Spiderweb smokescreens: spider trickster uses background noise to mask stalking movements

R. STIMSON WILCOX*, ROBERT R. JACKSON† & KRISTEN GENTILE*

**Department of Biological Sciences, Binghamton University*
†*Department of Zoology, University of Canterbury*

Abstract. The stalking behaviour of four species of jumping spiders, *Portia fimbriata, P. labiata, P. schultzi* and *P. africana*, was examined to determine whether *Portia* opportunistically exploits situations in which the prey spider is distracted by environmental disturbances. Disturbances were created mainly by wind blowing on webs and a magnet shaking webs. All four *Portia* species moved significantly further during disturbance than during non-disturbance, a behaviour labelled 'opportunistic smokescreen behaviour'. *Portia* can discriminate between spiders and other prey such as live insects, wrapped-up insects in the web, and egg sacs, because *Portia* used opportunistic smokescreen behaviour only against spiders and not against these other types of prey. If the location of disturbances and the location of prey differ, *Portia* can accurately discriminate between them. *Portia*'s smokescreen behaviour apparently is a true predatory tactic because *Portia* attacked prey more often during disturbances than at other times. Smokescreen behaviour appears to work in part because the disturbances that *Portia* uses for smokescreens interfere with the prey's ability to sense *Portia*'s stalking movements.

© 1996 The Association for the Study of Animal Behaviour

Predators use three main techniques to get near to their prey before attacking: stalking the prey, luring the prey in from ambush and passively waiting in ambush (reviewed in Curio 1976). Predators that use deceitful signals when stalking or luring from ambush have been called 'aggressive mimics' (reviews in Wickler 1968; Mitchell & Thompson 1986), and they include such well-known examples as firefly 'femmes fatales' (Lloyd 1986) and angler fish (Pietsch & Grobecker 1978).

In this paper we investigate the aggressive mimicry behaviour of *Portia*, a genus of jumping spiders. Like all jumping spiders, *Portia* has acute vision (Blest 1985; Land 1985). Typical jumping spiders are primarily cursorial hunters of insects (Forster 1982). Jumping spiders of the genus *Portia* are distinctive, however, because they specialize in preying on other spiders and because they are strikingly versatile aggressive mimics that

use a large repertoire of web-borne vibratory signals, emphasizing different signals when pursuing different prey spiders (Jackson & Blest 1982; Jackson & Hallas 1986; Jackson & Wilcox 1990), and determining which signals to use with some prey spider species by a flexible trial and error method (Jackson & Wilcox 1994).

Portia makes signals in two contexts when on other spiders' webs: (1) standing on the web and luring the spider in with signals that apparently imitate a struggling insect; (2) signalling while visually stalking across the web toward the prey spider on the web (reviewed in Jackson 1992). While studying *Portia*'s aggressive mimicry, we found that *Portia* appears to stalk prey spiders more rapidly when the prey's vibratory senses are subjected to background noise, such as when wind blows on their webs. We call this behaviour of *Portia* opportunistic 'smokescreen behaviour'.

The present paper is a laboratory study of *Portia*'s smokescreen behaviour. We provide experimental evidence demonstrating that *Portia* opportunistically responds to environmental noise in a variety of circumstances, is discriminating in its use of smokescreen behaviour, and attempts

Correspondence: R. S. Wilcox, Department of Biological Sciences, Binghamton University, Binghamton, NY 13902-6000, U.S.A. (email: fac273@bingvmb.cc.binghamton.edu). R. A. Jackson is at the Department of Zoology, University of Canterbury, Christchurch 1, New Zealand.

more captures of prey spiders during background disturbance than during periods of quiet. We also present evidence showing that smokescreen behaviour works in part because background noise interferes with the prey's ability to sense *Portia*'s stalking movements.

GENERAL METHODS

Throughout this study we used standard spider laboratory maintenance procedures, cage designs and terminology described in Jackson & Hallas (1986).

We conducted tests on four of the eight known species of *Portia*: *P. fimbriata* (populations from Queensland and Northern Territory, Australia, and from Sri Lanka); *P. labiata* (Sri Lanka); *P. schultzi* (Kenya); and *P. africana* (Kenya). We list below the spiders used for prey, where they were collected, and pertinent characteristics of the webs they build. (1) *Argiope appensa* (Araneidae): Queensland, Australia; orb web. (2) *Zosis genicularis* (Uloboridae): Queensland; orb web. (3) *Hygropoda dolomedes* (Pisauridae): Queensland; horizontal sheet web in the upper dihedral of single large leaves. (4) *Badumna longinquus* (Amaurobiidae): New Zealand; sheet web. (5) *Achaearanea* sp. (Theridiidae): New Zealand; space web. (6) *Achaearanea krausi*: Queensland; space web; hangs a curled leaf in web for a shelter. (7) *Argyrodes flavipes* (Theridiidae): Queensland; space web under leaves. (Unlike the better-known kleptoparasitic species of *Argyrodes*, *A. flavipes* lives exclusively in its own web: R. R. Jackson, unpublished data.) (8) *Pholcus phalangioides* (Pholcidae); New Zealand; space web. (9) *Philoponella variabilis* (Uloboridae): Queensland; social species; individual orb webs that break down into a communal space web when the number of spiders is large (R. R. Jackson, unpublished data). Before tests we removed all *P. variabilis* from webs except one individual, to eliminate confusion in *Portia* as to which spider to stalk. (10) *Stegodyphus sarasinorum* (Eresidae): Sri Lanka; social species in communal sheet web (Bradoo 1980). Before tests we removed all *S. sarasinorum* except one individual.

Web-building spiders generally rely on acute sensitivity to vibrations instead of vision for perceiving objects in their webs. Compared to salticid eyes, the eyes of the spiders that we used as prey are simple and not capable of acute vision (Homann 1971).

As in previous studies of salticid predatory behaviour (e.g. Jackson & Wilcox 1990), we defined four prey sizes by the approximate ratio of prey to predator body volume: very small prey (0.01:1), small prey (0.05:1), medium prey (1:1) and large prey (2:1).

