate-and-test algorithm (see Simon, 1969) where the generating capacity is especially large. The two tactics may often be combined, with trial-and-error signal derivation being used to complete predatory sequences after starting off with pre-programmed tactics (Jackson & Wilcox, 1998).

When deriving signals by trial and error, *Portia* first presents the resident spider with a kaleidoscope of different web signals. When one of these signals eventually elicits an appropriate response from the prey spider, *Portia* stops varying its signals and concentrates on repeating the signal that worked (Jackson & Wilcox, 1993a). If this signal stops working, *Portia* varies its signals again until another signal is found that triggers a favourable response from the prey spider. Using this trial and error tactic, *Portia* in the laboratory can communicate with, control and capture many kinds of spiders, including species that would never be encountered in nature (Wilcox & Jackson, 1998).

Theoretical accounts for why pronounced behavioural flexibility and problem-solving ability may be dominant features of *Portia*'s predatory strategy have emphasized three factors: the intimate contact this predator has with its prey's sensory system, the high level of risk entailed in attempting to gain dynamic fine control over the behaviour of another predator and the potential for predator-prey coevolution (Jackson, 1992; Jackson & Pollard, 1996). Little is known, however, about *Portia*'s problem-solving ability in contexts other than predation. One hypothesis might be that *Portia*'s facility at adopting trial and error, being a special-purpose ability that evolved specifically in the context of signal derivation, can be applied by *Portia* only in this particular context. Regardless of what the original use of trial and error may have been, an alternative hypothesis is that use of a generate-and-test algorithm serves as something like a general-process learning ability (see Beecher, 1988) that can be applied to problems with respect to which *Portia* might not have evolved solutions (see Johnston, 1985).

Here we investigate whether *Portia* uses trial and error to solve a confinement problem. Our experiments have similarities to Thorndike's (1911) confinement-test paradigm in which the goal was to test whether animals can derive methods for escaping from enclosed areas. However, two modifications make the present study comparable to the study of trial-and-error signal derivation by *Portia* (Jackson & Wilcox, 1993a):

1) *Portia* in a web often performs aggressive-mimicry signals while distant from the prey spider. This means that a particular signal might draw in a resident spider stepwise instead of immediately. When this happens, *Portia* experiences during the steps only partial success, with prey capture depending on repetition of the partially successful signals (Jackson & Wilcox, 1993a). Here we introduce partial success into a confinement-problem paradigm by requiring that *Portia* escape step-wise from confinement.

2) In the signal-generation study (Jackson & Wilcox, 1993a), the signal that would be successful was determined at random before each test began. Our confinement tests are made comparable by allowing choices (*i.e.* two possible ways by which *Portia* might escape from an enclosed area) where we decide beforehand, at random, which particular choice will succeed.

There is no reason to expect that, for these spiders in nature, situations would arise often, if ever, where there would be different rewards from choosing between subtly different methods for crossing water. The unrealistic character of the confinement problem was the very reason for choosing it for this study. We wanted to challenge the spider with a problem that would not be routine for them in nature.

## Materials and methods

All test subjects were juveniles (4-5 mm in body length) of *Portia fimbriata* taken from laboratory cultures (reared from eggs of more than 20 females in a controlled-environment laboratory). The cultures were initiated from animals collected in Queensland, Australia. Standard maintenance procedures were adopted (Jackson & Hallas, 1986a) in enriched environments (see Carducci & Jakob, 2000) under optimal diet (Li & Jackson, 1997).

Experimental apparatus (Fig. 1) was a water-filled rectangular plastic tray in which there was an 'island' surrounded by an 'atoll'. The inner edge of each shorter (210 mm) side of the atoll was 127.5 mm from the closest edge of the island and 127.5 mm from the closest edge of the tray. The edge of each longer (300 mm) side of the atoll was 77.5 mm from the closest edge of the island and 77.5 mm from the closest edge of the tray. Water in the tray came up to the height (20 mm) of the island and atoll. Preliminary testing established that the juvenile stages of *P. fimbriata* used as test subjects could not clear these distances by leaping.

