

## Influence of cues from the anterior medial eyes of virtual prey on *Portia fimbriata*, an araneophagic jumping spider

Duane P. Harland<sup>1,\*</sup> and Robert R. Jackson<sup>2</sup>

<sup>1</sup>Department of Biological Sciences, University of Sussex, Brighton BN1 9QG, East Sussex, UK and

<sup>2</sup>Department of Zoology, University of Canterbury, Private Bag 4800, Christchurch, New Zealand

\*e-mail: d.harland@biols.sussex.ac.uk

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### Summary

*Portia fimbriata* from Queensland, Australia, is a jumping spider (Salticidae) that preys on other spiders, including other salticids. Cryptic stalking (palps retracted, walking very slowly and freezing when faced) is a prey-specific tactic deployed exclusively against salticid prey. Using vision alone, *P. fimbriata* discriminates salticid from non-salticid prey, with the prey salticid's large anterior median (AM) eyes providing critical cues. Here, using computer-rendered virtual three-dimensional lures, we clarify experimentally some of the specific optical cues from AM eyes that influence the behaviour of *P. fimbriata*. Control lures were based on *Jacksonoides queenslandicus*, the salticid upon which *P. fimbriata* most commonly preys in nature. Experimental lures were modified to isolate specific combinations of AM eye features. For presentation to *P. fimbriata*, lures were projected on a

small screen positioned in front of a web-covered platform. Each individual *P. fimbriata* was tested once with a control lure and once with a lure on which some AM eye feature had been altered. *P. fimbriata* was affected by the presence-versus-absence of AM eyes, by the size and shape of these eyes and by AM eye position. Horizontal position on the face of a single AM eye had no discernible influence on whether *P. fimbriata* initiated cryptic stalking, but reduced how often *P. fimbriata* froze when faced by the prey. The implications of the findings are discussed in relation to perceptual processes underlying the predatory strategy of *P. fimbriata*.

Key words: *Portia fimbriata*, jumping spider, Salticidae, prey capture, vision, optical cue, anterior median eye, cryptic stalking, virtual prey.

### Introduction

For a predator, the advantages of acute eyesight might include rapid access, from a distance, to precise information about the location, size, identity and behaviour of prey animals, including different types of prey for which different predatory tactics are optimal (see Marler and Hamilton, 1966; Curio, 1976), and reliance on eyes with high-spatial-acuity vision ('acute eyesight') has evolved independently numerous times among animals that differ widely in body size (Land and Fernald, 1992). However, rapid translation of raw input from the eyes into intricate predatory strategies depends on the ability to discern relevant information in a typically complex and noisy environment (see Inglis, 2000).

Humans and other large animals that rely on spatially acute eyesight dedicate large tracts of the brain to visual processing. In insects, spiders and other animals with body size considerably smaller than that of humans, brain size is by necessity also relatively small. Small brain size means that the insect or spider has at its disposal vastly fewer neurones to devote to processing input from the eyes. Yet, in the face of size constraints, eyes that are adapted for resolving moderately fine spatial details have evolved in certain insects, honeybees (Srinivasan and Zhang, 1998), dragonflies (Sherk, 1978) and

hoverflies (Collett and Land, 1975) being especially notable examples. The eyes of most spider species are only poorly adapted for high spatial acuity. The most notable exceptions to this rule are the jumping spiders (Salticidae), which have complex eyes (Land, 1969a,b, 1985b) and exceptionally intricate vision-guided predatory strategies (Forster, 1982; Jackson and Pollard, 1996).

Salticids have eight eyes. Three pairs positioned along the sides of the cephalothorax (called the 'secondary eyes') have a combined field-of-view close to 360° laterally and serve primarily as movement detectors (Land, 1971, 1985a). However, it is a pair of proportionately much larger, forward-facing anterior median eyes (called the 'principal eyes' or 'AM eyes') that are specialized for high spatial acuity over a much smaller field of view (approx. 1–2°; Land, 1969a,b; Blest et al., 1981, 1990; Blest and Price, 1984). Salticid AM eyes, which are structurally very different from the compound eyes of insects, provide spatial acuity that is typically an order of magnitude finer than that of insect compound eyes (Land, 1985b; see also Land, 1997).