BASIC SMOKESCREEN EXPERIMENTS

Methods

We began each test by introducing *Portia* onto the web of a prey species. Introduction was done by holding *Portia*'s cage close to a prey's web and allowing *Portia* to leave its cage voluntarily and enter the web. Five minutes after the *Portia* had fixated visually on the prey and was stalking it, we started a timer that continuously indicated 30-s test segments and 90-s inter-test segments. During an experimental test segment we 'disturbed' the web with either wind or a shaking magnet that simulated struggling prey. During a control test segment we did not disturb the web.

Each test included five experimental and five control test segments, in random order. For each test segment we recorded how far *Portia* moved. For these recordings, we did not count pivoting in place, but recorded only the distance that the mid-point of the body moved. All distances are accurate to the nearest millimetre. Because the absolute distances that *Portia* travelled were not relevant to the questions we addressed, we only analysed the relative distances travelled during disturbance versus non-disturbance. Unless otherwise stated, a test ended either when *Portia* or the prey left the web, or 30 min elapsed. We also established a rule that a test would have ended when a prey caught *Portia*, but this never happened.

Some of the prey species we used had specialized patterns of defence. If, during a test, one of these spiders performed one of these specialized behaviour patterns, we cancelled the test. Also, if *Portia* groomed during a test, we terminated the test, then restarted it 30 min later. If *Portia* had one or more legs on a support at the edge of a web, we considered it to be out of the web, even if some legs were on the web. In certain special tests (called 'position tests'), we wanted to look specifically at whether *Portia* used opportunistic smokescreen behaviour even when some or all of its legs were off the web. To obtain these data, we relaxed the standard rule that *Portia* had to have all of its

Table I. Mean (± SD) distance (mm) moved by male and female juveniles and adult females (data pooled) of four species of *Portia*, and three populations of *P. fimbriata*, in response to *Badumna longinquus*, in the presence and absence of wind disturbance

	Wind disturbance	*Portia fimbriata* (NT) (9)	*Portia fimbriata* (Q) (12)	*Portia fimbriata* (SL) (7)	*Portia labiata* (9)	*Portia africana* (7)	*Portia shultzi* (7)
Badumna longinquus	Present	33 ± 16	32 ± 12	39 ± 19	25 ± 16	40 ± 18	32 ± 20
	Absent	10 ± 11	6 ± 5	15 ± 8	11 ± 9	9 ± 3	9 ± 5
		*	**	*	*	*	*

Number of tests is in parentheses. *Portia* size relative to prey size was always 1:1. Data analysis: Wilcoxon tests on distance moved by *Portia* during experimental test segments subtracted from distance moved during control test segments. Null hypothesis: distance moved in the two types of test segments are equal. *Portia* used smokescreen behaviour if $P<0.05$ (see text).
NT: Northern Territory, Australia; Q: Queensland, Australia; SL: Sri Lanka populations.
*$P<0.05$; **$P<0.005$.

legs on the silk during the test; then we used only those test segments in which the *Portia* spent five experimental and five control test segments with either all or some legs off the silk. For any one type of test, we used no *Portia* more than once, although we used some individuals in two or more different types of test. We tested each individual only once per day.

Disturbances

To make wind disturbance, we used a small electric motor that whirled a model airplane propeller positioned vertically 20 cm from *Portia*. 'Weak' wind was 15–20 cm/s, and 'strong' wind was 30–40 cm/s. We simulated the struggling of insect prey on the web by gluing a samarium-cobalt magnet to a 4-mm-square × 2-mm-thick piece of cork, adhering the cork to a web, then shaking the web by vibrating the cork with a 20 Hz sine wave (a major frequency found in many prey species of insects: R. S. Wilcox & R. R. Jackson, unpublished data) played through a power generator into a coil of magnet wire held near the cork (see Wilcox & Kashinsky 1980). Weak magnet 'struggles' oscillated the cork up and down about 2 mm, strong struggles about 5 mm. Unless stated otherwise, all wind and magnet tests reported here were 'weak'. Prey spiders were habituated to the magnet signal for 5 min before a test so they would not attack the magnet during the test.

Data analysis

For most types of tests, our interest centred on the differences in distance that *Portia* moved during experimental versus control test segments. We analysed this difference by using Wilcoxon matched-pairs signed-rank tests under the null hypothesis that distances moved during experimental and control test segments were equal. We found no evidence of differences in test results for age or sex classes; therefore, data for these classes were pooled unless stated otherwise.

During standard tests, *Portia* might be oriented in a variety of different directions relative to the prey spider. To determine whether *Portia*'s orientation affected whether it used opportunistic smokescreen behaviour, we defined three orientations: (1) directly towards the prey, (2) approximately 90° away from the prey and (3) approximately 180° away from the prey. Next, we tagged all tests in which *Portia* faced in each orientation in at least one experimental and one control test interval. To qualify, the *Portia* had to face in the specified orientation for the entire test segment. For each tagged test, we randomly chose one experimental and one control test segment with *Portia* oriented as specified. Pooling data from each appropriate test generated a data set for each orientation, which consisted of an experimental test segment paired with its control segment. These data sets differed from the previous standard test sets because the previous data pairs were sums from five experimental and five control test segments per *Portia*.