A plastic tube extended 60 mm below the tray. Its upper end went through a hole in the bottom of the tray and opened in the centre of the island (Fig. 1). The tray was set on a 100-mm high wood frame that allowed space for reaching the lower opening of the tube. *Portia fimbriata* was introduced into the bottom of this plastic tube and prodded up onto the island with a plunger (a cork, slightly smaller in diameter than the tube, with a stick handle attached below). Because of their acute eyesight, it can be assumed that the distant edge of the tray was discernible to the salticids.

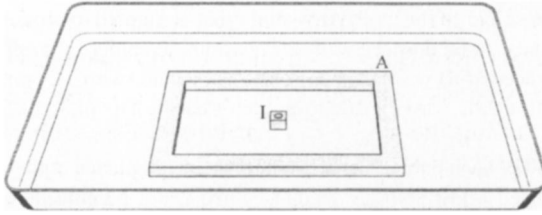


Fig. 1. Apparatus used in Experiment 1 for ascertaining whether *Portia fimbriata* uses trial and error to solve a confinement problem. Spider emerges on island (I) surrounded by an atoll (A) in water-filled tray and chooses either to leap or swim. Choice that would be successful determined at random before test begins. Successful choice: spider was moved to atoll. Unsuccessful choice: spider was returned to island. If first choice successful, spider makes second choice from atoll. If first choice unsuccessful, spider makes second choice from island. Island (I): 20 × 20 mm plastic square with hole in centre (entry point for spider). Atoll (A): 25-mm wide plastic walkway forming rectangle (300 × 210 mm) around island. Tray (T): 580 × 380 mm.

Preliminary testing established that *P. fimbriata* would leave the island, and attempt to cross the water, either by swimming or by leaping. Although it has been reported that salticids cannot swim (Ehlers, 1939; Foelix, 1996), *P. fimbriata* readily moved across water surfaces without sinking. When leaving the island by swimming, *P. fimbriata* slowly placed its forelegs on the water, pushed off with its rear legs, moved completely out into the water in a spread-eagle posture and then moved its legs in a stepwise fashion to propel itself across the water surface in much the same way as has been described for aquatic lycosid and pisaurid spiders (Schultz, 1987; Suter *et al.*, 1997; Suter, 1999). When leaving the island by leaping, *P. fimbriata* landed on the water (usually at a point about halfway across) then swam the rest of the way across. *Portia fimbriata*'s choice (leap or swim) was recorded once all legs were on the water. Using this criterion, the choice recorded was always unambiguous.

All trials were carried out between 0830 and 1100 hours (laboratory photoperiod 12L:12D, lights on at 0800 hours). Between trials, the island and atoll were cleaned with 80% ethanol and water, then dried, and the water in the tray was changed. Lighting was provided by a 200 W incandescent lamp positioned c. 300 mm above the tank. Overhead florescent lamps provided additional ambient lighting. All statistical analyses are from Sokal & Rohlf (1995). No individual spider was used in more than one test.

## Experiment 1

### Methods

Test spiders were assigned at random to two groups, spiders with leaping pre-determined to be successful ( $N = 40$ ) and spiders with swimming pre-determined to be successful ( $N = 40$ ). Any spider that attempted to cross the water using the choice (swimming or leaping) pre-determined to be successful was helped to the atoll. This was done, once the choice was made, by placing a small plastic scoop between the spider and the island, then gently making

waves to propel the spider to the atoll. Any spider that attempted to cross the water using the choice pre-determined to be unsuccessful (e.g. swimming spider in group with leaping pre-determined to be successful) was pushed back to the island (with scoop placed between the spider and the atoll, gentle waves made to propel it back). The plastic scoop never touched the spider.

Once on the atoll or back on the island, whether the consequence of the first choice (reward or setback) influenced a test spider's second choice could be considered. The reward for making the correct choice was only 'partial success' at escaping from the water-filled tray (i.e. a correct first choice got the spider only part of the way to the tray). On the atoll, a spider had to choose again how to cross the water before it could reach the edge of the tray. It might either repeat its first choice or switch. Repetition was predicted by the trial-and-error hypothesis. A spider forced back to the island after an unsuccessful first choice had to try again to reach the atoll. It might repeat its earlier choice or switch. Switching was predicted by the trial-and-error hypothesis.