The use of different prey-capture tactics against different types of prey ('predatory versatility'; Curio, 1976) appears to

be widespread in salticids (Richman and Jackson, 1992) and is especially pronounced among araneophagic species (i.e. a minority group of salticids for which the preferred prey are other spiders; Jackson, 1992). Pronounced predatory versatility may make araneophagic salticids especially suitable for studying how visual information is processed by animals that are subject to severe size constraints: by adopting prey-specific prey-capture behaviour, the salticid effectively tells the researcher how it has classified the prey (see Harland and Jackson, 2000a, 2001).

*Portia fimbriata* from Queensland, Australia, the most extensively studied of the araneophagic salticids (Jackson and Wilcox, 1998), preys on spiders and on insects, both of which may be captured away from webs, in webs that *P. fimbriata* built itself and in webs built by other spiders (Jackson and Blest, 1982). Away from webs, *P. fimbriata* preys especially on salticids belonging to other genera, deploying against them a special tactic termed 'cryptic stalking' (Jackson and Blest, 1982).

The appearance and walking gait of *P. fimbriata* are unlike those of any other salticid. Resting in a web, *P. fimbriata* resembles a piece of detritus (Wanless, 1978), detritus mimicry when walking being preserved by a slow, choppy gait (each leg moves jerkily and out of phase with the movement of the other legs). Resting in a web, *P. fimbriata* adopts a special posture, called the 'cryptic rest posture' (Jackson and Blest, 1982). In this posture, with the legs close to the body and the palps retracted beside the chelicerae, the outlines of the appendages are hidden.

When cryptic stalking is adopted, the Queensland *P. fimbriata* retracts its palps, as in the cryptic rest posture, and exaggerates the slow, choppy character of its gait. When salticids detect movement, they sometimes turn to face the cryptically stalking *P. fimbriata*, but *P. fimbriata* freezes until the salticid once again faces away (Jackson and Blest, 1982). While stalking a spider of any type other than a salticid, or while stalking an insect, the Queensland *P. fimbriata* does not consistently retract its palps, nor does it consistently freeze when faced. Other studied species of *Portia* (*P. africana*, *P. albimana*, *P. labiata* and *P. schultzi*) and *P. fimbriata* from sites other than Queensland (Northern Territory of Australia, Malaysia, Sri Lanka) attempt to capture salticids, but they do not adopt cryptic stalking and they are considerably less successful than the Queensland *P. fimbriata*. When cryptically stalked by a Queensland *P. fimbriata*, salticids typically give no evidence of recognizing the presence of a predator (Jackson and Blest, 1982). When stalked by other *Portia* species, however, they may flee or else turn on the *Portia*, attack it and drive it away (Jackson and Hallas, 1986).

Cryptic stalking by the Queensland *P. fimbriata* appears to be an example of local adaptation to a locally abundant type of prey (Jackson, 1992). *Jacksonoides queenslandicus* Wanless is by far the most abundant salticid on tree trunks, boulders and rock walls where *P. fimbriata* hunts (Jackson, 1988), but many salticid species are present in the rain-forest habitat of the

Queensland *P. fimbriata*. From standardised tests carried out on 114 salticid species (Harland and Jackson, 2001), the optical cues that trigger cryptic stalking are known not to be unique to *J. queenslandicus*. In these tests, only optical cues were available to *P. fimbriata* (prey enclosed in a small glass vial within a large cage). Despite testing with species that differed considerably in appearance (including beetle mimics, species with unusual body shapes and species with a wide variety of camouflaging markings), all except *Myrmarachne* spp. (ant mimics) triggered cryptic stalking by *P. fimbriata*. This suggests that some commonly present salticid features serve as cryptic-stalking cues.

The specific optical cues used by *P. fimbriata* to identify salticids have been investigated experimentally using odourless lures made from dead prey on which various combinations of features were altered (Harland and Jackson, 2000b). *P. fimbriata* adopted cryptic stalking only against intact salticid lures and modified lures on which the large anterior median (AM) eyes were visible. Ordinary stalking was usually adopted when the AM eyes were not visible on the lure. There was no evidence that cues from the legs, cephalothorax and abdomen of prey salticids influenced the choice of stalking style of *P. fimbriata*.