Results

The results from the standard experimental procedure using wind and magnet disturbance

Table II. Mean (± SD) distance (mm) moved by male and female juveniles and adult females (data pooled) of *Portia* (Queensland) in response to 9 prey species of varying size, in the presence and absence of wind disturbance

Prey species	Wind disturbance	Predator: prey body size			
		0.1	0.5	1.0	2.0
Argiope appensa	Present	—	13 ± 3	20 ± 11	—
	Absent		3 ± 2	7 ± 5	
			* (12)	*** (35)	
Argyrodes flavipes	Present	—	8 ± 2	6 ± 3	—
	Absent		3 ± 3	2 ± 1	
			* (8)	*** (12)	
Achaeranea sp.	Present	13 ± 2	15 ± 6	33 ± 13	19 ± 11
	Absent	7 ± 4	10 ± 2	10 ± 7	4 ± 3
		* (7)	* (7)	*** (25)	* (6)
Badumna longinquus	Present	23 ± 8	21 ± 10	32 ± 12	26 ± 18
	Absent	9 ± 5	7 ± 7	6 ± 5	6 ± 6
		* (7)	* (6)	*** (12)	* (8)
Hygropoda dolomedes	Present	11 ± 2	13 ± 6	15 ± 8	11 ± 6
	Absent	4 ± 1	5 ± 5	6 ± 3	5 ± 3
		* (6)	* (8)	* (11)	* (8)
Philopoella variabilis	Present	23 ± 11	16 ± 16	8 ± 4	—
	Absent	12 ± 6	7 ± 4	4 ± 3	
		** (21)	* (10)	*** (22)	
Pholcus phalangioides	Present	—	—	28 ± 15	—
	Absent			10 ± 6	
				*** (29)	
Stegodyphus sarasinorum	Present	—	—	28 ± 8	—
	Absent			10 ± 5	
				*** (12)	
Zosis geniculatus	Present	27 ± 18	20 ± 7	30 ± 13	17 ± 7
	Absent	11 ± 5	10 ± 6	8 ± 6	4 ± 4
		* (7)	** (9)	*** (27)	* (8)

—: Data were not collected. Number of tests is in parentheses. *Portia* size relative to prey size was always 1:1. Data analysis: Wilcoxon tests on distance moved by *Portia* during experimental test segments subtracted from distance moved during control test segments. Null hypothesis: distance moved in the two types of test segments are equal. *Portia* used smokescreen behaviour if $P<0.05$ (see text).
*$P<0.05$; **$P<0.01$; ***$P<0.005$.

showed that *Portia* opportunistically capitalized on background noise as a smokescreen against all 10 prey species of spider we used. *Portia* moved significantly further during experimental test segments in which there was disturbance than during control test segments in which there was no disturbance (see Tables I–V). These results were true for male and female juveniles and adult females of each of the four species of *Portia*, including all three populations of *P. fimbriata* that we tested (Table I), for a wide variety of sizes of prey species (Table II), and for adult males of three species of

Portia, including two populations of *P. fimbriata* (Table III).

Disturbance using the magnet gave the same results as disturbance using wind for *P. fimbriata* and *P. labiata*, against a variety of prey species (Table IV). *Portia* also used opportunistic smokescreen behaviour while oriented in different directions relative to the prey (Table V). Because *Portia* often does not take the shortest, most direct, route towards a spider and may face in various orientations when stalking a spider (Jackson & Hallas 1986), these orientations

Table III. Mean ($\pm$ SD) distance (mm) moved by adult males of three species of *Portia* in response to three pey species, in the presence and absence of wind disturbance

Prey species	Wind disturbance	*P. fimbriata* (Q)	(NT)	*P. labiata*	*P. schultzi*
Achaeranea sp.	Present	42 $\pm$ 15	50 $\pm$ 15	51 $\pm$ 26	30 $\pm$ 13
	Absent	30 $\pm$ 24	28 $\pm$ 17	23 $\pm$ 14	18 $\pm$ 13
		* (11)	* (6)	* (11)	* (7)
Badumna longinquus	Present	47 $\pm$ 29	—	—	
	Absent	24 $\pm$ 25			
		NS (5)			
		$P=0.28$			
Zosis genicularis	Present	35 $\pm$ 12		—	—
	Absent	14 $\pm$ 5			
		* (6)			
All prey species (pooled data)	Present	41 $\pm$ 19			
	Absent	22 $\pm$ 18			
		* (16)			

—: Data were not collected. Number of tests is in parentheses. *Portia* size relative to prey size was always 1:1. Data analysis: Wilcoxon tests on distance moved by *Portia* during experimental test segments subtracted from distance moved during control test segments. Null hypothesis: distance moved in the two types of test segments are equal. *Portia* used smokescreen behaviour if $P<0.05$ (see text). Q: Queensland; NT; Northern Territory, Australia.
*$P<0.05$; NS: not significant.

Table IV. Mean ($\pm$ SD) distance (mm) moved by male and female juveniles and adult females (data pooled) of *Portia fimbriata* and *P. labiata* in response to six prey species, in the presence and absence of magnet disturbance

Prey species	Magnet disturbance	*P. fimbriata*	*P. labiata*
Argiope appensa	Present	16 $\pm$ 7	—
	Absent	8 $\pm$ 5	
		** (16)	
Achaearanea sp.	Present	39 $\pm$ 13	—
	Absent	16 $\pm$ 12	
		* (8)	
Badumna longinquus	Present	35 $\pm$ 13	36 $\pm$ 17
	Absent	10 $\pm$ 9	16 $\pm$ 7
		* (9)	* (6)
Zosis genicularis	Present	31 $\pm$ 35	44 $\pm$ 12
	Absent	14 $\pm$ 10	9 $\pm$ 4
		* (20)	* (8)
Hygropoda dolomedes	Present	23 $\pm$ 7	—
	Absent	4 $\pm$ 2	
		* (7)	
Philoponella variabilis	Present	8 $\pm$ 3	—
	Absent	3 $\pm$ 2	
		* (7)	

—: Data were not collected. Number of tests is in parentheses. *Portia* size relative to prey size was 1:0.5–1. Data analysis: Wilcoxon tests on distance moved by *Portia* during experimental test segments subtracted from distance moved during control test segments. Null hypothesis: distance moved in the two types of test segments are equal. *Portia* used smokescreen behaviour if $P<0.05$ (see text).
*$P<0.05$; **$P<0.005$.