Four possible outcomes were defined operationally with no claims being made about spider's understanding of the outcomes: (1) both the first and the second choice succeeded; (2) neither the first nor the second choice succeeded; (3) the first choice succeeded but the second choice failed; (4) the first choice failed but the second choice succeeded. Initial choices were always made from the island. When the spider's first choice failed, the second choice was again made from on the island. When the first choice succeeded, the second choice was made from the atoll. Whether the consequence of the first choice influenced the second choice was considered by using tests of independence, analysing separately data for spiders that leapt first and spiders that swam first.

Forty tests (i.e. half of the total number of tests) were video taped, providing detailed records of spider behaviour (swimming pre-determined to be successful in 20; leaping pre-determined to be successful in the other 20). This included latencies to make choices and second-by-second records (tabulated for each spider separately for when on the island and when on the atoll) of behaviour and orientation (called collectively 'categories'; categories are not mutually exclusive): (1) facing outward (oriented more closely to edge than centre of tray); (2) facing inward (oriented more closely to centre than edge of tray); (3) stationary; (4) walking (changing location by stepping); (5) pivoting (turning about while staying in one place); (6) grooming; (7) leaning out (having some, but not all, leg tarsi in contact with the water, but with other leg tarsi remaining on the island or atoll). Each spider provided seven scores, each score being calculated as the percentage of the total time in seconds during which the spider's activity or orientation corresponded to the specified category. For example, a spider's score for facing outward while on the atoll was the time in seconds during which it was facing outward while on the atoll divided by total time spent on the atoll (multiplied by 100 and expressed as a percentage). Changes in location were not recorded when spiders were on the island where space available was not much larger than the spider itself, but second-by-second records were kept of sector changes when spiders were on the atoll: 46 sectors, each being a 20 mm length of the atoll.

Movement data, and scores for behaviour and orientation (i.e. categories), were compared by using Mann-Whitney U-tests for paired comparisons after separating out two groups: spiders for which the first choice succeeded (FCS) and spiders for which the first choice failed (FCF). FCS spiders were on the atoll when making their second choices, whereas FCF spiders were back on the island when making their second choices.

After a test spider came up the tube, out of the hole and onto the island, testing was aborted if it failed to stay on the platform for at least 10 s before making its first choice or failed to make its first choice within 10 min. Tests were also aborted whenever a spider (1) failed to make its second choice within 10 min after its first (*i.e.* after reaching the atoll or being returned to the island) or (2) failed to remain on the island or atoll for at least 10 s before making its second choice. Only 12% of the tests had to be aborted. Spiders from aborted tests were not used again. There were no instances in which a spider on the island went back into the hole or a spider on the atoll attempted to return to the island.

### *Results and discussion*

First choices (from the island) were about equally often to leap (37) or to swim (43) (test of goodness of fit, null hypothesis 50/50, NS). Spiders that leapt first (Table 1) and succeeded at reaching the atoll always leapt again (row 1 and 2), whereas spiders that leapt first, but failed to reach the atoll, usually switched to swimming (row 3 and 4). Spiders that swam first and succeeded at reaching the atoll usually swam again (row 1 and 2), whereas spiders that swam first, but failed to reach the atoll, usually switched to leaping (row 3 and 4).

When choosing for the first time, spiders on the island spent most of their time facing outward (Table 2), apportioning time especially between

TABLE 1. *Data from Experiment 1. Portia fimbriata surrounded by water. Chooses twice in succession to leap or to swim*

		Spider leapt first	Spider swam first
<i>N</i>		37	43
Row 1	Spider repeated successful first choice	17	17
Row 2	Spider switched when first choice was successful	0	3
Row 3	Spider switched when first choice was unsuccessful	17	19
Row 4	Spider repeated unsuccessful first choice	3	4
Test of independence*		$\chi^2 = 26.73$ $p < 0.001$	$\chi^2 = 19.57$ $p < 0.001$

Findings (analysed separately for leapt first and swam first) show that success or failure of first choice influences second choice.

\* Shows second choice depends on consequence of first choice.