Here, we investigate in greater detail the cryptic-stalking cues provided by salticid AM eyes. This is a step towards a long-term goal of clarifying the perceptual processes governing the predatory behaviour of araneophagic salticids. Our rationale for concentrating on cues from AM eyes is that a fine-grain understanding of how *P. fimbriata* discriminates between salticid and non-salticid spiders may elucidate more general low-level mechanisms underlying acute vision.

Unlike in the earlier study (Harland and Jackson, 2000b), here we used computer-generated virtual lures instead of physical lures. Clark and Uetz (1990, 1992, 1993) pioneered the use of video playback and simple video-derived animated lures in research with salticids. Our methods differ from theirs because, instead of playing back video recordings, we use a computer-generated three-dimensional animation projected as a two-dimensional image onto a small screen. Specifically, we investigate whether a virtual salticid lure will elicit cryptic stalking and whether, as in the study based on physical lures, the presence-versus-absence of AM eyes influences the decision of *P. fimbriata* to use cryptic or ordinary stalking. We then extend the earlier study by considering some initial questions about the specific cues from AM eyes that may influence the predatory decisions of *P. fimbriata*. In particular, we investigate the influence of cues from the size, number, position and shape of the AM eyes.

## Materials and methods

As in numerous earlier studies (see Harland and Jackson, 2000b), laboratory cultures of *Portia fimbriata* (Doleschal) were used, all individuals being reared from eggs under standardized conditions. Testing was carried out between 09:00h and 17:00h (laboratory photoperiod 12h:12h L:D,

lights on at 08:00 h). For each specific test, the individuals to be tested were chosen at random from the stock culture. Hunger state was standardized by keeping each individual without prey for the 5 days immediately before testing.

#### Lures

In the previous study (Harland and Jackson, 2000b), the physical lures used were constructed from dead specimens of *Jacksonoides queenslandicus*. Appendages and sometimes entire body parts were removed from these lures. To us, a salticid's AM eyes appear as dark glossy hemispheres protruding from the anterior surface of the carapace, one on either side of the body's sagittal plane. 'Removal' of the lure's eyes in the previous study was achieved by carefully obscuring the hemispheres with red paint.

In preliminary studies, it was exceedingly difficult to control for other potential influences on the response of *P. fimbriata* when altering details of the principal eyes on a physical lure, but this goal is readily achievable using computer-generated virtual lures. For a standard, we developed a virtual lure depicting an intact adult *J. queenslandicus* female (Fig. 1A). Next, for investigating how specific abstracted features of the AM eyes influenced the behaviour of *P. fimbriata*, we made six experimental virtual lures by systematically altering the appearance of the standard lure (Fig. 1B–G).

Lures were drawn and modified using commercially available computer software packages on a standard IBM PC clone computer (450 MHz Pentium II with 128 MB RAM, running Microsoft Windows 98). Using as references scanned taxonomic drawings and captured video-stills of dissected parts of specimens through a microscope, each part of the body was carefully sculpted with Macromedia Extreme 3D2. The finished virtual three-dimensional lure was rendered in monochrome as a standard (bitmap) movie file and animated so that it rotated by 360° about its vertical axis. Macromedia Director 7 was used for writing a test harness program that presented the rendered movies of the various lures to *P. fimbriata* and allowed us to manipulate the behaviour of the lures on screen. Using the test harness, we could move each lure horizontally and vertically across the screen and rotate it smoothly by 360° around its vertical axis. Smooth rotation of the lure's entire body was chosen over more realistic motion involving the legs because our specific interest was the optical cues provided by form in the absence of potential cues from prey-specific motion. On command, rotating lures suddenly stopped in place or else suddenly stopped rotating and then immediately faced forward.

