

# BEHAVIOURAL AND COGNITIVE INFLUENCES OF KAIROMONES ON AN ARANEOPHAGIC JUMPING SPIDER

by

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## Summary

In laboratory experiments, *Portia fimbriata*, an araneophagic salticid from Queensland, was influenced by olfactory and contact-chemical cues from *Jacksonoides queenslandicus*, an abundant salticid on which *P. fimbriata* preys. Four distinct effects were revealed: *P. fimbriata* (1) moved into and remained in the vicinity of *J. queenslandicus*, (2) performed undirected leaping, behaviour known to function as speculative hunting by inducing a turning response from not-yet-seen *J. queenslandicus*, (3) adopted a posture (retracted palps) known to be routine when stalking salticids and (4) showed enhanced attention to optical cues from *J. queenslandicus*. Laboratory experiments provided no statistical evidence that chemical cues from other prey species affected *P. fimbriata*, that *J. queenslandicus* was affected by chemical cues from *P. fimbriata* or that allopatric *Portia* were sensitive to chemical cues from *J. queenslandicus*.

**Keywords:** spiders, Salticidae, predation, kairomones, attentional priming.

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## Introduction

Routine encounters with dangerous prey may favour the evolution of exceptionally intricate predatory strategies (Forbes, 1989). Here we examine chemoreception-based predatory decisions in *Portia fimbriata*, an unusual jumping spider (Salticidae). Small, soft-bodied and more or less harmless insects dominate the diet of most salticids (Jackson and Pollard, 1996), a group with unique complex eyes and acute vision (Land, 1969a, b; Blest *et al.*, 1990; Harland *et al.*, 1999). However, *Portia* is exceptional, because the species in this largely tropical genus are versatile predators (Jackson, 1992) with a preference for an exceptionally dangerous type of prey, other spiders (Li *et al.*, 1997). Besides hunting away from webs, these araneophagic salticids also make predatory raids into other spiders' webs where they eat ensnared insects, the resident spider's eggs and the resident spider. Spiders in alien webs are not simply stalked or chased down, but instead deceived and manipulated by aggressive-mimicry signals before being attacked (Jackson & Wilcox, 1998; Wilcox & Jackson, 1998). Besides preying frequently on web-building spiders, the Queensland *P. fimbriata* (Doleschall) prefers salticids to other spiders as prey (Li & Jackson, 1996) and captures salticids in sequences based on cryptic stalking, a predatory tactic used exclusively against cursorial salticids (Jackson & Blest, 1982): approaches very slowly; holds palps beside the chelicerae ('retracted-palps posture'), thereby obscuring the palps' outlines; freezes whenever faced by the salticid being stalked (Jackson & Blest, 1982).

Although many salticid species are present in the rain-forest habitat of the Queensland of *P. fimbriata*, *Jacksonoides queenslandicus* Wanless appears to be by far the most abundant salticid on tree trunks, boulders and rock walls where *P. fimbriata* hunts (Jackson, 1988). *J. queenslandicus* rarely defends itself when cryptically stalked by the Queensland *P. fimbriata*, but often flees or attacks when tested in the laboratory with allopatric *Portia* which do not adopt cryptic stalking (Jackson & Hallas, 1986).

In encounters between *P. fimbriata* and *J. queenslandicus*, being the first spider to detect the other's presence might be especially advantageous. Our working hypothesis is that kairomones are critical in this predator-prey system, kairomones being chemicals that provoke responses beneficial to the receiver but not the sender of the signal, where the sender and receiver belong to different species (Brown *et al.*, 1971). The early warning provided by

detecting chemical cues from *P. fimbriata* might give *J. queenslandicus* time to flee or take other precautions against attack by *P. fimbriata*. Conversely, preparation by *P. fimbriata* for encounters with an unseen *J. queenslandicus* might lessen the likelihood of *J. queenslandicus* escaping. Safety may also be a factor for *P. fimbriata* because *J. queenslandicus* preys not only on insects but also on spiders (Jackson, 1988). Whether *P. fimbriata* becomes *J. queenslandicus*' prey, instead of *vice versa*, may depend on which spider sees the other first.

While walking about in the environment, salticids routinely lay down silk draglines (Foelix, 1996). Many spiders rely on dragline-associated and olfactory pheromones in the context of courtship and mating (Kaston, 1936; Millot, 1945; Robinson, 1982; Tietjen & Rovner, 1982; Pollard *et al.*, 1987; Schulz & Toft, 1993; Trabalon *et al.*, 1997; Papke *et al.*, 2001), including salticids (Jackson, 1987; Clark & Jackson, 1994, 1995; Taylor, 1998), but less is known about how chemical cues might influence the predatory behaviour of spiders (see Blanke, 1972; Persons & Uetz, 1996; Persons & Rypstra, 2000). Here we investigate whether *J. queenslandicus* avoids regions where there are draglines from *P. fimbriata* and whether draglines from *J. queenslandicus* encourage *P. fimbriata* to spend time in regions recently occupied by *J. queenslandicus*, and to adopt the posture (retracted palps) and behaviour (undirected leaping) known to facilitate prey capture by *P. fimbriata* (Clark & Jackson, 2000a). We also examine whether dragline-associated and olfactory cues heighten *P. fimbriata*'s attention to optical cues from prey.

Opportunities arise for *P. fimbriata* to encounter *J. queenslandicus* in or near webs (Clark & Jackson, 2000b). *J. queenslandicus* neither builds webs nor practises aggressive mimicry, but does enter the webs of other spiders where dead leaves and other detritus are often adopted as nest sites (Jackson, 1988). *J. queenslandicus* also practises araneophagy, either by leaping from outside onto spiders in webs or by walking into webs and chasing down the resident spider. Here we investigate how chemical cues influence web-based encounters of *P. fimbriata* with *J. queenslandicus*.

By testing *P. fimbriata* with prey other than *J. queenslandicus*, we examine whether *P. fimbriata*'s predatory responses to *J. queenslandicus* are specific to this particular prey species or generalised responses to a wide range of prey. By testing allopatric *Portia* (*P. fimbriata* from the Northern Territory of Australia, *P. fimbriata* from Sri Lanka, *P. africana* from Kenya, *P. labiata*

from the Philippines and *P. labiata* Sri Lanka), we clarify whether the Queensland *P. fimbriata*'s reliance on chemical cues from *J. queenslandicus* is a local adaptation by *P. fimbriata* to this particular prey.

## Materials and methods

Standard procedures for spider maintenance were adopted in a controlled-environment laboratory, as detailed elsewhere (Jackson & Hallas, 1986). All testing was between 0830 and 1100 hours (laboratory photoperiod, 12L:12D; lights on at 0800 hrs), this having been determined in earlier studies (Tarsitano & Jackson, 1997) to be the optimal time for testing. All individuals of *Portia* and *Jacksonoides* used in experiments were derived from laboratory rearing to second or third generation. The laboratory-rearing environment was 'enriched' (spacious cages, a frame of twigs inside each cage) in a manner comparable to that described by Carducci & Jakob (2000). Maintenance diet for *Portia* consisted of a variety of spider and insect species, as this diet has been shown to be optimal for growth and survival (Li & Jackson, 1997). Maintenance diet did not, however, include *J. queenslandicus*.

Because choice-test procedures were in basic respects as described elsewhere (Clark & Jackson, 1994, 1995), minimal detail is provided here. All spiders used (Table 1) were adult females (3-10 mm in body length) and no individual spider was tested in more than one experiment or provided data more than once per experiment. No individual spider provided draglines or odour more than once, and no individual spider was used as a lure more than once. All spiders were fed to satiation 5 days before testing, before being used for making a lure or before being used as a source spider (see below).

Unless stated otherwise, '*P. fimbriata*' always refers to the Queensland population. All spiders used were adult females unless stated otherwise. When data were skewed or of unequal variance, non-parametric statistics were used (Sokal & Rohlf, 1995). Acceptance levels for multiple comparisons were adjusted using Bonferroni corrections (Rice, 1989).

## Dragline-discrimination tests

### Methods

For all tests, there was a test spider and a source spider. The source spider provided draglines. *J. queenslandicus* was tested with draglines of the Queensland *P. fimbriata*. The Queensland *P. fimbriata* was tested with the draglines of *J. queenslandicus* and with the draglines of other spiders. *Portia africana*, *P. labiata*, the Sri Lanka *P. fimbriata* and the Northern Territory *P. fimbriata* were tested with the draglines of *J. queenslandicus*.

To collect draglines, a source spider (adult female or juvenile one moult from maturity for *J. queenslandicus*; adult female for all others) was placed in a clean petri dish (diameter 90 mm) in which there were two circular pieces of blotting paper (diameter 90 mm), one taped to the inside top (ceiling) and one taped to the inside bottom (floor) of the dish. Each spider was left in the petri dish for 2 h, during which time it was seen to walk about and leave draglines on the paper. After dragline collection, the two circles of blotting paper from the source spider's cage were cut in half.