TABLE 2. *Details of behaviour of 40 Portia fimbriata in Experiment 1. Spiders on island before making first choice*

	Latency (s)	Facing outward (%)	Stationary (%)	Walking (%)	Pivoting (%)	Grooming (%)	Leaning out (%)
Median	276	100	38	19	26	0	8
First quartile	215	97	31	8	21	0	4
Third quartile	392	100	46	28	36	4	15
Minimum	79	92	7	0	14	0	2
Maximum	571	100	68	37	50	23	29

Latency: time elapsing before making choice. Score for each category (facing outward, *etc.*): time (expressed as percentage of total time elapsing before first choice) engaged in stated category.

walking, pivoting and being stationary. After making a first choice, spiders tended to stay stationary for close to half the time leading up to their second choice (Table 3 & 4). Scores for grooming and for leaning out were low before both the first and the second choice (Table 2-4). Although spiders moved about on the atoll, they rarely went very far (Table 3). Both the first and second choices were usually made after about 5 min (Table 2-4).

When making second choices, FCS (first choice succeeded: Table 3) and FCF (first choice failed: Table 4) spiders had statistically indistinguishable latencies (Mann-Whitney *U*-test, NS) and statistically indistinguishable scores for remaining stationary (NS) and grooming (NS), but they differed in other ways. Compared with FCF spiders (on the island), FCS spiders (on the atoll) had higher scores for facing outward ( $p < 0.001$ ) and walking about ( $p < 0.005$ ), and lower scores for pivoting ( $p < 0.005$ ) and leaning out ( $p < 0.05$ ).

Spiders began tests on an island surrounded by water where they could choose to leap or choose to swim. Choosing had one of two consequences. Either the spider failed to get closer to the edge of the water-filled tray (*i.e.* it landed back on island) or it succeeded at getting closer to the edge of the water-filled tray (*i.e.* it landed on the atoll). Which consequence held for each potential choice was arbitrary (decided at random before the test). These tests can be envisaged as attempts to train spiders either to leap or to swim, and most spiders were trained in one trial to leap or in one trial to swim.



TABLE 3. Details of behaviour 22 *Portia fimbriata* in Experiment 1. Spiders on atoll after successful first choice (FCS in text)

	Latency (s)	Facing outward (%)	Stationary (%)	Walking (%)	Pivoting (%)	Grooming (%)	Leaning out (%)	Moving (%)	Sector changes (%)
Median	289	99	43	19	18	6	2	9	4
First quartile	232	96	32	10	14	0	0	3	1
Third quartile	411	100	62	31	21	16	5	21	9
Minimum	109	37	27	2	7	0	0	0	0
Maximum	468	100	77	41	35	42	8	65	15

Latency: time elapsing before making choice. Score for each category (facing outward, etc.): time (expressed as percentage of total time elapsing before first choice) engaged in stated category.

TABLE 4. Details of behaviour of 18 *Portia fimbriata* in Experiment 1 (see text) while on island after unsuccessful first choice (FCF in text)

	Latency (s)	Facing outward (%)	Stationary (%)	Walking (%)	Pivoting (%)	Grooming (%)	Leaning out (%)
Median	280	86	45	5	28	7	6
First quartile	233	75	40	4	20	0	3
Third quartile	342	91	51	16	33	14	10
Minimum	75	50	27	0	13	0	0
Maximum	481	98	65	25	37	24	41

Latency: time elapsing before making choice. Score for each category (facing outward, etc.): time (expressed as percentage of the total time elapsing before first choice) engaged in stated category.

Spiders for which the first choice was leaping always leapt again when leaping succeeded and usually switched to swimming when leaping failed. Spiders for which the first choice was swimming usually swam again when swimming succeeded and usually switched to leaping when swimming failed. These findings suggest that spiders perceive whether the consequence of the first choice is failure (*i.e.* whether, after choosing, they are no closer to the edge of the tray) or success (*i.e.* whether, after choosing, they land closer to the edge of the tray) and use this feedback when choosing the second time. The findings may also suggest an inherent reluctance to switch that makes training to repeat easier than training to switch, but firm conclusions on this possibility await further study.