#### Apparatus

Lures, rear projected from a computer projector, were presented to *P. fimbriata* on a white screen (23.5 mm wide × 17.5 mm high). The image from the projector was reduced by using an array of lenses, with the brightness of the image being controlled by using neutral-density filters placed

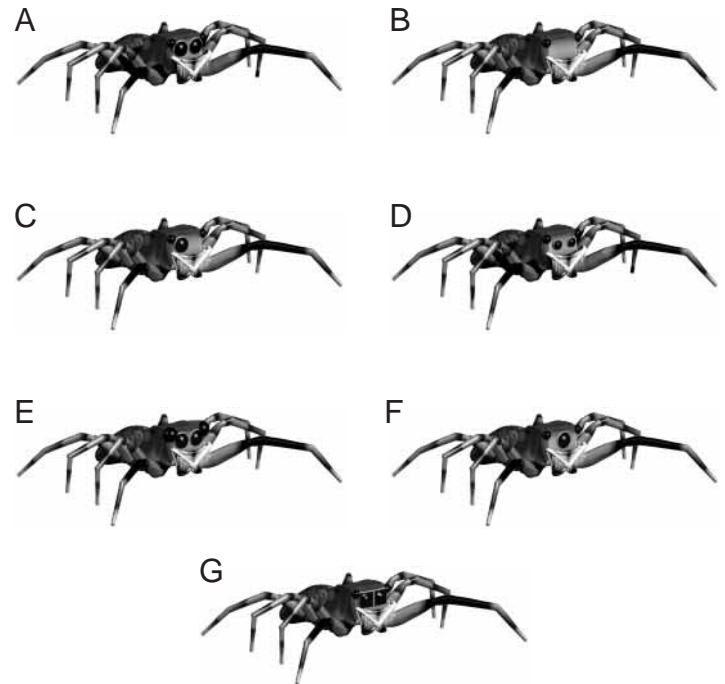


Fig. 1. Virtual lures based on *Jacksonoides queenslandicus* females: (A) intact (i.e. not modified), (B) with both anterior median (AM) eyes removed, (C) with the left AM eye removed, (D) with the AM eyes reduced to the size of the anterior lateral (AL) eyes, (E) with the AL eyes enlarged to the size of the AM eyes, (F) with one AM eye removed and the other centred on the face (Cyclops), (G) with square AM eyes. All lures are facing 45° away.

behind and in front of the screen. We adjusted image scale to where the projected lure's carapace width was the same (to the nearest 0.1 mm) as that of a typical adult *J. queenslandicus* female. During testing, illumination came from the projector screen (approximately 675 lx at platform surface) and from fluorescent tube ceiling lights 1.5 m above the platform.

The testing platform (80 mm long × 65 mm wide) was placed on a table in front of, and level with, the bottom of the projector screen (Fig. 2). It was 160 mm above the table surface. The platform was a rectangular wire frame (brass welding wire, diameter 1.5 mm) over which were stretched multiple layers of non-sticky (structural) silk threads taken in the field from webs of *Badumna longinquus* (Desidae), a spider that is common on buildings in Christchurch, New Zealand. Silk threads were stretched over the frame in quantities sufficient to make a dense matting with no holes large enough for *P. fimbriata* to pass through. As a precaution against possible chemical traces left by previously tested *P. fimbriata*, the web platform was washed in a bath of 80% ethanol, then allowed to dry for at least 30 min between tests.

Having *P. fimbriata* on a silk-covered platform facilitated testing. Although *J. queenslandicus* is not a web-building species, *P. fimbriata* in nature encounters *J. queenslandicus* both in and away from webs, web-based encounters being common (Clark and Jackson, 2000) because *J. queenslandicus*