TABLE 1. *Spider species used in experiments*

Species	Family	Origin
<i>Portia fimbriata</i> (Doleschal)	Salticidae	Australia (Queensland & Northern Territory), Sri Lanka
<i>Portia africana</i> (Simon)	Salticidae	Kenya
<i>Portia labiata</i> (Thorell)	Salticidae	Philippines, Sri Lanka
<i>Jacksonoides queenslandicus</i> Wanless	Salticidae	Queensland
<i>Bavia aericeps</i> Simon	Salticidae	Queensland
<i>Cosmophasis micarioides</i> (L. Koch)	Salticidae	Queensland
<i>Cytaea</i> sp.	Salticidae	Queensland
<i>Euophrys parvula</i> Bryant	Salticidae	New Zealand
<i>Euryattus</i> sp.	Salticidae	Queensland
<i>Helpis minitabunda</i> (L. Koch)	Salticidae	Queensland
<i>Marpissa marina</i> Goyen	Salticidae	New Zealand
<i>Mopsus mormon</i> Karsch	Salticidae	Queensland
<i>Myrmarachne lupata</i> L. Koch	Salticidae	Queensland
<i>Plexippus paykulli</i> (Savigny & Audouin)	Salticidae	Queensland
<i>Tauala lepidus</i> Wanless	Salticidae	Queensland
<i>Trite auricoma</i> Urquhart	Salticidae	New Zealand
<i>Trite planiceps</i> Urquhart	Salticidae	New Zealand
<i>Zenodorus orbiculatus</i> (Keyserling)	Salticidae	Queensland
<i>Hygropoda dolomedes</i> Simon	Pisauridae	Queensland
<i>Achaearana krausi</i> Chrysanthus	Theridiidae	Queensland

All Queensland species sympatric with *Portia fimbriata*.

Another petri dish of the same size was used as a test chamber (Fig. 1). A half piece of clean blotting paper was taped to one side of the test chamber's ceiling, and another half piece of clean blotting paper was aligned with the top piece and taped to the floor directly below ('control side'). Dragline-covered pieces of blotting paper were then taped to the ceiling and floor of the other half of the petri dish ('experimental side'). A triangle (each side 15-mm long), cut out of the paper, straddled the control and experimental side ('neutral area'). A horseshoe-shaped metal divider straddled the neutral area, making it impossible for the test spider to see immediately that there was no source spider in the petri dish (see Clark & Jackson, 1994).

The test spider was introduced into the neutral area. Once it walked onto one of the pieces of blotting paper, it was observed for the following 10 min. To ascertain whether chemical cues rather than other properties (e.g. tactile) of *J. queenslandicus*' silk were responsible for the Queensland *P. fimbriata*'s reactions, testing was repeated using *J. queenslandicus* draglines treated in one of two ways (washed in 80% ethanol or aged for 1 week). These two treatments for inactivating chemical cues have been used successfully in earlier studies on salticid pheromones (Jackson, 1987).

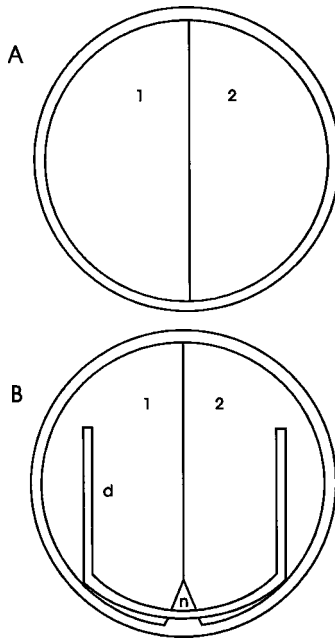


Fig. 1. Chamber made from a petri dish (diameter 90 mm). Used for dragline-discrimination tests. A: Top of dish. B: Bottom of dish. 1. Blotting paper covered by draglines of one source spider. 2. Blotting paper covered by draglines of different source spider. N: Neutral area (space with no draglines present). d: Metal divider that prevents test spider from seeing entire test chamber at start of test.

### Results and discussion

The Queensland *P. fimbriata* spent more time on the experimental than on the control side when tested with fresh draglines of *J. queenslandicus* ( $p < 0.01$ , Wilcoxon test for paired comparisons, Fig. 2A-B). The time spent on the two sides of the chamber did not differ significantly when the Queensland *P. fimbriata* was tested with draglines from any other species (Fig. 2E-T), or when allopatric *Portia* were tested with draglines from *J. queenslandicus* (Fig. 3) or when *J. queenslandicus* was tested with draglines from the Queensland *P. fimbriata* (Fig. 4). Dragline-associated cues appear to be chemical: when the dragline tests were repeated after washing silk in ethanol or ageing silk for one week, *P. fimbriata*'s reaction to blotting paper coated with silk of *J. queenslandicus* and clean blotting paper were not significantly different (Fig. 2C-D).

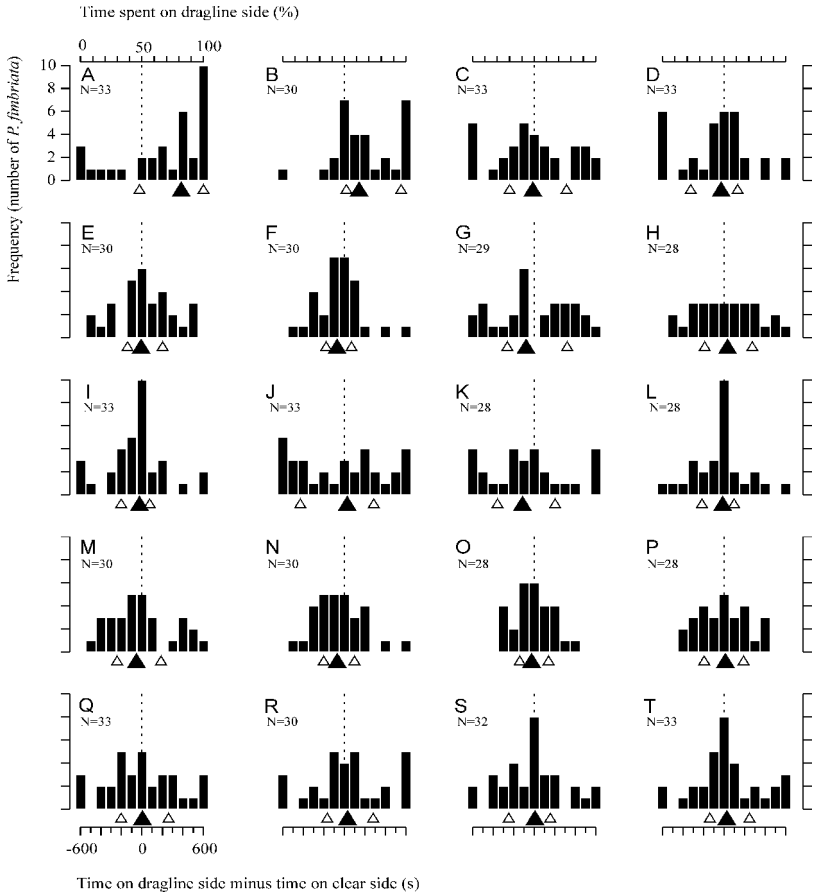


Fig. 2. Difference scores from testing the Queensland *Portia fimbriata* in dragline-choice experiment. Score defined as time *P. fimbriata* spent on dragline-covered blotting paper (untreated draglines unless stated otherwise) minus time *P. fimbriata* spent on clean blotting paper. Filled and unfilled triangles indicate medians and quartiles, respectively. Except where stated otherwise, all source spiders were salticids and all were adult females. (A) Adult *Jacksonoides queenslandicus* females. (B) *J. queenslandicus* juveniles. (C) Adult *J. queenslandicus* females (draglines aged 2 weeks). (D) Adult *J. queenslandicus* females (draglines washed in ethanol). (E) Adult *Achaeranea krausi* females (web-building theridiid spiders). (F) Adult *Hygropoda dolomedes* females (web-building pisaurid spiders). (G) *Bavia aericeps*. (H) *Cosmophasis micarioides*. (I) *Cytaea* sp. (J) *Euophrys parvula*. (K) *Euryattus* sp. (L) *Helpis minitabunda*. (M) *Marpissa marina*. (N) *Mopsus mormon*. (O) *Myrmarachne lupata*. (P) *Plexippus paykulli*. (Q) *Tauala lepidus*. (R) *Trite auricoma*. (S) *T. planiceps*. (T) *Zenodorus orbiculatus*. *P. fimbriata* spent significantly more time on untreated draglines from *J. queenslandicus* (a, b) than on clean blotting paper. For all other source-spider species and all other treatments, difference scores were not significantly different from zero.