Table V. Mean (± SD) distance (mm) moved by male and female juveniles and female adults of *Portia* in response to prey spiders, in the presence and absence of wind and magnet disturbance, in standard tests and position tests conducted to determine whether *Portia*'s orientation relative to its prey affects *Portia*'s inclination to use opportunistic smokescreen behaviour

		Disturbance	
Portia	Disturbance present/absent	Wind	Magnet
Orientation			
Facing directly towards prey	Present	5 ± 4	5 ± 4
	Absent	1 ± 2	1 ± 2
		** (361)	** (70)
Facing 90° away from prey	Present	8 ± 5	8 ± 6
	Absent	4 ± 4	1 ± 2
		** (246)	* (38)
Facing 180° away from prey	Present	10 ± 7	12 ± 22
	Absent	4 ± 4	7 ± 10
		** (71)	NS *P*=0.09 (19)
Position			
Completely in web	Present	26 ± 16	32 ± 23
	Absent	10 ± 9	10 ± 8
		** (370)	* (59)
Completely off web, on solid substrate	Present	5 ± 4	—
	Absent	5 ± 4	
		* (18)	

Data are pooled from all species and sex–age classes, against a wide variety of prey species and prey sizes. —: Data were not collected. Number of tests is in parentheses. Data analysis: Wilcoxon tests on distance moved by *Portia* during experimental test segments subtracted from distance moved during control test segments. Null hypothesis: distance moved in the two types of test segments are equal. *Portia* used smokescreen behaviour if $P<0.05$ (see text).
*$P<0.01$; **$P<0.001$; NS: not significant.

represent normal predatory behaviour of *Portia*. *Portia* used smokescreen behaviour not only when in a web, but also when completely off a web, on a solid substrate beside the web (Table V).

ARTIFICIAL PLAYBACK CONTROL

Methods

To control for the artificiality of our wind and magnet playback procedure, we examined whether *Portia* would respond to background noise made by struggling insects in the same way as it responded to wind and magnet playbacks. We put a locust, *Locusta migratoria*, and a prey spider, *Stegodyphus sarasinorum*, in a web, then induced the locust to struggle by brushing it lightly with a bristle. We discarded tests in which a locust struggled spontaneously. Otherwise, the methods in these tests were the same as in standard tests.

Results

When locusts were struggling in a web that also contained a prey spider, *Portia* performed smokescreen behaviour in synchrony with the insect's struggling noise, while always stalking the spider rather than the insect (Wilcoxon: N=11, $P<0.005$; disturbance, $\bar{X}\pm$ SD$=9\pm4$ mm; non-disturbance, 4 ± 3 mm).

CIRCUMSTANCES IN WHICH SMOKESCREEN BEHAVIOUR IS NOT USED

We conducted a variety of tests to examine the circumstances under which *Portia* does not use smokescreen behaviour. We predicted that if smokescreen behaviour is used against dangerous prey that could potentially capture *Portia*, or against prey that could escape or use defensive

measures if they detected *Portia*, then *Portia* would restrict the use of smokescreen behaviour to circumstances in which dangerous or easily frightened prey were present (e.g. other spiders). We therefore conducted a series of experiments in which non-spider prey were used, all of which *Portia* has previously been observed to attack in nature (Jackson & Blest 1982). We predicted that *Portia* would not use smokescreen behaviour when approaching these prey, all of which were defenceless and unable to flee.

Methods

We conducted standard smokescreen experiments, with the following conditions for *Portia*: (1) alone in a bare cage, with no web present, (2) alone in its own web, (3) alone in a vacant alien web, (4) alone in an alien web, feeding on a spider but with no other spider present; alone in an alien web, with (5) egg sacs, (6) a wrapped-up insect or (7) a live moth present. None of these first seven prey are spiders, in contrast to the following two circumstances, which were: (8) *Portia* in its own web, stalking prey spiders and (9) *Portia* in a *Philoponella variabilis* web, eating a *P. variabilis* and simultaneously stalking another *P. variabilis*.

Results

As predicted, *Portia* did not show smokescreen behaviour when no prey were present or when stalking non-spider prey, and did show this behaviour when spider prey were present (Table VI). *Portia* accurately identified egg sacs and insects (a noctuid moth), and it used smokescreen behaviour when in its own web and pursuing a spider. Thus *Portia* was not inhibited from smokescreen behaviour by being in its own web. Nor does feeding itself inhibit *Portia*'s smokescreen behaviour, because *Portia* used smokescreen behaviour not only when feeding on one spider but also when pursuing another spider in a web (Table VI).

SMOKESCREEN BEHAVIOUR IS A PREDATORY TACTIC

Methods

If opportunistic smokescreen behaviour is indeed a predatory tactic, we might expect *Portia* to attack and catch its prey more often when a disturbance is present than when it is absent. We went through the transcripts of standard tests and tagged all tests in which *Portia* attacked the prey spider, pooling data from tests with wind and with magnets.

Results

Of 16 instances in which *Portia* caught prey during the test, there were nine instances of prey capture during experimental test segments, but only one during a control test segment, resulting in a significant difference between the experimental and control tests (goodness-of-fit test, null hypothesis of equal capture frequency in experimental and control: $\chi^2 = 4.900$, $P < 0.05$). Six other captures were during intervals between test segments. The results supported the prediction that *Portia* catches prey more often during disturbances than at other times.

These data from standard tests came from a small sample size, because *Portia* did not often catch prey during the short standard tests. Therefore we conducted additional tests to gather more data, and specifically to investigate the relationship between prey capture and disturbances.

Methods

For these tests, we used *Z. genicularis*. Test methods were as in the standard tests with wind except for the following modifications. We used only one test segment per test instead of 10, which could last up to 4 h. Before starting the test, we waited until *Portia* was within five body lengths of the *Z. genicularis*, then waited another 1, 2, 3, 4 or 5 min (decided randomly), after which we conducted either an experimental or a control test segment. We cancelled the test if (1) *Portia* failed to get to within five body lengths of the *Z. genicularis* within 4 h after entering the web, (2) *Portia* failed to stay within five body lengths of the *Z. genicularis* during the interval between approaching within five body lengths and the start of the test segment, or (3) if *Portia* attacked the *Z. genicularis* during the waiting interval. If a test was cancelled, we made another attempt with the same *Portia* on the next day or on each successive day until we obtained a successful test. We used each individual *Portia* in a pair of tests, usually on successive days, with the experimental test segment on one day and the control segment on the other day (order decided randomly). All tests were with male and female juveniles and adult females of *P. fimbriata*, and *Portia*