Alternative hypotheses related to latency appear to have been ruled out. For example, had the experience of being pushed back to the island induced spiders to wait longer before making a second choice ('spider was stunned') or had being pushed forward induced spiders to choose again more quickly ('spider's momentum from first choice carried through to second choice'), then an alternative hypothesis might have been that the spider's inclination to repeat choices simply decreases as the time interval between choices increases. However, this hypothesis is not supported: success or failure of first choice did not vary significantly in relation to latency to make second choice.

However, other variables can not be ruled out so easily. Scores for facing outward and walking when making second choices were higher for FCS (first choice succeeded) spiders on the atoll than for FCF (first choice failed) spiders on the island, whereas FSF spiders had significantly higher scores for pivoting and leaning out. Differences in these scores appear to be consequences of the experimental design.

FCS spiders usually walked across the sector of the atoll on which they arrived, then paused, thereby coming to a stop facing outward. FCF spiders usually paused where they landed on the island (facing inward), perhaps because the hole in the middle of the island inhibited walking immediately across.

FCS spiders (on the atoll) having, compared with FCF spiders (on the island), higher scores for walking and lower scores for pivoting before making second choices was probably a consequence of FCS spiders having more room for walking on the atoll than on the island. FCS spiders having

lower scores for leaning out was probably a consequence of the atoll affording more space than the island for avoiding contact with the water.

FCS spiders arrived at a new locality (the atoll), whereas FCF spiders returned to a locality (the island) from which they had only recently departed. Perception of the island as familiar might be mediated by detection of silk draglines or other traces left behind (see Clark & Jackson, 1994, 1995).

How many of these potential consequences of the experimental design might have made FCS spiders more likely to repeat their first choices and FCF spiders more likely to switch is unclear, but we can not rule out the possibility that these or other unappreciated factors might explain our findings. This problem has similarities to the problem of ruling out 'contextual variables', a notorious difficulty in cognitive research (Bitterman, 1965; McPhail, 1985; Kamil, 1988, 1998).

Confidence in the conclusion that spiders based second choices on their perception of the success or failure of first choices is, however, enhanced by another two experiments in which we disconnect arrival at the atoll from perception of success and disconnect return to the island with perception of failure. From the trial-and-error hypothesis, we predict that spiders arriving on the atoll after a failure will switch (Experiment 2) and spiders arriving on the island after a success will repeat (Experiment 3).

## Experiment 2

### *Methods*

Apparatus and methods were as in Experiment 1 (Fig. 1) except that the test spider made its first choice from the atoll ( $N = 28$ ) and, regardless of whether its first choice was to swim or leap, it was pushed back to the atoll (*i.e.* these spiders always had to make their second choices from the atoll and their first choices always failed). This reversed the situation in Experiment 1 where spiders choosing from the atoll were always the spiders that had experienced success at getting closer to the shoreline (edge of the tray).

Testing was initiated by using a plunger (see Experiment 1) to entice the spider out of a hand-held plastic tube (same length and diameter as tube in Experiment 1) onto one of the long sides of the atoll. Testing was aborted if the test spider: (1) came out facing inward (toward island) (happened 5 times); (2) left the atoll before a 10-s period elapsed after being placed on it (happened 4 times); (3) spent more than 10 min on the atoll without leaving (happened 3 times); (4) left in direction of island (happened once).

*Results and discussion*

For data analysis, the spiders were divided into two groups: spiders that leapt first and spiders that swam first. Experiment 1 provided data for spiders making their second choices on the atoll after having made successful first choices (*i.e.* after having made a first choice, swim or leap, that brought them closer to the edge of the tray). The present experiment provided data on the reverse: spiders making their second choices on the atoll after having made unsuccessful first choices (*i.e.* after a choice, swim or leap, that brought them no closer to the edge of the tray).

Spiders that chose to leap first always leapt again when they were on the atoll after a success (Experiment 1), but usually switched to swimming when they were on the atoll after a failure (Experiment 2). Spiders that chose to swim first usually swam again when they were on the atoll after a success (Experiment 1), but usually switched to leaping when they were on the atoll after a failure (Experiment 2) (Table 5).

For these comparisons, being on the atoll when making second choices is a constant. The variable that appears to matter is whether the first choice succeeded or failed to bring the spider closer to the shoreline.