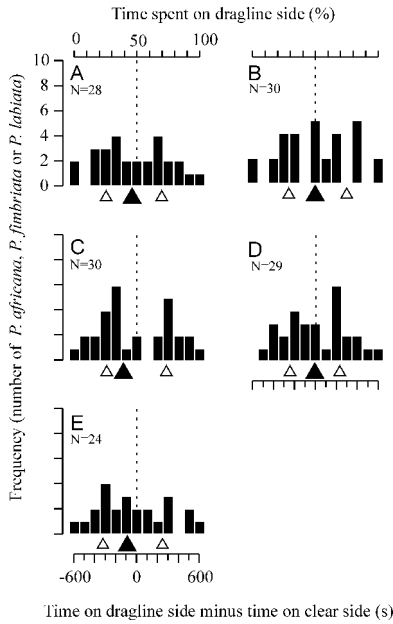


Fig. 3. Difference scores (see Fig. 2) from testing (a) *Portia fimbriata* from the Northern Territory, (b) *P. fimbriata* from Sri Lanka, (c) *P. africana* from Kenya, (d) *P. labiata* from Sri Lanka and (e) *P. labiata* from the Philippines in dragline-choice experiment. Filled and unfilled triangles indicate medians and quartiles, respectively. Difference scores were not significantly different from zero for any test-spider category.

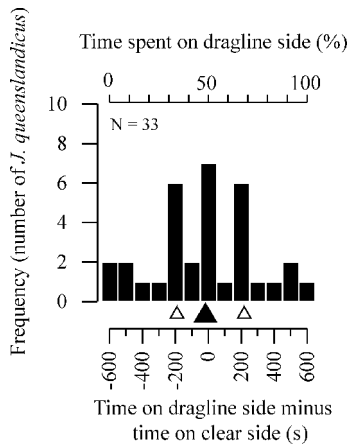


Fig. 4. Difference scores (see Fig. 2) from testing *Jacksonoides queenslandicus* in dragline-choice experiment. Filled and unfilled triangles indicate median and quartiles, respectively. Difference scores not significantly different from zero.

In the confined space of the simple chamber we used, no postural changes or undirected leaping by the Queensland *P. fimbriata* were evident. Postural changes might have been expected, but the absence of undirected leaping appears easy to explain. When making undirected leaps, *P. fimbriata* suddenly propels itself more or less directly upward, with no target being evident. These leaps elicit turning responses from *J. queenslandicus*, these turns giving *J. queenslandicus*' location away to *P. fimbriata* (Clark & Jackson, 2000a). In the confinement of a petri dish, there was no space for making these leaps.

## Effects of draglines on behaviour and posture

### Methods

We evaluated whether, in a more natural environment, the retracted-palps posture and undirected leaping would be elicited by chemical cues from *J. queenslandicus*. By repeating these tests with draglines from another sympatric salticid, *Tauala lepidus*, we investigated whether it is cues from specifically *J. queenslandicus* that influence the Queensland *P. fimbriata*.

The test chamber was a cage (length 211 mm, width 144 mm, height 44 mm) made from transparent Perspex. The cage was cleaned with distilled water and 80% ethanol after each test. Dry twigs and leaves ('vegetation') were evenly spaced over the bottom surface of the cage, covering *ca* 30% of the area. New vegetation was provided for each test. The vegetation was collected in New Zealand gardens and had never been in contact with any of the spider species used in this experiment. Before use, all vegetation was microwaved (900 W) for 10 min and then held in the container (kept closed) for a waiting period of 20-30 days. This procedure ensured that there were no small arthropods active on the vegetation during testing.

Before starting experimental tests, a source spider (*J. queenslandicus* or a closely related salticid, *Tauala lepidus*) was left for 2 h in the cage, during which time it walked about, actively laying down draglines on all surfaces of the cage and on the vegetation. After the 2-h period, the source spider was removed and the test spider (*P. fimbriata*) was introduced. A test spider was taken into a plastic tube (65 mm long; internal diameter 11 mm) beforehand, and one end of the tube was connected to a hole in the base of the cage. The other end was kept closed. Testing began when the test spider, on its own accord, walked out of the tube and into the test chamber. Whenever a test spider failed to enter the test chamber within 5 min, the test was aborted.

Each test lasted for 15 min, during which time the test spider's behaviour and posture were recorded. Each test spider was used twice: experimental test on one day and control test on the preceding or the succeeding day (decided at random). No source spider had occupied the control test chamber during the pre-test interval (*i.e.* no draglines were present). Otherwise, control tests were identical to experimental tests. There were 41 test pairs for each species of source spider.

### *Results and discussion*

Test spiders never retracted their palps (*i.e.* they never adopted the palp posture that characterizes how *P. fimbriata* typically stalks salticids) and never made undirected leaps in experimental tests where *T. lepidus* was the source spider nor in any of the control tests. However, 13 test spiders retracted their palps (McNemar test for significance of changes,  $\chi^2 = 13.00$ ,  $p < 0.001$ ) and 15 made undirected leaps ( $\chi^2 = 15.00$ ,  $p < 0.001$ ) in experimental tests where *J. queenslandicus* was the source spider. All individuals that retracted their palps also made undirected leaps.

Retraction of *P. fimbriata*'s palps is routine when pursuing *J. queenslandicus* and is readily triggered by optical cues alone (Harland & Jackson, 2000, 2001). Finding that *P. fimbriata* often retracted its palps when *J. queenslandicus* draglines are present, despite no optical cues from *J. queenslandicus* being present, suggests that contact chemical cues enable *P. fimbriata* to prepare for an encounter with this prey species before sighting it.

### **Effect of draglines on attention to optical cues**

#### *Methods*

In the previous experiments, where we considered how *P. fimbriata* responded to substrates over which *J. queenslandicus* had walked, there were no optical cues from prey in the test arena. Next we investigated whether draglines from prey influence how quickly *P. fimbriata* reacts to optical cues from motionless lures.

Lures were presented on a test ramp (Fig. 5) comparable to that used in numerous earlier studies where fuller details can be found (see Li & Jackson, 1996). The lure sat at the top of the ramp and was surrounded by four evenly spaced corks. In preliminary trials, without the corks, *P. fimbriata* reacted quickly to the lure in both the experimental and the control tests, making dragline effects difficult to discern. The rationale for having the corks was to slow *P. fimbriata* down by making the lure less conspicuous.

Four spider species were used for making lures (body length always 10 mm) and the same four species were also used as dragline sources. Spiders used for lures were first immobilised under carbon dioxide, then preserved in 80% ethanol. A lure was made by removing the spider, letting it dry, then mounting it in a lifelike posture centred on a disc-shaped piece of cork (diameter *ca*  $1.25 \times$  spider's body length). The mounted dead spider and the cork were coated with plastic aerosol (Crystal Clear Lacquer, Atsco Australia Pty) for preservation and to mask chemical traces that might have remained on the dead spider.

During testing, a strip of white blotting paper was placed on top of the ramp. There were draglines from a source spider on the paper during experimental tests, but no draglines were present during control tests. There were four controls, the lure being made from a different one of the four spider species in each control. There were four experimental tests in which

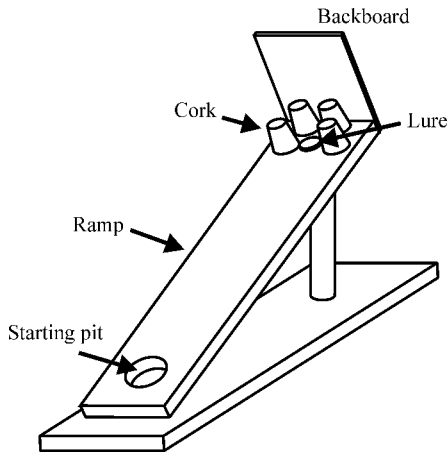


Fig. 5. Apparatus for testing how draglines affect the Queensland *Portia fimbriata*'s attention to optical cues from lures. Wooden ramp (320 mm long, 70 mm wide) inclined at  $20^\circ$  from horizontal and supported by two wooden poles (diameter 20 mm) placed at 75 mm (shown) and 150 mm (not shown), respectively, from the far end of the base. Poles slotted into holes in 100-mm wide wooden base. Pit (diameter 30 mm) centred 50 mm from bottom end of ramp (used for holding test spider before testing). Screen (80 mm high, 70 mm wide) glued to top of ramp (served as a background against which *Portia fimbriata* viewed lure). Lure placement: centred on ramp 40 mm from base of screen. Four corks positioned in semicircle around lure. Diameter of each cork at base: 13 mm. Distance between the lure and each cork: 12 mm. Distance between neighbouring corks: 9 mm. Lure faced  $45^\circ$  away from pit. Ramp and base 17 mm thick. Ramp, base, screen and poles made of custom-wood (two coats of water-resistant polyurethane). White blotting paper (not shown) covered ramp from 50 mm above the upper edge of the pit to 15 mm below front edge of lure. Lure present during control tests (paper clean) and during experimental tests (draglines on paper).

the lure and source spiders were the same species. In another three experimental tests, a *J. queenslandicus* lure was used in conjunction with different species as source spiders. In yet another three experimental tests, the source spider was *J. queenslandicus*, but the lures were made from different species.