Table VI. Mean (± SD) distance (mm) moved by male and female juveniles and adult females (data pooled) of three species of *Portia* in response to a variety of conditions, in the presence and absence of wind (W) and magnet (M) disturbance

Condition	Disturbance present/absent	*P. fimbriata* (Q)	*P. labiata*	*P. schultzi*
Alone in bare cage	Present	25 ± 16	—	—
	Absent	30 ± 19		
		NS *P*=0.39		
		(20) (W)		
Alone in its own web	Present	8 ± 6	6 ± 5	3 ± 5
	Absent	5 ± 5	11 ± 9	6 ± 7
		NS *P*=0.07	NS *P*=0.053	NS *P*=0.18
		(12) (W)	(12) (W)	(5) (W)
	Present	23 ± 21		
	Absent	33 ± 29		
		NS *P*=0.29		
		(14) (M)		
In vacant *Badumna longinquus* web	Present	15 ± 13	12 ± 9	—
	Absent	17 ± 13	19 ± 18	
		NS *P*=0.38	NS *P*=0.13	
		(17) (W)	(17) (W)	
			10 ± 11	
			17 ± 21	
			NS *P*=0.42	
			(14) (M)	
Alone in alien web, eating a spider				
Alien webs				
Badumna longinquus	Present	5 ± 8	—	—
	Absent	8 ± 8		
		NS *P*=0.58		
		(7) (W)		
Achaeranea sp.	Present	9 ± 11	—	—
	Absent	7 ± 7		
		NS *P*=0.42		
		(9) (W)		
In alien web, stalking spider egg sacs				
Alien webs				
Achaeranea sp.	Present	17 ± 7	23 ± 8	24 ± 18
	Absent	23 ± 9	23 ± 9	25 ± 21
		NS *P*=0.18	NS *P*=0.11	NS *P*=0.79
		(5) (W)	(4) (W)	(3) (W)
Argiope appensa	Present	22 ± 16	—	—
	Absent	36 ± 33		
		NS *P*=0.86		
		(4) (W)		
Zosis genicularis	Present	16 ± 8	19 ± 9	—
	Absent	16 ± 6	29 ± 2	
		NS *P*=0.93	NS *P*=0.11	
		(7) (W)	(4) (W)	
In *Badumna longinquus* web, stalking wrapped-up fly	Present	12 ± 7	—	—
	Absent	17 ± 12		
		NS *P*=0.17		
		(10) (W)		
In *Badumna longinquus* web, stalking noctuid moth	Present	18 ± 14	—	—
	Absent	22 ± 12		
		NS *P*=0.27		
		(12) (W)		

Table VI. *Continued*

Condition	Disturbance present/absent	*P. fimbriata* (Q)	*P. labiata*	*P. schultzi*
In its own web, stalking prey spiders				
Pholcus phalangioides	Present	23 ± 12	—	—
	Absent	6 ± 5		
		**		
		(12) (W)		
	Present	10 ± 4		
	Absent	4 ± 2		
		*		
		(12) (M)		
Achaeranea krausi	Present	11 ± 5	—	—
	Absent	3 ± 2		
		**		
		(12) (W)		
In *Philoponella variabilis* web, eating a	Present	8 ± 2	—	—
P. variabilis and stalking another	Absent	0.5 ± 1		
P. variabilis		**		
		(16) (W)		

Tests were designed to determine whether *Portia* is selective as to when to use smokescreen behaviour. —: Data were not collected. Number of tests is in parentheses. *Portia* size relative to prey size was always 1:1. Data anlysis: Wilcoxon tests on distance moved by *Portia* during experimental test segments subtracted from distance moved during control test segments. Null hypothesis: distance moved in the two types of test segments are equal. *Portia* used smokescreen behaviour if $P<0.05$ (see text).
*$P<0.01$; **$P<0.005$.

size relative to prey size was always 1:1. For a pair of tests with a given *Portia*, there were four possible results: *Portia* caught the *Z. genicularis* (1) only in the experimental test, (2) only in the control test, (3) in both tests, or (4) in neither test. Being paired data, the appropriate analysis was a McNemar test for significance of changes, which could only be calculated on results (1) and (2).

Results

Portia caught the *Z. genicularis* only in the experimental test nine times, only in the control once, in both no times, and in neither 58 times ($P<0.05$), supporting the hypothesis that smokescreen behaviour is a predatory tactic. This hypothesis is further supported by results of the following study.

WHY DOES THE OPPORTUNISTIC SMOKESCREEN TACTIC WORK?

We investigated the hypothesis that *Portia*'s smokescreen tactic works because background noise interferes with the prey's ability to detect *Portia*'s stalking movements.

Continuous Disturbance versus No Disturbance: Helping *Portia* Capture Prey

Methods

We tested whether we could help *Portia* in prey capture by providing a smokescreen disturbance that continued during the entire test. We predicted that *Portia* would capture prey spiders more effectively during disturbance than during no disturbance.

All tests were with juveniles and adult females of *P. fimbriata*, and *Portia* size relative to prey size was always 1:1. Prey spiders were *A. appensa*, *Z. genicularis*, and *B. longinquus*, each of which has readily recognizable defences against potential predators: *A. appensa* pumps rapidly in its orb web (Jackson et al. 1993), *Z. genicularis* tugs sharply on its web or leaves the web entirely, and *B. longinquus* attacks by rushing aggressively forward.

Each test lasted 60 min, and differed from standard tests (in which experimental or control segments were brief and alternated randomly) in that each test was either an experimental condition involving continuous disturbance (wind or magnet) throughout the test, or a control

Table VII. Effectiveness of *Portia*'s smokescreen tactic on the webs of *Argiope appensa*, *Badumna longinquus* and *Zosis genicularis* (data pooled), in the presence (experimental) and absence (control) of continuous wind disturbance

	Experimentals only	Controls only	Both experimentals and controls	Neither experimentals nor controls	P*
Prey attacks *Portia* or performs defensive behaviour	15	73	23	192	<0.001
Portia catches prey spider	80	28	35	160	<0.001
Portia walked from edge completely onto web	14	4	0	55	<0.05
Portia walked off web	11	1	0	62	<0.01

Null hypothesis: there is no difference in experimental versus control results. The tests used male and female juveniles and adult females of *Portia fimbriata* (Q). *Portia* size relative to prey size=1:0.5 or 1:1 (see text).
*McNemar test.

involving no disturbance at all throughout the test. For each *Portia* we conducted either an experimental or a control test, on successive days (order decided randomly). The results were analysed with the McNemar test for significance of changes. For each *Portia*, the possible results from a pair of tests, with respect to prey capture and with respect to the prey's defence behaviour, could be capture or defence in (1) both tests, (2) neither test, (3) only the experimental test or (4) only the control test.