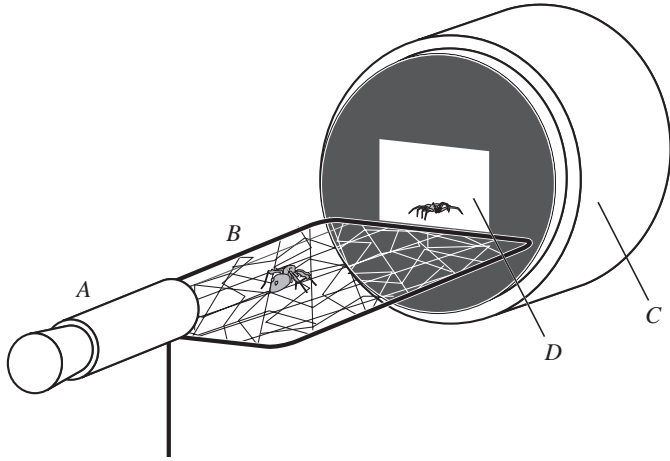


Fig. 2. Arrangement for presenting virtual lures to *Portia fimbriata*. A, opaque tube, stoppered at one end. The non-stoppered end was fringed with hair (not shown). *P. fimbriata* emerges from the non-stoppered end. B, web platform (a wire frame matted with silk). *P. fimbriata* is depicted in the centre and facing the screen. C, the lens array for reducing the image from the computer projector (not shown) to life-like size and manipulating the image brightness and contrast. D, the image from the lens array on screen: a virtual salticid lure on a uniform white background.

often enters other spiders' webs, including the webs of *Badumna* spp. (Jackson, 1988).

#### Testing protocol

Before each test, an individual of *P. fimbriata* was transferred from its cage to a small plastic Petri dish (diameter 35 mm). From the Petri dish, *P. fimbriata* was introduced into a narrow opaque tube (internal diameter 13 mm, length 45 mm) attached to the end of the platform opposite the screen (Fig. 2). A small soft-tipped paintbrush was used to coax the spider into and out of the Petri dish.

The tube faced the projector screen and virtual lure, with one end of the tube touching the web. *P. fimbriata* was introduced into the end of the tube that was away from the screen, and this end was then stoppered to ensure that *P. fimbriata* had to exit from the end of the tube that faced the screen. The top and the two sides of this end of the tube were fringed with human hair (fringe approximately 7.5 mm long, held in place with tape), but the bottom was left free. Being reluctant to move over the hair fringe, *P. fimbriata* almost always walked out from the bottom of the tube and onto the web. In rare instances when *P. fimbriata* left *via* the top or a side of the end of the tube and failed to walk onto the web, the test was aborted.

Whenever *P. fimbriata* failed to leave the tube after 15 min had elapsed, a small soft-tipped brush was used to direct it gently until it was facing the screen, after which it was allowed an additional 15 min to emerge. Should it still fail to emerge, the test was aborted. Before *P. fimbriata* left the tube, the lure was moved erratically back and forth on the screen. Once *P. fimbriata* walked out of the tube and onto the platform, erratic

lure movement continued until *P. fimbriata* oriented towards it. Once *P. fimbriata* turned to face the lure, erratic movement ceased and the lure was moved smoothly to the centre of the screen. Once stalking began, the lure was rotated by 45° (whether left or right was decided at random) and the style of stalking of *P. fimbriata* was recorded.

Two specific tests were carried out next. The lure was moved 10 mm (whether to the left or the right was decided at random) to ensure that *P. fimbriata* was actually stalking the lure, rather than just walking towards the part of the screen where the lure happened to be situated. If *P. fimbriata* continued moving towards the lure (i.e. changed in its path appropriately), we recorded this as confirmation of stalking. The test continued whenever stalking was confirmed, but it was aborted whenever stalking was not confirmed.

When *P. fimbriata* had stalked to within 50 mm of the lure, a second test was carried out to determine whether *P. fimbriata* would freeze when suddenly faced by the lure: a lure that was initially facing 45° to the side was suddenly (i.e. without any in-between steps) made to face directly towards *P. fimbriata*. Whether *P. fimbriata* froze (i.e. stopped all movement) within 0.5 s of being faced was recorded. The 'freezing test' was repeated at 5 s intervals until *P. fimbriata* touched the glass (projector screen) or until a total of three freezing tests had been completed. Instances in which *P. fimbriata* touched the glass after only one freezing test were rare, and testing was aborted whenever this happened.

*Portia fimbriata* sometimes freezes when its prey (including non-salticid prey) stops moving, even if the prey does not turn and face the *P. fimbriata* (Wilcox et al., 1996). To distinguish freezing when the prey simply stops moving from freezing when faced by a salticid, the lure was kept stationary for 2 s after being rotated by 45° to the left of *P. fimbriata* but before being made suddenly to face *P. fimbriata*. If *P. fimbriata* froze during the 2 s pause, the lure was kept stationary until stalking resumed (i.e. the lure was not made to face the *P. fimbriata*).