Before testing began, the test spider (*P. fimbriata*) was placed in a pit at the base of the ramp. The paper on the ramp was positioned so that its bottom edge was 50 mm from the top edge of the pit and its top edge was 15 mm from the lure at the top of the ramp. The pit was kept covered with a clear plastic petri dish until the test spider became quiescent. The pit was uncovered to start a test. Tests were aborted whenever test spiders failed to leave the pit within 30 min or left the pit and then moved off the top of the ramp before reaching the blotting paper. Spiders from aborted tests were not tested again.

A 200 W incandescent lamp, positioned *ca* 600 mm over head, lit the entire apparatus. Fluorescent ceiling lamps provided additional ambient lighting. A white cardboard screen surrounded the apparatus on three sides, the open side being for the observer. The ramp was positioned so that during the test the salticid moved away from the open side and the observer. Between tests, the used blotting paper was discarded. The apparatus was then wiped off with

80% ethanol and distilled water and then allowed to dry for at least 30 min, after which new blotting paper was positioned on the ramp.

Test spiders usually walked up the ramp, thereby getting closer to the lure. They never began stalking lures before moving at least 50 mm up the ramp (*i.e.* they were always on to the paper when they began stalking the lure). We recorded whether the test spider began stalking (defined as maintaining orientation toward the lure while walking more or less directly toward it) within 60 min after beginning the test. Once a test spider began stalking, observation continued until it stopped stalking, got close (defined as when the spider moved to within 15 mm of the lure; *i.e.* when it moved off the paper at end of the ramp that was closest to the lure) or 60 min had elapsed since stalking began, whichever came first.

We also recorded starting latency (defined as time elapsing between when the spider stepped onto the paper and when it began stalking the lure) and getting-close latency (defined as time elapsing from when the spider stepped onto the paper until it got to within 15 mm of the lure). When calculating starting latency, we excluded any test spiders that failed to begin stalking. Likewise, any test spiders that failed to get close were excluded when calculating getting-close latency. Latency data were compared using one-way ANOVA and frequency data were compared using tests of independence.

## Results and discussion

When incidence of starting to stalk, incidence of getting close, starting latency and getting-close latency were considered, data from all of the controls (*i.e.* tests with no draglines present) were comparable (*i.e.* not significantly different):  $3 \times 2$  tests of independence (incidence of starting to stalk,  $\chi^2 = 0.35$ ,  $p = 0.84$ ; incidence of getting close,  $\chi^2 = 1.43$ ,  $p = 0.49$ ;  $df = 2$  for both); ANOVA (latency to start stalking,  $F = 2.99$ ,  $p = 0.055$ ; latency to get close,  $F = 0.03$ ,  $p = 0.960$ ). However, with the exception of latency to get close, pooled data from control tests where salticid lures were used differed from data from control tests where *Hygropoda dolomedes* lures were used (Fig. 6): frequencies of starting to stalk and of getting close were less in tests where *H. dolomedes* lures were used and latency to start stalking was shorter in tests where salticid lures were used.

Our experiments suggest that contact chemical cues heightened *P. fimbriata*'s ability to detect location-revealing optical cues from *J. queenslandicus*. Evidence came from *P. fimbriata* having a stronger inclination, and shorter latency, to start stalking and to get close when in the presence of *J. queenslandicus* contact chemicals. 'Enhanced reaction' will be used as a collective term for whenever any of these attention effects were significant.

First we compare, for each type of lure (*i.e.* each prey species), control tests (no draglines present) with experimental tests where the same species

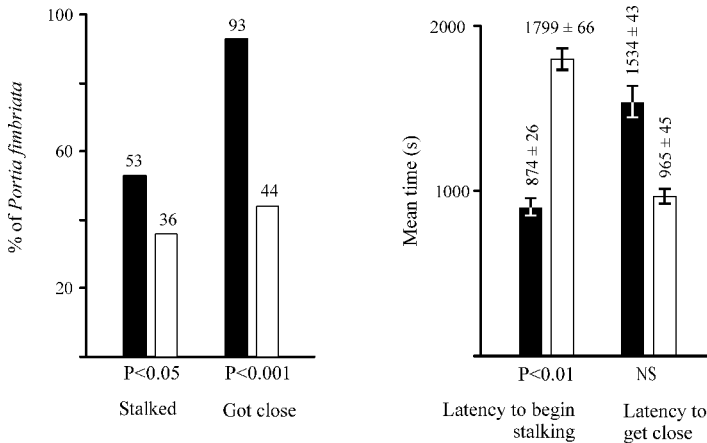


Fig. 6. Data from control tests (no draglines present) in experiment on how draglines affect the Queensland *Portia fimbriata*'s attention to optical cues from lures. Black bars: data for *Portia fimbriata* stalking salticid lures in control tests. Data for the three salticid lures (*Jacksonoides queenslandicus*, *Tauala lepidus* and *Zenodorus orbiculatus*) not significantly different (only pooled data displayed). White bars: data for *Portia fimbriata* stalking lure made from a web-building spider, *Hygropoda dolomedes*, in control tests. Left: percentage of *P. fimbriata* that stalked ('stalking tendency') and, of those that stalked, percentage that got close. Right: mean latency for *P. fimbriata* to begin stalking and, of those that stalked, mean latency to get close. Bars: standard error of the mean. For N, see Fig. 7. Significant differences were found for all comparisons except latency to get close.

was used as the lure and the dragline source. The only enhanced reactions that were evident came from testing *P. fimbriata* with *J. queenslandicus* (Fig. 7).

Additional testing suggested that it was specifically the draglines of *J. queenslandicus*, and not the draglines of some wider group of spiders, that heightened *P. fimbriata*'s attention to optical cues from *J. queenslandicus*. That is, *Portia fimbriata*'s reactions when on draglines from *J. queenslandicus* were enhanced compared with when on draglines from any of the other three prey species used (Fig. 8).

Other testing showed that it was the optical cues specifically from *J. queenslandicus* to which *P. fimbriata* attended more strongly when in the presence of *J. queenslandicus*' draglines. That is, we ruled out an alternative hypothesis: that *J. queenslandicus* draglines elicited enhanced attention more or less equally to optical cues from some wider array of prey such as spiders or salticids in general. Although *J. queenslandicus* draglines enhanced (relative to controls) reaction to optical cues from all four prey species tested

(bottom of Fig. 8), reaction to *J. queenslandicus* lures was also enhanced relative to the other three types of lures (top of Fig. 8).

In most instances, *J. queenslandicus* draglines seemed to facilitate how quickly lures got *P. fimbriata*'s attention (*i.e.* enhanced reaction was a consequence of higher incidence of starting to stalk or shorter starting latency, or both). When testing with *H. dolomedes* lures, facilitated gaining of attention was not evident. Instead, *P. fimbriata* got close to *H. dolomedes* lures in the presence of *J. queenslandicus* draglines more often than in controls (Fig. 8), suggesting that *J. queenslandicus* draglines were good at keeping *P. fimbriata*'s attention once stalking of *H. dolomedes* had begun.

The methods used in the control tests were similar to prey-choice testing methods in numerous earlier salticid studies (*e.g.* Li & Jackson, 1996; Li *et al.*, 1997) except that the controls in the present study can be envisaged as staging a stronger challenge to *P. fimbriata*'s visual system. In the earlier studies, because the background was simpler (no corks surrounding the lure), it may have been easier for *P. fimbriata* to see the lures. Despite this difference, comparing data from the different control tests (no draglines present) corroborates conclusions from earlier studies (Li & Jackson, 1996) by showing that the Queensland *P. fimbriata* prefers salticids to other spiders as prey and that optical cues alone, in the absence of prey movement, enable *P. fimbriata* to distinguish salticids from other prey (Harland & Jackson, 2000).