Results

There was no evidence that the species of prey spider affected the outcome of the tests, nor that data from tests in which we used wind differed from tests in which we used magnets (tests of independence, NS). Therefore, we pooled data from these different sets. As expected, there were significantly more instances of prey spider defence during the control tests and more instances of prey capture during the experimental tests (Table VII). Also, *Portia* not only entered from a solid onto webs significantly more often during disturbance, but also left webs more during disturbance (Table VII).

Continuous Disturbance versus No Disturbance: Helping Prey Defend Against *Portia*

Methods

Having postulated that opportunistic smoke-screen behaviour interferes with a prey spider's ability to detect approaching *Portia*, we designed a procedure to help the prey spider perceive *Portia*'s presence when *Portia* stalked it during background disturbance. This procedure was identical to the preceding tests with continuous wind throughout a test, except that the disturbance was perceived by *Portia* but did not affect the prey spider's ability to detect *Portia*. We achieved this by duping *Portia* into performing smokescreen behaviour when there was in fact no disturbance present on the web containing both *Portia* and the prey.

All tests were with male and female juveniles and adult females of *P. fimbriata*, and *Portia* size relative to prey size was always 1:1. Before each test, we set up two vertically oriented glass-fronted cages (cages A and B), one on either side of a square transparent plastic cage (cage C) (Fig. 1). Cage C contained a *Z. genicularis* in a horizontal web. Cages A and B each contained a vertical web of a *Z. genicularis*, but no spider, and the webs contained detritus and egg sacs. The glass sides were in place on cages A and B on the sides between them and cage C, but we removed the sides of these cages away from cage C. At the start of a test, we introduced *Portia* into cage C. We carried out tests as in standard tests with wind, except that the wind struck only the webs in cages A and B, the glass blocking the wind from hitting the web in the cage C. Thus, although *Portia* could not feel the wind, it could see the webs in cages A and B, with their detritus and egg sacs moving. Having two cages receive wind ensured that *Portia* would see the neighbouring webs blowing in the wind, regardless of its orientation on the web in cage C. We used strong wind to
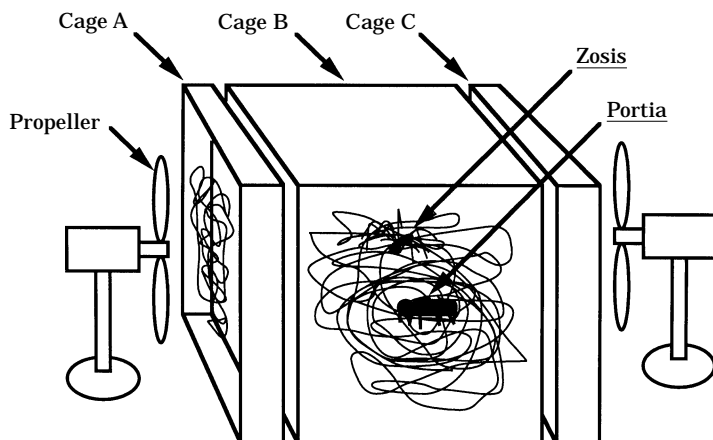
Figure 1. Experimental set-up to induce *Portia* to perform smokescreen behaviour from visual stimuli only. Vertical cages A and B had webs of *Z. genicularis* in them, but no spiders. Glass fronts of cages A and B were removed on the sides near the propellers, but not on the sides by cage C, which was constructed of glass; thus the web in cage C receives no wind stimulus. Square cage C contained a *Z. genicularis* web with a *Z. genicularis* in it. A *Portia* was introduced onto the web in cage C, and wind was blown by the propellers onto the vacant webs in cages A and B, making egg sacs and detritus move in the webs. *Portia* could not feel the wind, but saw webs in cages A and B moving and performed smokescreen behaviour while stalking the *Z. genicularis*.

make the movement of detritus and egg sacs conspicuous.

We predicted that *Portia* would be less successful at prey capture during these tests, and the prey spider would be more likely to perform defence behaviour, than during standard tests using wind for disturbance. We therefore used tests of independence to compare data from these tests with data from previous standard tests.

Results

Portia responded to the sight of the wind-disturbed webs with smokescreen behaviour as in standard tests, only now there was no wind to conceal *Portia*'s movements from the *Z. genicularis*. *Portia* caught the *Z. genicularis* in 32 of 76 tests with continuous 'actual' wind, but in only 28 of 148 tests with continuous 'visual' wind ($\chi^2 = 12.61$, $P < 0.001$). *Zosis genicularis* performed defence behaviour in 28 of 148 tests in visual wind, but in only five of 76 tests in actual wind ($\chi^2 = 6.09$, $P < 0.01$). These results supported our prediction that smokescreen behaviour interfered with the prey spider's ability to detect the predator on the web.

PORTIA'S SMOKESCREEN BEHAVIOUR: IRRITATION OR PREDATORY TACTIC?

Our hypothesis is that *Portia* performs smokescreen behaviour as a predatory tactic. An alternative hypothesis, however, is that this behaviour is simply an artefact of *Portia* being irritated by the stimulus we used for a disturbance. We therefore evaluated how *Portia* responded to irritation from wind blowing on it or from a magnet vibrating its web, and predicted that *Portia* would be more irritated by a strong disturbance than by a weak disturbance. We therefore conducted two sets of tests comparable to previous tests with weak disturbances, only now with strong disturbance stimuli also.