#### Experimental design

A paired design was adopted: each individual of *P. fimbriata* was tested once with an intact lure (called 'control') and once with a modified lure (called 'experimental'), with testing order (intact lure then modified lure or modified lure then intact lure) decided at random for each individual *P. fimbriata*. The *P. fimbriata* was returned to the small plastic Petri dish and placed out of sight of the testing apparatus during the interval (10–15 min) between the first and second test.

We chose not to consider the question of whether or not any stalking at all was elicited by the experimental lures (stalking tendency) because it is the stalking style that provides unambiguous evidence that *P. fimbriata* has 'classified' a lure as a salticid (see Harland and Jackson, 2000b, 2001). Therefore, sequences in which *P. fimbriata* stalked neither the control nor the experimental lure were terminated.

Paired frequency data were analysed using  $\chi^2$  McNemar tests for significance of changes (see Sokal and Rohlf, 1995).

## Results

### *Influence of the presence-versus-absence of AM eyes*

*Portia fimbriata* often adopted cryptic stalking against the standard virtual lure but never against the lure with no AM eyes ( $P < 0.001$ ). When faced by the standard lure, *P. fimbriata* more often froze than when faced by the lure from which both AM eyes had been removed ( $P < 0.001$ ) (Fig. 3A) (Tables 1, 2). These two findings, being consistent with findings from the previous study (Harland and Jackson, 2000b) in which physical lures were used, confirm that using animation-derived lures is an effective method for testing *P. fimbriata*.

### *Influence of the number of AM eyes*

A lure with only one AM eye (Fig. 1C) was made by removing the left AM eye from a copy of the standard virtual lure. Results (frequency of adopting cryptic stalking and of freezing) in tests with the lure that had only one AM eye were not significantly different from the findings with the standard lure (Fig. 3A) (Tables 1, 2).

### *Influence of the size and relative size of AM eyes*

Two lures (Fig. 1D,E) were made. On one, the diameters of the AM eyes were reduced to that of the anterior lateral (AL) eyes (Fig. 1D). On the other, the AL eyes were enlarged to the diameter of AM eyes (Fig. 1E). The position of the centre point of each AM and AL eye was preserved for both these lures

*P. fimbriata* often adopted cryptic stalking against the control lure, but only once against the lure that had small AM eyes ( $P < 0.001$ ). *P. fimbriata* also froze when faced by the control lure more often than when faced by the lure with small AM eyes ( $P < 0.001$ ) (Fig. 3B) (Tables 1, 2). However, the frequencies with which