## Olfactometer tests

### Methods

A Y-shaped olfactometer (Fig. 9) with airflow adjusted to 1500 ml/min (Matheson FM-1000 flowmeter) was used to assess *P. fimbriata*'s response to airborne prey odours. At the airflow setting used, there was no evidence of impaired locomotion or any other adverse effects on *P. fimbriata*'s behaviour. Air was pushed by a pump from a tap through two separate flowmeters into two chambers, a stimulus chamber which contained a spider used as an odour source and control chamber which was empty. For each test, whether the stimulus chamber was on the left or right side of the olfactometer was decided at random. Air moved from the stimulus chamber to the stimulus arm, and independently from the control chamber to the control arm. Collectively, the two are referred to as the 'choice arms'. Air moved from the two choice arms into the 'test arm' (*i.e.* the stem of the Y). There was a test spider in a holding chamber at the far end of the test arm. The spider used for an odour source was placed in the stimulus chamber 30 min before each test. This 30-min period allowed air to circulate evenly and ensured that air pressure was comparable throughout the olfactometer. A removable metal

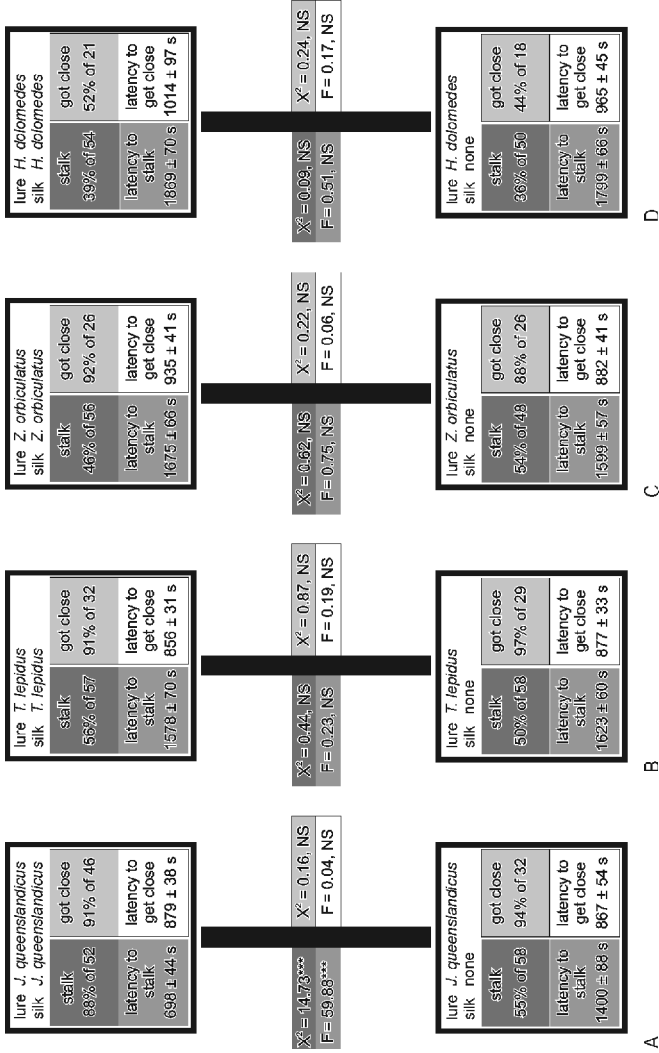


Fig. 7. Data from testing how draglines affect the Queensland *Portia fimbriata*'s attention to optical cues from lures. Control and experimental tests where lure and draglines were from the same species: (a) *Jacksonoides queenslandicus*; (b) *Tanala lepidus*; (c) *Zenodorus orbiculatus*; (d) *Hygroploda dolomedes*. Boxes represent results from one test condition (lure type and dragline type at top). Comparison line: thick black line between boxes. Statistical metrics (chi-square tests of independence and ANOVA) at midpoint of comparison line are shade coded to match the shading in the test condition boxes: dark grey, percentage that stalked; intermediate grey, latency to begin stalking; light grey, percentage that got close; white, latency to get close). Latencies are to nearest second. Standard error of the mean is given. \*\*\* $p < 0.001$ .

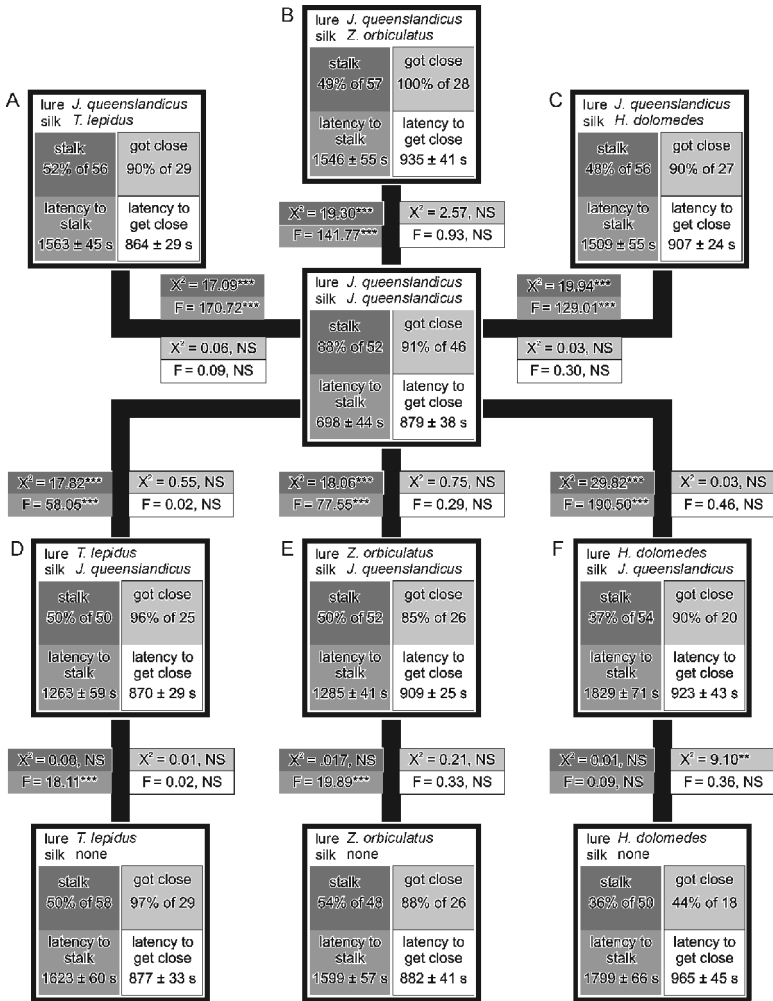


Fig. 8. Data from testing how draglines affect the Queensland *Portia fimbriata*'s attention to optical cues from lures. Test conditions: lure from one species and draglines from another species (a, b and c: *J. queenslandicus* lure, but draglines from *Taula lepidus*, *Zenodorus orbiculatus* and *Hygropoda dolomedes*, respectively; d, e and f: draglines from *J. queenslandicus*, but lures from *T. lepidus*, *Z. orbiculatus* and *H. dolomedes*, respectively). Other test conditions provided for comparison (see Fig. 7). Boxes represent results from one test condition (lure type and dragline type at top). Comparison line: thick black line between boxes. Statistical metrics (chi-square tests of independence and ANOVA) at midpoint of comparison line are shade coded to match shading in the test condition boxes: dark grey, percentage that stalked; intermediate grey, latency to begin stalking; light grey, percentage that got close; white, latency to get close. Latencies are to nearest second. Standard error of the mean is given. \*\* $p < 0.01$ . \*\*\* $p < 0.001$ .

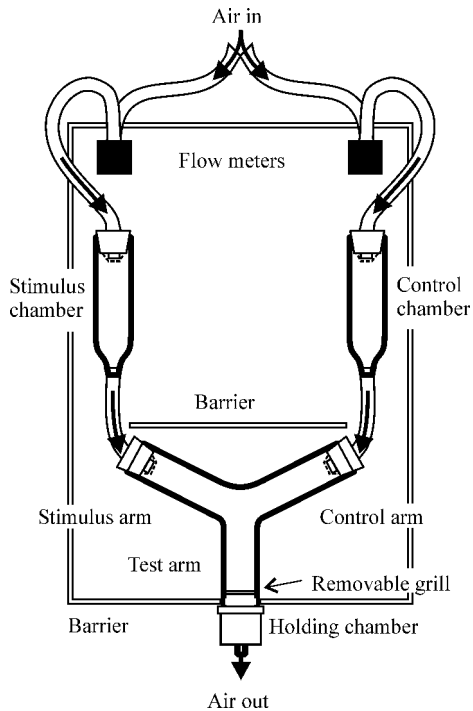


Fig. 9. Olfactometer. Arrows indicate direction of airflow. Stimulus chamber contains source spider. Control chamber empty. Dimensions of stimulus chamber and of control chamber: length 115 mm, internal diameter 25 mm. Holding chamber (location of test spider at start of test): length 40 mm, internal diameter 20 mm. Start of test: test spider released from holding chamber (grill removed), giving it access to the test arm, control arm and stimulus arm. Dimensions of test arm, control arm and stimulus arm: length 90 mm, internal diameter 20 mm. Opaque barriers prevent test spider from seeing source spider and minimise disturbances to test spider caused by movement outside the test apparatus. Diagram not to scale.

grill fit into a slit in the chamber roof, blocking access between the test arm and the holding chamber. The grill was lifted to start a test.

Spiders usually walked about actively in the olfactometer. After leaving the holding chamber, the spider was allowed 1 h to make a choice (definition: entered a choice arm and remained there for 30 s). We recorded the test spider's latency to choose and the arm it chose. As a precaution against the potential effects of traces left by spiders that had been tested previously, the olfactometer was dismantled and cleaned with 80% ethanol and then with distilled water between tests.