Portia Alone in Its Own Web

Methods

We tested *Portia*'s response to differences solely of disturbance intensity by first noting *Portia*'s response when alone in its own web, thereby establishing baseline information on how *Portia* responds to irritation, with no other distractions.

Table VIII. Mean ($\pm$ SD) distance (mm) moved by male and female juveniles and adult females of *Portia fimbriata* (Q) alone or in response to *Badumna longinquus*, in the presence and absence of wind (W) and magnet (M) disturbance, of weak and strong intensity

		Wind or magnet disturbance	
Portia	Disturbance present/absent	Weak	Strong
Alone in own web	Present	6 ± 5	24 ± 8
	Absent	8 ± 7	9 ± 6
		NS $P=0.17$	*
		(34) (W)	(63) (W)
	Present	23 ± 21	44 ± 16
	Absent	33 ± 29	18 ± 10
		NS $P=0.29$	*
		(14) (M)	(6) (M)
In occupied *Badumna longinquus* web	Present	33 ± 16	10 ± 6
	Absent	10 ± 7	12 ± 5
		*	NS $P=0.43$
		(53) (W)	(15) (W)
	Present	30 ± 14	9 ± 8
	Absent	13 ± 8	7 ± 4
		*	NS $P=0.98$
		(15) (M)	(14) (M)

Number of tests is in parentheses. *Portia* size relative to prey size was always 1:1. Data analysis: Wilcoxon tests on distance moved by *Portia* during experimental test segments subtracted from distance moved during control test segments. Null hypothesis: distance moved in the two types of test segments are equal. *Portia* used smokescreen behaviour if $P<0.05$ (see text).
*$P<0.05$.

Results

During weak wind disturbance *Portia* did not move more during disturbance than during non-disturbance; that is, *Portia* essentially ignored weak disturbance, and did not perform smokescreen behaviour. During strong disturbance, however, *Portia* moved significantly more during disturbance than non-disturbance (Table VIII). Moreover, during strong disturbance, *Portia* moved more rapidly and produced more loco-motory vibrations than when performing smokescreen behaviour during weak disturbance.

Portia in an Occupied Alien Web

Methods

We next tested *Portia* in an alien web under strong disturbance to see whether that provoked a different response from that to weak disturbance.

Results

From our previous studies, we knew that a weak wind disturbance stimulated *Portia* in a web

containing a *B. longinquus* to respond with smoke-screen behaviour (Table VIII). Under strong wind disturbance, however, *Portia* showed no difference between experimental and control test segments (Table VIII). Furthermore, we did not see the unguarded style of locomotion that *Portia* showed when alone in its own web and stimulated by strong disturbance (Table VIII). We concluded that *Portia* suppressed its irritation response to strong wind and acted cautiously in the presence of *B. longinquus*. These results support our hypothesis that smokescreen behaviour is a predatory tactic and not an irritation response when in the presence of a prey spider.

DISCUSSION

Smokescreen behaviour appears to be a means of moving in the presence of other spider species. It is probably a general behavioural characteristic of the genus *Portia*, because male and female juveniles, adult males and females of all four

species and all populations of *Portia* tested responded with smokescreen behaviour to both wind and magnet disturbance. The behaviour seems to be effective against a wide range of spider prey species, because *Portia* used it when in the webs of all 10 spider prey species, and against spiders of widely different sizes within each prey species. The tests using live insects supported previous evidence that *Portia* accurately discriminated between insects and spiders on the same web, and preferred spiders as prey (Jackson & Wilcox 1993).

Portia apparently does not have to see a spider to use smokescreen behaviour effectively, because *Portia* performed smokescreen behaviour when at any orientation relative to the prey spiders. This behavioural pattern is likely to be related to a feature of *Portia*'s stalking strategy: *Portia* sometimes shows 'detour behaviour', a behaviour previously described in jumping spiders by Hill (1979), in that it does not stalk directly towards a prey spider, but instead takes a circuitous route, often not looking at the prey when doing so and even going around obstacles that cut off the prey spider from view (Jackson & Wilcox 1993; Tarsitano & Jackson 1994).

Because *Portia* attacked spider prey more often during disturbance than during non-disturbance periods, and prey spiders appeared less able to sense the presence of *Portia* on their webs during disturbance periods, *Portia*'s smokescreen behaviour appears to be a genuine predatory tactic. The evidence suggests that the ploy works by interfering with the prey spiders' ability to detect *Portia*. Our results show that *Portia* uses smokescreen behaviour when entering, stalking in, and leaving webs, which makes sense from two viewpoints. First, many of *Portia*'s spider prey are dangerous to *Portia*, and *Portia* is occasionally captured by its intended prey (e.g. Jackson & Hallas 1986). Second, some of the prey spiders that *Portia* attacks specifically respond to the vibration patterns from *Portia* walking on their webs by leaving the web altogether. No other genus of spiders that we have tested has caused a prey spider species to leave its web entirely (R. S. Wilcox & R. Jackson, unpublished data). Thus, smokescreen behaviour appears also to be a strategy to prevent prey spiders from leaving the web.

The slower, low-vibration movement that *Portia* showed when on a *B. longinquus* web under strong wind disturbance appears to be a sensible behaviour on *Portia*'s part, because *B. longinquus* is one of the more dangerous prey *Portia* stalks. This interesting ability of *Portia* to control its irritation response to strong wind when in a dangerous situation indicates that *Portia* discriminates between weak and strong disturbances, and the results are consistent with our hypothesis that strong disturbance is an irritation, and weak disturbance is a cue to perform smokescreen behaviour.

Portia's smokescreen behaviour appears similar to descriptions of certain kleptoparasitic spiders moving stealthily across their host's web towards ensnared prey when the host spider is motionless, but moving more rapidly when the host is feeding on prey or moving around on its web (*Argryodes elevatus*, Theriidae: Vollrath 1979; *Mysmenopsis furtiva*, Mysmenidae: Coyle et al. 1991). A different but related situation is the 'vibratory camouflage' displayed by certain grasshoppers to avoid capture by ctenid spiders on banana leaves (Barth et al. 1988), characterized by a slow, cautious 'vibrocryptic' gait that may be imitating the low-frequency vibrations made by wind. The opportunistic smokescreen behaviour of *Portia*, in contrast, appears to capitalize on the concealing or masking effect of the wind on a prey spider's web. Although the kleptoparasitic spiders and the grasshoppers seem likely to benefit from their stealthy behaviour, experimental evidence is lacking.