TABLE 5. *Spiders making second choice from atoll*

		Spider leapt first	Spider swam first
Row 1	Spider repeated successful first choice	17	17
Row 2	Spider switched when first choice was successful	0	3
Row 3	Spider switched when first choice was unsuccessful	12	13
Row 4	Spider repeated unsuccessful first choice	1	2
Test of independence		$\chi^2 = 26.15$ $p < 0.001$	$\chi^2 = 17.74$ $p < 0.001$

Data for first choice succeeding came from Experiment 1. Data for first choice failing came from Experiment 2. Repetition of choice (swim or leap) depends on its consequences regardless of whether spiders leapt or swam first.

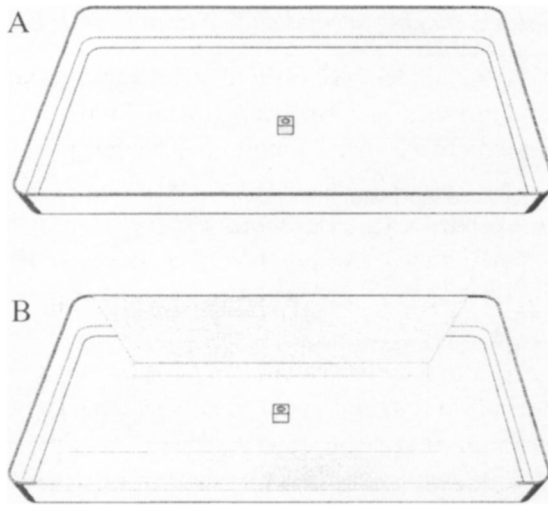


Fig. 2. Apparatus used in Experiment 3 for ascertaining whether *Portia fimbriata* derives solutions to a confinement problem by trial and error when second choice is made from same location (island) as first choice. Spider emerges on island in centre of water-filled tray (A). Two slanted metal sheets put into place after spider makes first choice (B) and left in place if choice is successful, but immediately removed if choice is unsuccessful.

### Experiment 3

#### Methods

Apparatus and methods were as in Experiment 1 (Fig. 1) except that no atoll was present, the spider was always pushed back to the island after its first choice and a manipulation was introduced for generating partial success despite the spider being returned to the island.

Arriving on the island for the first choice, the spider faced a distant shoreline (edge of tray) and a wide expanse of water. Depending on the group to which the spider was assigned at random, it faced either the same distant shoreline (Group 1,  $N = 30$ ) or else a closer shoreline (Group 2,  $N = 30$ ) when it made its second choice from the island. As soon as a spider in Group 1 was returned to the island, the metal sheets (sloped down from the tray edge to water level) (Fig. 2) were put into place. The distance from the island to the closer (*i.e.* water-level) side of each metal sheet corresponded to the distance from the island to the atoll in Experiment 1. If the spider had been assigned to Group 1, then the metal sheets were immediately removed. If the spider had been assigned to Group 2, then the metal sheets were left in place. This meant that spiders in Group 2, despite being back on the same island from which they made their first choice, had achieved partial success because the expanse of water had shrunk.

#### Results and discussion

Data were analysed separately for spiders that leapt first and spiders that swam first. Of spiders that leapt first, those in Group 1 (shoreline remained

TABLE 6. *Spiders making second choice from island (Experiment 3)*

		Spider leapt first	Spider swam first
<i>N</i>			
Row 1	Spider repeated successful first choice	12	14
Row 2	Spider switched when first choice was successful	3	1
Row 3	Spider switched when first choice was unsuccessful	13	11
Row 4	Spider repeated unsuccessful first choice	2	4
Test of independence		$\chi^2 = 13.39,$ $p < 0.001$	$\chi^2 = 13.89,$ $p < 0.001$

After successful first choice, shoreline brought closer. After unsuccessful first choice, shoreline remained as distant as before first choice. Repetition of choice (swim or leap) depends on its consequence regardless of whether spiders leapt or swam first.

distant) usually switched whereas those in Group 2 (shoreline came closer) usually repeated their first choices (test of independence,  $p < 0.05$ , Table 6). Of spiders that swam first, those in Group 1 usually switched whereas those in Group 2 usually repeated their first choices (Table 6).