*Results and discussion*

When *J. queenslandicus* was the odour source, the Queensland *P. fimbriata* chose the stimulus arm more often than the control arm (26 chose the stimulus arm, 4 chose the control arm; binomial test of independence,  $p < 0.001$ ). When other spider species were used as odour sources, how often the Queensland *P. fimbriata* chose the stimulus arm was not significantly different from how often it chose the control arm. When *J. queenslandicus* was used as the odour source, there was no significant difference in how often allopatric *Portia* chose the stimulus arm instead of the control arm, nor was *J. queenslandicus*' choice influenced by odour from *P. fimbriata* (Table 2).

TABLE 2. *Olfactometer arm chosen by test spider*

Test spider	Source spider	Chose stimulus arm	Chose control arm
Queensland <i>Portia fimbriata</i>	<i>Jacksonoides queenslandicus</i>	26	4
<i>Jacksonoides queenslandicus</i>	Queensland <i>Portia fimbriata</i>	15	15
Northern Territory <i>Portia fimbriata</i>	<i>Jacksonoides queenslandicus</i>	14	14
Sri Lanka <i>Portia fimbriata</i>	<i>Jacksonoides queenslandicus</i>	16	10
Kenya <i>Portia africana</i>	<i>Jacksonoides queenslandicus</i>	15	15
Philippines <i>Portia labiata</i>	<i>Jacksonoides queenslandicus</i>	12	13
Sri Lanka <i>Portia labiata</i>	<i>Jacksonoides queenslandicus</i>	15	15
Queensland <i>Portia fimbriata</i>	<i>Achaearanea krausi</i>	10	20
Queensland <i>Portia fimbriata</i>	<i>Bavia aericeps</i>	15	15
Queensland <i>Portia fimbriata</i>	<i>Cosmophasis micaroides</i>	11	19
Queensland <i>Portia fimbriata</i>	<i>Cytaa</i> sp.	12	18
Queensland <i>Portia fimbriata</i>	<i>Euophrys parvula</i>	17	13
Queensland <i>Portia fimbriata</i>	<i>Euryattus</i> sp.	18	12
Queensland <i>Portia fimbriata</i>	<i>Helpis minitabunda</i>	16	14
Queensland <i>Portia fimbriata</i>	<i>Hygropoda dolomedes</i>	14	16
Queensland <i>Portia fimbriata</i>	<i>Marpissa marina</i>	17	13
Queensland <i>Portia fimbriata</i>	<i>Mopsus mormon</i>	14	15
Queensland <i>Portia fimbriata</i>	<i>Myrmarachne lupata</i>	13	17
Queensland <i>Portia fimbriata</i>	<i>Plexippus paykulli</i>	14	15
Queensland <i>Portia fimbriata</i>	<i>Tauala lepidus</i>	15	14
Queensland <i>Portia fimbriata</i>	<i>Trite auricoma</i>	13	16
Queensland <i>Portia fimbriata</i>	<i>Trite planiceps</i>	16	15
Queensland <i>Portia fimbriata</i>	<i>Zenodorus orbiculatus</i>	16	16

All test and source spiders were adult females. Data analysis: tests of goodness-of-fit (null hypothesis: stimulus and control arm chosen indiscriminately): row 1:  $\chi^2 = 16.133$ ,  $p < 0.001$ ; all other rows, NS.

Although arrestment (detection at close range followed by settling in the region of the stimulus) may account for dragline-mediated effects, attraction (detection from a distance followed by movement to the source) is implied by the findings from the olfactometer tests. The attraction and arrestment effects of kairomones in this salticid-salticid predator-prey system are comparable to the effects of kairomones in some other predator-prey systems (Sabelis & van de Baan, 1983; Sabelis *et al.* 1984; Dicke *et al.*, 1990; Vet & Dicke, 1992; Raffa & Dahlsten, 1995; Teerling *et al.*, 1993; Heimpel & Hough-Goldstein, 1994; Yasuda, 1997; Janssen 1999), as well as in parasitoid-host (Tumlinson *et al.*, 1992) and competitor systems (de Jong & Sabelis, 1988; Poland & Borden, 1994; Janssen *et al.*, 1995a, b, 1997; Pallini *et al.*, 1997).

## Effect of olfactory cues on attention to optical cues

### Methods

Two species of prey, *J. queenslandicus* and a theridiid spider, *Achaearanea krausi* Chrysanthus, were used for making lures and as odour sources. The test chamber was a wooden frame cage (interior dimensions 200 × 200 × 200 mm) with four sliding glass sides. The top and the bottom of the cage were made of wood. Four holes (diameter 13 mm) were spaced in a square (110 × 110 mm) centred on the top of the cage. A glass tube (length 60 mm, diameter 13 mm) was positioned in each hole. A capless glass vial (length 20 mm, width 13 mm) was connected to the distal end of each tube. Wire screening was in place between the open end of the vial and the tube and between the tube and the cage. Each tube had a 90° bend (elbow) at its midline, angled so that the vial was positioned toward the nearest corner of the cage top and out of view from inside the cage.

There was another hole (diameter 13 mm) centred at the bottom of the cage. This hole was kept plugged with a cork until the test began. The cage sat on a wooden frame that permitted easy access to the bottom without lifting the cage.

The test spider (Queensland *P. fimbriata*) was put into the cage 5-7 days prior to testing, during which time it spun a web. No prey were provided and no vials were attached to the tubes during this time. The hole in the bottom of the cage was kept stoppered with a bare cork (*i.e.* there was no lure on the cork: see below). After the waiting period, the four vials were attached to tubes. For experimental tests, one spider (odour source) was placed in each vial. With the spiders in the vials, odour could diffuse into the cage. Each of the four spiders belonged to the same species. In control tests, each vial was empty.

Testing began 60 min later. The cork was removed and a lure (dead spider mounted on a cork, as described earlier) was inserted through the hole in the cage floor. However, testing was aborted if the test spider was out of its web when the 60-min interval elapsed.

'Stalking' and 'getting close' were as defined earlier (see Effect of draglines on attention to optical cues), but an additional response, dropping on draglines, was also relevant to this experiment (after attaching a dragline to the web, *P. fimbriata* dropped toward the lure, making intermittent brief pauses along the way: see Clark & Jackson, 2000b). For *P.*

*fimbriata*, dropping on draglines functions as an alternative to walking to get close to prey (*i.e.* by descending on a dragline, *P. fimbriata* can get close enough to make a sudden downward attack).

Except for the absence of source spiders, controls were the same as experimental tests. Each test spider was used twice: in an experimental test on one day and in a control test on the preceding or succeeding day (decided at random). A separate set of tests was carried out using each of the following four combinations: (1) *J. queenslandicus* as lure and source spider, (2) *A. krausi* as lure and source spider, (3) *J. queenslandicus* as lure and *A. krausi* as source spider, and (4) *A. krausi* as lure and *J. queenslandicus* as source spider.

### *Results and discussion*

*Portia fimbriata* dropped on draglines towards *J. queenslandicus* lures more often when *J. queenslandicus* odour was present than when no odour was present (Table 3), suggesting that *J. queenslandicus*' odour enhances *P. fimbriata*'s ability to detect location-revealing optical cues from *J. queenslandicus*. *P. fimbriata* also got close in more experimental tests when *J. queenslandicus* served as both lure and odour source than in control tests (Table 4). Latency to get close to *J. queenslandicus* lures was significantly shorter when *J. queenslandicus* odour was present than when no odour was present (Fig. 10).

### **Discussion**

The rationale for this study was the idea that being the first to detect the other would be advantageous to both predator and prey, but we found no evidence that the prey, *J. queenslandicus*, is alerted by kairomones from the predator, *P. fimbriata*. How strongly predation by *P. fimbriata* impacts on populations of *J. queenslandicus* in nature is unclear. Although *J. queenslandicus* may be a dominant prey for *P. fimbriata*, *J. queenslandicus* populations are very large (Jackson, 1988). Perhaps predation by *P. fimbriata* has only minor impact on *J. queenslandicus* in nature. Kairomones from *J. queenslandicus*, however, appear to assist *P. fimbriata* in a variety of ways.