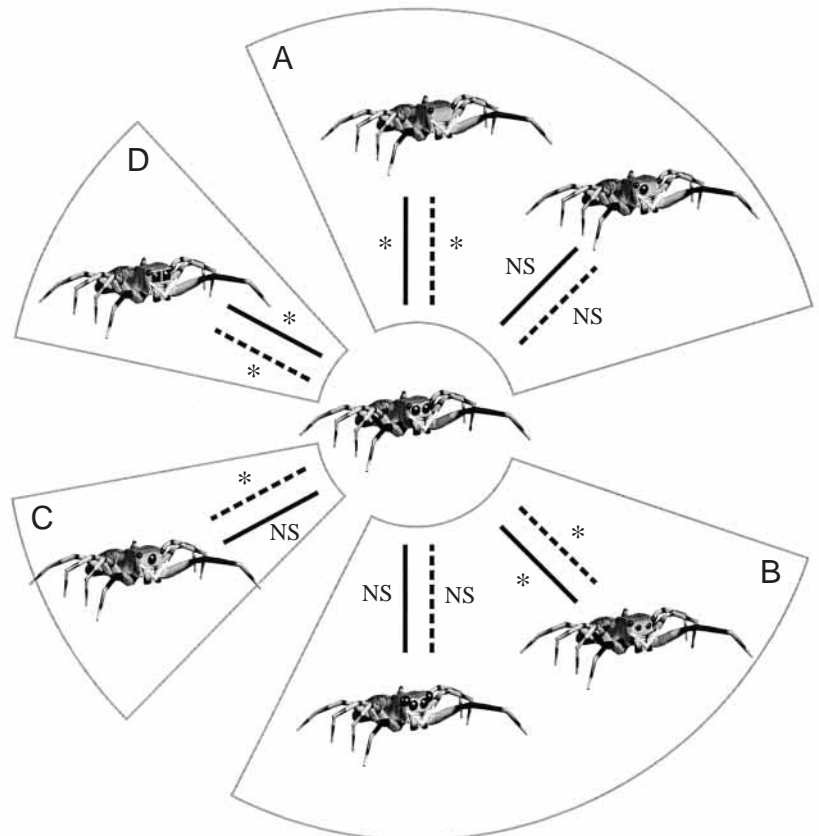


Fig. 3. Results from paired tests. Compared findings are from using an intact salticid lure (centre) and one modified lure. Comparisons of the tendency of individual *Portia fimbriata* to adopt cryptic stalking (solid line) and the tendency to freeze when faced by a lure (broken line). (A) Modified lures used to test the effect of the number of anterior median (AM) eyes. (B) Modified lures used to test the effect of AM eye size. (C) Lure used to test the effect of AM eye position. (D) Lure used to test the effect of AM eye shape. NS, not significant;  $*P < 0.001$ .

individuals adopted cryptic stalking against, or froze when faced by, the lure with enlarged AL eyes were not significantly different from these frequencies in tests with the control lure (Fig. 3B) (Tables 1, 2).

Table 1. *Stalking style adopted by Portia fimbriata when tested with Jacksonoides queenslandicus virtual lures*

Experimental lure	<i>N</i>	Cryptic stalking adopted with experimental lure only	Cryptic stalking adopted with standard lure only	Cryptic stalking adopted with both lures	Cryptic stalking adopted with neither lure	McNemar test
No AM eyes	24	0	14	0	10	$P < 0.001$
One AM eye	46	5	6	22	13	NS
(normal position)						
Small AM eyes	26	1	17	0	8	$P < 0.001$
Large AL eyes	32	4	4	11	13	NS
One AM eye (Cyclops)	43	5	8	10	20	NS
Square AM eyes	25	1	15	2	7	$P < 0.001$

In all instances, the test subject stalked both experimental and control lures.

Data are presented for whether or not cryptic stalking was adopted.

AL, anterior lateral; AM, anterior median; NS, not significant.

Table 2. Results from freezing tests (see text) during encounters between *Portia fimbriata* with *Jacksonoides queenslandicus* virtual lures

Experimental lure	N	Froze when faced by experimental lure only	Froze when faced by standard lure only	Froze when faced by both lures	Froze when faced by neither lure	McNemar test
No AM eyes	24	1	18	2	3	$P < 0.001$
One AM eye (normal position)	46	11	14	17	4	NS
Small AM eyes	26	1	20	3	2	$P < 0.001$
Large AL eyes	32	9	8	13	2	NS
One AM eye (Cyclops)	43	1	28	8	6	$P < 0.001$
Square AM eyes	25	1	15	6	3	$P < 0.001$

In all instances, the test subject stalked both experimental and control lures.

Data are presented for whether *P. fimbriata* froze at least twice when faced by lures.

AL, anterior lateral; AM, anterior median; NS, not significant.

#### *Influence of the position of the AM eyes*

A lure was made with one AM eye removed, the other eye being repositioned horizontally so that it was, Cyclops-fashion, in the centre of the spider's 'face' (Fig. 1F). The frequency with which individuals adopted cryptic stalking when faced by the Cyclops-like lure was not significantly different from this frequency with the control lure (Table 1). However, individuals more often ( $P < 0.001$ ) froze when faced by the control lure than when faced by the Cyclops (Fig. 3C) (Table 2).

#### *Influence of AM eye shape*

A lure was made by replacing both round AM eyes of the standard lure with square eyes, each side of the square being equal to the diameter of the standard's AM eye (Fig. 1G). The central region of each square AM eye was rendered so that it appeared to bulge out to the same extent as the normal AM eye, thereby preserving the specular spots and preserving the shape of the eye when viewed from the side.

Compared with the lure that had square AM eyes (Fig. 3D), the control lure more often elicited cryptic stalking ( $P < 0.001$ ) and freezing when faced ( $P < 0.001$ ) (Tables 1, 2).