Being on an island and being in a familiar locality were ruled out as variables that might have accounted for the findings. No matter what first choices were made, all spiders got pushed back. Each spider had to make its first and its second choice from the same place. These findings imply that whether the first choice succeeded or failed to bring the spider closer to the shoreline was the variable that influenced the spider.

## General discussion

For *P. fimbriata*, use of trial-and-error, a generate-and-test algorithm, appears not to be restricted to signal derivation. By repeating successful choices and switching after failures, *P. fimbriata* solved a confinement problem. However, signal derivation apparently relies on a much greater generating capacity. For solving the confinement problem, choice was between only two potential methods of crossing an expanse of water, but the number of signals *P. fimbriata* may generate appears almost limitless. Another difference is that, in trial-and-error signal-generation study (Jackson &

Wilcox, 1993a), whether *Portia* would switch signals after failure was not explicitly considered. Only repetition of successful signals was shown. However, trial-and-error derivation apparently works both ways: *P. fimbriata* solved a confinement problem both by repeating successes and by switching after failure.

A routine problem *Portia* is known to face in nature was simulated in the trial-and-error signal-generation study (Jackson & Wilcox, 1993a) but the confinement problem was deliberately artificial. Although *Portia* in nature might sometimes need to cross water, there is no evidence that crossing water is a routine occurrence. The manipulations performed in this study (being helped forward or forced back) are almost surely alien to anything *Portia* might routinely encounter in nature.

Detouring behaviour is yet another example of *Portia*'s flexibility (Tarsitano & Andrew, 1999). *Portia* reaches prey by taking indirect routes (detours) when direct routes are unavailable (Tarsitano & Jackson, 1992), including 'reverse-route detours' (detours that can be completed only by initially moving away from, and losing sight of, the prey) (Tarsitano & Jackson, 1994, 1997). In encounters with certain types of prey, such as spitting spiders, which are particularly dangerous (Li *et al.*, 1999), *Portia* takes detours by choice even when shorter direct routes are available (Jackson & Wilcox, 1993b; Jackson *et al.*, 1998). In all of these studies, *Portia* solved a path-finding problem by selecting a route ahead of time. Although detour problems and confinement problems all entail decisions related to locomotion, trial-and-error solutions have not been allowed for in detour studies. Whether *Portia* would, in an appropriately designed experiment, apply trial-and-error to solve detour problems has not been investigated.

Learning, or the modification of behaviour by experience (Lorenz, 1965; Stephens, 1991), differs from other types of phenotypic plasticity (West-Eberhard, 1989) by being cognitive in character. That spider behaviour is modified by experience is firmly established (Grunbaum, 1927; Bays, 1962; LeGuelte, 1969; Lahue, 1973; Seyfarth *et al.*, 1982). Numerous recent studies have demonstrated how prior experience influences spider intraspecific interactions, web-building behaviour and foraging decisions (Sebrier & Krafft, 1993; Sandoval, 1994; Edwards & Jackson, 1994; Whitehouse, 1997; Morse, 1999, 2000a, b; Heiling & Herberstein, 1999; Nakata & Ushimura, 1999; Tso, 1999; Venner *et al.*, 2000).

Trial and error by *Portia* appears to be at least a rudimentary example of learning (Staddon, 1983), or more technically an example of operant conditioning (Skinner, 1938). At least short-term memory is implied (Davis & Dougan, 1988) because *Portia* must remember the last decision and its consequence. Questions pertaining to how long memory traces persist are currently being investigated and have important cognitive implications. However, a different cognitive issue, problem-solving ability, may be of more interest.

A compelling argument might be made for how *Portia*'s predatory strategy, being based on web invasion and close interplay with another predator, might favour especially pronounced problem-solving in the context of signal derivation and during other stages in predatory sequences. It has been argued that complex systems, such as those implied by learning and cognition, may often enable animals to respond flexibly and adaptively to problems outside the context in which these systems evolved (Johnston, 1985; Papaj, 1986; Dukas, 1998b). In *Portia*, perhaps a predatory strategy that routinely demands fine control over the behaviour of dangerous prey has set the stage for the evolution of problem-solving abilities that, as a spin-off, can be readily applied to novel situations, including confinement problems.

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