In the natural environment where vegetation and the physical features of a complex habitat are likely to obstruct *P. fimbriata*'s line of sight, sensitivity to both olfactory and contact chemical cues may provide complementary advantages. Being volatile plumes subject to rapid dissipation and diffusion in the air (Bossert & Wilson, 1963; Alberts, 1992), olfactory cues may be especially useful at revealing from a distance the presence

TABLE 3. Experiment testing how odours affect the *Queensland Portia fimbriata*'s attention to optical cues from lures

Source spider (odour)	Lure	Dropped on dragline during experimental test only	Dropped on dragline during control test only	Dropped on dragline during both tests	Dropped on dragline during neither test	McNemar test for significance of changes
<i>Jacksonoides queenslandicus</i>	<i>Jacksonoides queenslandicus</i>	18	1	6	55	$\chi^2 = 15.211, p < 0.001$
	<i>Achaearanae krausi</i>	3	2	0	75	
<i>Achaearanae krausi</i>	<i>Achaearanae krausi</i>	3	1	2	74	NS
	<i>Jacksonoides queenslandicus</i>	4	2	6	69	NS

TABLE 4. Experiment testing how odours affect the *Queensland Portia fimbriata* attention to optical cues from lures

Source spider (odour)	Lure	Got close during experimental test only	Got close during control test only	Got close during both tests	Got close during neither test	McNemar test for significance of changes
<i>Jacksonoides queenslandica</i>	<i>Jacksonoides queenslandica</i>	22	3	8	47	$\chi^2 = 14.440, p < 0.001$
	<i>Achaearanae krausi</i>	6	6	8	60	
<i>Achaearanae krausi</i>	<i>Achaearanae krausi</i>	4	3	5	68	NS
	<i>Jacksonoides queenslandicus</i>	7	5	13	55	NS

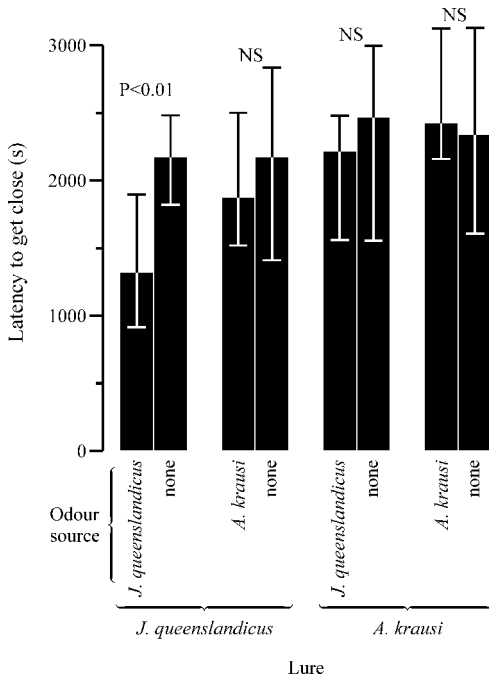


Fig. 10. Data from testing how odours affect the Queensland *Portia fimbriata*'s attention to optical cues from lures. Latency to get close. Bars represent medians (data non-normal) and error bars represent upper and lower quartiles. Data analysis, Mann-Whitney *U*-tests.

and identity of any unseen *J. queenslandicus* that may currently be in the environment. Contact cues, on the other hand, tend to be detectable over only short distances, but they usually remain in the environment for longer than olfactory cues. Rather than revealing the current whereabouts of prey, the importance of contact cues may be related more to informing *P. fimbriata* of the presence of an area that is frequented by *J. queenslandicus*.

We also found that *J. queenslandicus*' draglines and odour affect *P. fimbriata*'s responses to optical cues. These effects appear to be examples of attentional priming (see Roitblat, 1987). However, attentional priming has traditionally been considered in the context of perception of optical cues influencing the processing of subsequent optical input (e.g. Blough, 1989, 1992). What we have shown for *P. fimbriata* is different, this being an instance of specific chemical stimuli priming response to specific optical stimuli. What we have shown is also unusual because the effect on *P. fimbriata* appears to be pre-programmed, whereas traditional examples of

attentional priming are based on the individual's prior experience. A key feature that this example and the more traditional examples of attentional priming, along with the related processes of using search images (Tinbergen, 1960; Bond, 1983; Langley *et al.*, 1996), have in common is that they all suggest a cognitive explanation (*i.e.* the calling up of a representation of an expected, but not seen, prey).

There was no evidence from our experiments that draglines or odour from other species had comparable attraction, arrestment or attention effects on *P. fimbriata*, suggesting that the chemical cues that influence *P. fimbriata* are derived specifically from *J. queenslandicus*. Data on starting latency in the controls of the experiment on how draglines affect attention to optical cues suggest that *P. fimbriata* is also biased to attend more strongly to optical cues from *J. queenslandicus* than to optical cues from other salticids even in the absence of kairomones: latency in controls was less when *P. fimbriata* was tested with *J. queenslandicus* lures than with *Tauala lepidus* or *Zenodorus orbiculatus* lures. However, independent of any attention bias for optical cues from *J. queenslandicus* in the absence of draglines, our findings imply that *J. queenslandicus* draglines heighten *P. fimbriata*'s attention to optical cues from spiders in general, more strongly heighten attention to optical cues from salticids in particular and especially strongly heighten attention to optical cues from *J. queenslandicus*.

The behaviour of five species of *Portia* (*P. africana*, *P. albimana*, *P. fimbriata*, *P. labiata* and *P. schultzi*) from a wide range of African, Asian and Australian habitats has been studied (Jackson & Hallas, 1986), but only the Queensland *P. fimbriata* practises cryptic stalking. Using cryptic stalking, the Queensland *P. fimbriata* is uniquely effective at preying on a wide range of salticid species (Harland & Jackson, 2001). Although it may be tempting to argue that cryptic stalking evolved as a tactic for capturing salticids in general, the highly focussed kairomone system revealed by the present study suggests an alternative hypothesis. Perhaps *J. queenslandicus* has exerted the primary selective pressure responsible for the evolution of cryptic stalking. As a group, cursorial salticids are exceptionally abundant in the Queensland habitat of *P. fimbriata*, but *J. queenslandicus* appears to be by far the most abundant salticid species in this habitat (Jackson, 1988). Perhaps the usefulness of cryptic stalking for capturing salticids other than *J. queenslandicus* is, to a significant degree, incidental.

## References

- Alberts, A.C. (1992). Constraints on the design of chemical communication systems in vertebrates. — *Am. Nat.* 139, p. 62-89.
- Blanke, R. (1972). Untersuchungen zur Ökophysiologie und Ökethologie von *Cyrtophora citricola* Forskål (Araneae, Araneidae) in Andalusien. — *Forma et Functio* 5, p. 125-206.
- Blest, A.D., O'Carroll, D.C. & Carter, M. (1990). Comparative ultrastructure of Layer 1 receptor mosaics in principal eyes of jumping spiders: the evolution of regular arrays of light guides. — *Cell Tissue Res.* 262, p. 445-460.
- Blough, P.M. (1989). Attentional priming and visual search in pigeons. — *J. Exp. Psychol. Anim. Behav. Process* 15, p. 358-365.
- — (1992). Detectability and choice during visual search: joint effects of sequential priming and discriminability. — *Anim. Learn. Behav.* 20, p. 293-300.
- Bond, A.B. (1983). Visual search and selection of natural stimuli in the pigeon: the attentional threshold hypothesis. — *J. Exp. Psychol. Anim. Behav. Process* 9, p. 292-306.
- Bossert, W.H. & Wilson, E.O. (1963). The analysis of olfactory communication among animals. — *J. theor. Biol.* 5, p. 443-469.
- Brown, W.L., Eisner, T. & Whittaker, R.H. (1971). Allomones and kairomones: transpecific chemical messengers. — *BioScience* 20, p. 21-22.
- Carducci, J.P. & Jakob, E.M. (2000). Rearing environment affects behaviour of jumping spiders. — *Anim. Behav.* 59, p. 39-46.
- Clark, R.J. & Jackson, R.R. (1994). Self recognition in a jumping spider: *Portia labiata* females discriminate between their own draglines and those of conspecifics. — *Ethol. Ecol. Evol.* 6, p. 371-375.
- — & — — (1995). Araneophagic jumping spiders discriminate between the draglines of familiar and unfamiliar conspecifics. — *Ethol. Ecol. Evol.* 7, p. 185-190.
- — & — — (2000a) Speculative hunting by an araneophagic salticid spider. — *Behaviour* 137, p. 1601-1612.
- — & — — (2000b). Web use during predatory encounters between *Portia fimbriata*, an araneophagic jumping spider, and its preferred prey, other jumping spiders. — *N.Z. J. Zool.* 27, p. 129-136.
- de Jong, M.C.M. & Sabelis, M.W. (1988). How bark beetles avoid interference with squatters: an ESS for colonization by *Ips typografus*. — *Oikos* 51, p. 88-96.
- Dicke, M., Beek, T.A., Posthumus, M.A., Ben Dom, N., van Bokhoven, H. & de Groot, A.E. (1990). Isolation and identification of volatile kairomone that affects acarine predator-prey interactions. — *J. Chem. Ecol.* 16, p. 381-396.
- Foelix, R.F. (1996). *Biology of spiders*. — Oxford University Press, New York.
- Forbes, L.S. (1989). Prey defense and predatory handling behaviour: the dangerous prey hypothesis. — *Oikos* 55, p. 155-158.
- Harland, D.P. & Jackson, R.R. (2000). Cues by which *Portia fimbriata*, an araneophagic jumping spider, distinguishes jumping spider prey from other prey. — *J. Exp. Biol.* 203, p. 3485-3494.
- — & — — (2001). Prey classification by *Portia fimbriata*, a salticid spider that specializes at preying on other salticids: species that elicit cryptic stalking. — *J. Zool. Lond.* 255, p. 445-460.