There are obvious advantages for a predator that can exploit situations in which a prey's predator-detection abilities are handicapped. Predatory tactics comparable to *Portia*'s opportunistic smokescreen behaviour, although rarely investigated, may be widespread. It would be enlightening to take a closer look, not only at other spiders, but also at other species as well. For example, Shaller (1972) noted that lions not only hunt more often during the night, but also preferentially hunt when cloud cover suddenly obscures the moon, making the night vision of prey less effective. As another example, Brown (1980) noted that he was trained by his Apache Indian teacher to stalk game by taking advantage of background noise in the environment that would mask the sounds of his stalking. We suspect that many intriguing stories will emerge from future studies on smokescreen behaviour in various species.

REFERENCES

Barth, F., Bleckmann, H., Bohnenberger, J. & Seyfarth, E.-A. 1988. Spiders of the genus *Cupiennius* Simon 1891 (Araneae, Ctenidae). II. On the vibratory environment of a wandering spider. *Oecologia (Berl.)*, **77**, 194–201.

Blest, D. 1985. Fine structure of spider photoreceptors in relation to function. In: *Neurobiology of Arachnids* (Ed. by F. Barth), pp. 79–102. New York: Springer-Verlag.

Bradoo, B. L. 1980. Feeding behaviour and recruitment display in the social spider *Stegodyphus sarasinorum* Karsch (Araneae, Eresidae). *Tijdschr. Entomol.*, **123**, 89–104.

Brown, T. 1980. *The Search: The Continuing Story of the Tracker*. Englewood Cliffs, New Jersey: Prentice-Hall.

Coyle, F. A., O'Shields, T. C. & Perlmutter, D. G. 1991. Observations on the behavior of the kleptoparasitic spider, *Mysmenopsis furtiva* (Araneae, Mysmenidae). *J. Arachnol.*, **19**, 62–66.

Curio, E. 1976. *The Ethology of Predation*. Berlin: Springer-Verlag.

Forster, L. 1982. Vision and prey-catching strategies in jumping spiders. *Am. Scient.*, **70**, 165–175.

Hill, D. E. 1979. Orientation by jumping spiders of the genus *Phidippus pulcherrimus* (Araneae: Salticidae) during the pursuit of prey. *Behav. Ecol. Sociobiol.*, **5**, 301–322.

Homann, H. 1971. Die Augen der Araneae. Anatomie, Ontogenie und Bedeutung fur die Systematik (Chelicerata, Arachnida). *Z. Morphol. Ökol. Tiere*, **69**, 201–272.

Jackson, R. R. 1992. Eight-legged tricksters, spiders that specialize in catching other spiders. *BioScience*, **42**, 590–598.

Jackson, R. R. & Blest, D. 1982. The biology of *Portia fimbriata*, a web-building jumping spider (Araneae,

Salticidae) from Queensland: utilization of webs and predatory versatility. *J. Zool., Lond.*, **196**, 255–293.

Jackson, R. R. & Hallas, S. 1986. Comparative biology of *Portia africana, P. albimana, P. fimbriata, P. labiata*, and *P. schultzi*, araneophagic, web-building jumping spiders (Araneae, Salticidae): utilisation of webs, predatory versatility, and intraspecific interactions. *N.Z. Jl Zool.*, **13**, 423–489.

Jackson, R. R., Rowe, R. J. & Wilcox, R. S. 1993. Antipredator defences of *Argiope appensa* (Araneae, Araneidae), a tropical orb-weaving spider. *J. Zool., Lond.*, **229**, 121–132.

Jackson, R. R. & Wilcox, R. S. 1990. Aggressive mimicry, prey-specific predatory behaviour and predator-recognition in the predator–prey interactions of *Portia fimbriata* and *Euryattus* sp., jumping spiders from Queensland. *Behav. Ecol. Sociobiol.*, **26**, 111–119.

Jackson, R. R. & Wilcox, R. S. 1993. Observations in nature of detouring behaviour by *Portia fimbriata*, a web-invading aggressive mimic jumping spider from Queensland. *J. Zool., Lond.*, **230**, 135–139.

Jackson, R. R. & Wilcox, R. S. 1994. Spider flexibly chooses aggressive mimicry signals for different prey by trial and error. *Behaviour*, **127**, 21–36.

Land, M. 1985. The morphology and optics of spider eyes. In: *Neurobiology of Arachnids* (Ed. by F. Barth), pp. 53–78. New York: Springer-Verlag.

Lloyd, J. 1986. Firefly communication and deception: 'oh, what a tangled web'. In: *Deception: Perspectives on Human and Nonhuman Deceit* (Ed. by R. Mitchell & N. Thompson), pp. 113–128. Albany, New York: State University of New York Press.

Mitchell, R. & Thompson, N. 1986. *Deception: Perspectives on Human and Nonhuman Deceit*. Albany, New York: State University of New York Press.

Pietsch, T. & Grobecker, D. 1978. The compleat angler: aggressive mimicry in an antennariid angler fish. *Science*, **201**, 369–370.

Shaller, G. 1972. *The Serengeti Lion*. Chicago: University of Chicago Press.

Tarsitano, M. S. & Jackson, R. R. 1994. Jumping spiders make predatory detours requiring movement away from prey. *Behaviour*, **131**, 65–73.

Vollrath, F. 1979. Behaviour of the kleptoparasitic spider *Argyrodes elevatus* (Araneae, Theridiidae). *Anim. Behav.*, **27**, 515–521.

Wickler, W. 1968. *Mimicry*. New York: McGraw-Hill.

Wilcox, R. S. & Kashinsky, W. 1980. A computerized method of analysing and playing back vibratory signals. *Behav. Meth. Instrumn*, **12**, 361–363.