- — — & Macnab A.M. (1999). Distances at which jumping spiders (Araneae: Salticidae) distinguish between prey and conspecific rivals. — *J. Zool. Lond.* 247, p. 357-364.
- Heimpel, G.E. & Hough-Goldstein, J.A. (1994). Search tactics and response to cues by predatory stink bugs. — *Entomol. Exp. Appl.* 73, p. 193-197.
- Jackson, R.R. (1987). Comparative study of releaser pheromones associated with the silk of jumping spiders (Araneae, Salticidae). — *N.Z. J. Zool.* 14, p. 1-10.
- — — (1988). The biology of *Jacksonoides queenslandicus*, a jumping spider (Araneae: Salticidae) from Queensland: intraspecific interactions, web-invasion, predators, and prey. — *N.Z. J. Zool.* 15, p. 1-37.
- — — (1992). Eight legged tricksters. — *BioScience* 42, p. 590-598.
- — — & Blest, A.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, p. 255-292.
- — — & Hallas, S.E.A. (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. J. Zool.* 13, p. 423-489.
- — — & Pollard, S.D. (1996). Predatory behavior of jumping spiders. — *Ann. Rev. Ent.* 41, p. 287-308.
- — — & — — — (1997). Jumping spider mating strategies: sex among cannibals in and out of webs. — In: *The evolution of mating systems in insects and arachnids* (J. Choe & B. Crespi, eds). Cambridge University Press, Cambridge, p. 340-350.
- — — & Wilcox, R.S. (1998). Spider-eating spiders. — *Amer. Sci.* 86, p. 350-357.
- Janssen, A. (1999). Plants with spider-mite prey attract more predatory mites than clean plants under greenhouse conditions. — *Entomol. Exp. Appl.* 90, p. 191-198.
- — —, Bruin, J., Jacobs, G., Schraag, R. & Sabelis, M.W. (1997). Predators use volatiles to avoid prey patches with conspecifics. — *J. Anim. Ecol.* 66, p. 223-232.
- — —, van Alphen, J.J. M., Sabelis, M. W. & Bakker, K. (1995a). Odour-mediated avoidance of competition in *Drosophila* parasitoids: the ghost of competition. — *Oikos* 73, p. 356-366.
- — —, — — —, — — — & — — — (1995b). Specificity of odour-mediated avoidance of competition in *Drosophila* parasitoids. — *Behav. Ecol. Sociobiol.* 36, p. 229-235.
- Kaston, B.J. (1936). The senses involved in the courtship of some vagabond spiders. — *Ent. Amer.* 16, p. 97-167.
- Land, M.F. (1969a). Structure of the retinae of the principal eyes of jumping spiders (Salticidae: Dendryphantinae) in relation to visual optics. — *J. Exp. Biol.* 51, p. 443-470.
- — — (1969b). Movements of the retinae of jumping spiders (Salticidae, Dendryphantinae) in response to visual stimuli. — *J. Exp. Biol.* 51, p. 471-493.
- Langley, C.M., Riley, D.A., Bond, A.B. & Goel, N. (1996). Visual search for natural grains in pigeons (*Columba livia*): search images and selective attention. — *J. Exp. Psychol. Anim. Behav. Proc.* 22, p. 139-151.
- Li, D. & Jackson, R.R. (1996). Prey preferences of *Portia fimbriata*, an araneophagic, web-building jumping spider (Araneae: Salticidae) from Queensland. — *J. Insect Behav.* 9, p. 613-642.

- — & — — (1997). Influence of diet on survivorship and growth in *Portia fimbriata*, an araneophagic jumping spider (Araneae: Salticidae). — *Can. J. Zool.* 75, p. 1652-1658.
- —, — — & Barrion, A. (1997). Prey preferences of *Portia labiata*, *P. africana*, and *P. schultzi*, araneophagic jumping spiders (Araneae: Salticidae) from the Philippines, Sri Lanka, Kenya, and Uganda. — *N.Z. J. Zool.* 24, p. 333-349.
- Millot, J. (1945). Sens chimiques et sens visuel chez les araignées. — *L'Année Biologique* 22, p. 1-21.
- Papke, M.D., Reichert, S.E. & Schulz, S. (2001). An airborne female pheromone associated with male attraction and courtship in a desert spider. — *Anim. Behav.* 61, p. 877-886.
- Pallini, A., Janssen, A. & Sabelis, M.W. (1997). Odour-mediated responses of phytophagous mites to conspecific and heterospecific competitors. — *Oecologia* 110, p. 179-185.
- Persons, M.H. & Rypstra, A.L. (2000). Preference for chemical cues associated with recent prey in the wolf spider *Hogna helluo* (Araneae: Lycosidae). — *Ethology* 106, p. 27-35.
- — & Uetz, G.W. (1996). Wolf spiders vary patch residence time in the presence of chemical cues from prey (Araneae, Lycosidae). — *J. Arachnol.* 24, p. 76-79.
- Poland, T.M. & Borden J.H. (1994). Semiochemical-based communication in interspecific interactions between *Ips pini* (Say) and *Pityogenes knechteli* (Swaine) (Coleoptera: Scolytidae) in lodgepole pine. — *Trends Ecol. Evol.* 7, p. 151-154.
- Pollard, S.D., Macnab, A.M. & Jackson, R.R. (1987). Communication with chemicals: pheromones and spiders — In: *Ecophysiology of spiders* (W. Nentwig, ed.). Springer Verlag, Berlin. p. 133-141.
- Raffa, K.F. & Dahlsten, D.L. (1995). Differential responses among natural enemies and prey to bark beetle pheromones. — *Oecologia* 102, p. 17-23.
- Rice, W.R. (1989). Analysing tables of statistical tests. — *Evolution* 43, p. 223-225.
- Robinson, M.H. (1982). Courtship and mating behavior in spiders. — *Ann. Rev. Ent.* 27, p. 1-20.
- Roitblat, H.L. (1987). Introduction to comparative cognition. — W.H. Freeman and Co, New York.
- Sabelis, M.W., Vermaat, J.E. & Groeneveld A. (1984). Arrestment response of the predatory mite *Phytoseiulus persimilis* to steep odour gradients of a kairomone. — *Physiol. Entomol.* 9, p. 437-446.
- — & van de Baan, H.E. (1983). Location of distant spider mite colonies by phytoseiid predators: demonstration of specific kairomones emitted by *Tetranychus urticae* and *Panonychus ulmi*. — *Entomol. Exper. Appl.* 33, p. 303-314.
- Schulz, S. & Toft, S. (1997). Identification of sex pheromone from a spider. *Science* 260, p. 1635-1637.
- Sokal, R.R. & Rohlf, F.J. (1995). *Biometry: the principles and practice of statistics in biological research*. — Third edition. W.H. Freeman and Co., New York.
- Taylor, P.W. (1998). Dragline-mediated mate-searching in *Trite planiceps* (Araneae, Salticidae). — *J. Arachnol.* 26, p. 330-334.
- Tarsitano, M.S. & Jackson, R.R. (1997) Araneophagic jumping spiders discriminate between detour routes that do and do not lead to prey. — *Anim. Behav.* 53, p. 257-266.
- Teerling, C.R., Gillespie, D.R. & Borden, J.H. (1993). Utilization of western flower thrips alarm pheromone as a prey-finding kairomone by predators. — *Can. Entomol.* 125, p. 431-437.
- Tietjen, W.J. & Rovner, J.S. (1982) Chemical communication in lycosids and other spiders. — In: *Spider communication: mechanisms and ecological significance* (P.N. Witt & J.S. Rovner, eds). Princeton University Press, Princeton, New Jersey, p. 249-279.

- Tinbergen, L. (1960). The natural control of insects in pinewoods. Factors influencing the intensity of predation by songbirds. — *Archs Neer. Zool.* 13, p. 265-343.
- Trabalon, M., Bagnères, A.G. & Roland, C. (1997). Contact sex signals in two sympatric spider species, *Tegenaria domestica* and *Tegenaria pagana*. — *J. Chem. Ecol.* 23, p. 747-758.
- Tumlinson, J.H., Turlings, T.C.J. & Lewis, W.J. (1992). The semiochemical complexes that mediate insect parasitoid foraging. — *Agr. Zool. Rev.* 5, p. 221-252.
- Vet, L.E.M. & Dicke, M. (1992). Ecology of infochemical use by natural enemies in a tritrophic context. — *Ann. Rev. Entomol.* 37, p. 141-172.
- Wilcox, R.S. & Jackson, R.R. (1998). Cognitive abilities of araneophagic jumping spiders. — In: *Animal cognition in nature: the convergence of psychology and biology in laboratory and field* (R.P. Balda, I.M. Pepperberg & A.C. Kamil, eds). Academic Press, New York, p. 411-433.
- Yasuda, T. (1997). Chemical cues from *Spodoptera litura* larvae elicit prey-locating behavior by the predatory stink bug, *Eocanthecona furcellata*. — *Entomol. Exper. Appl.* 82, p. 349-354.
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