### Discussion

Intact virtual lures elicited cryptic stalking, whereas virtual lures with no AM eyes were ineffective, supporting one of the major conclusions (i.e. that the presence-versus-absence of AM eyes is an important cryptic-stalking cue for *P. fimbriata*) from the earlier study (Harland and Jackson, 2000b). Other findings suggest precisely what AM eye features matter to *P. fimbriata*.

For initiating cryptic stalking and provoking the freezing response, the presence of two AM eyes was not necessary. Even a lure with one AM eye removed and the other AM eye in its normal off-centre position sufficed. Size, however, did matter. A lure with AM eyes reduced in size triggered cryptic stalking and the freezing responses less often than intact lures.

Eye shape also appears to matter. When the lure had square-

edged AM eyes, *P. fimbriata* rarely appeared to classify it as a salticid at all (i.e. cryptic stalking was usually not initiated and freezing was usually not provoked when faced). Evidently, the shape of the edges of the AM eyes is an important salticid-identification cue.

The anterior lateral (AL) eyes face more-or-less forward and are visible face on. On the standard lure, the AM eyes are large relative to the AL eyes, suggesting that, for a *P. fimbriata* trying to decide whether to initiate cryptic stalking and whether to freeze when faced, a relevant cue might be the size of the AM relative to the AL eyes. Our findings, however, did not support this hypothesis. When we used a virtual lure on which we had enlarged the AL eyes while leaving the AM eyes at their typical large size, there was no evidence that the response of *P. fimbriata* was different from its response to the standard lure.

Yet *P. fimbriata* cannot be using absolute AM eye size as a salticid-detection cue. The salticids on which *P. fimbriata* preys in nature vary considerably in body size, which means that they vary considerably in absolute AM eye size as well. Furthermore, the distance between *P. fimbriata* and its salticid prey varies when cryptic stalking is initiated, which means that the image size of an AM eye will vary considerably even for salticid prey of similar body size.

Although our findings suggest that *P. fimbriata* does not pay attention to AM eye size relative to AL eye size, AM/AL relative size was not the only change brought about when we altered AM eye size on our virtual lures. For example, reducing the size of the two AM eyes, while preserving the position of the centre of each, altered the positions of the AM eye edges relative to each other, relative to the AL eye edges and relative to the edges of the carapace. These or other parameters may have influenced the reactions of *P. fimbriata* to the experimental lures.

Findings from testing with a Cyclops-like lure (a single AM eye centred between the two AL eyes) suggest that the horizontal position of the AM eyes influences the decision of *P. fimbriata* to freeze when faced by salticid prey (i.e. *P. fimbriata* more often froze when a lure had two AM eyes

instead of a single centrally positioned AM eye), but not the decision of *P. fimbriata* to initiate cryptic stalking. In nature, *P. fimbriata* may often initiate cryptic stalking prior to getting a clear face-on view of the salticid prey. Horizontal positioning of an AM eye may not be so readily discernible in many instances, and it might not be optimal for *P. fimbriata* to base an early decision on difficult-to-discern details. However, deciding to freeze or not appears to depend on information about specifically whether a salticid is facing or not.

Findings from testing with the Cyclops may have other implications regarding how *P. fimbriata* determines AM eye size. Centring the AM eye on the face horizontally altered the horizontal component of distances between the edge of the AM eye and other facial features. In particular, the distances between the edges of the AL eyes and left and right sides of the carapace increased. This was also true for the lure with reduced AM eyes. However, *P. fimbriata* tended to adopt cryptic stalking against the lure with one horizontally centred AM eye, but not against the lure with reduced AM eyes. This suggests that the horizontal component of distances between the edge of the AM eye and other facial features is not used to determine AM eye size. However, the story might not be so simple.

‘Cryptic stalking’ is a term used for a predatory tactic that has distinct components: palp posture, walking gait and a tendency to freeze when faced by the prey. Using a single term, ‘cryptic stalking’, for this collection of integrated components may be convenient, but should not be envisaged as implying that all components are governed in the same way by the same cues. The findings from using the Cyclops-like lure particularly strongly suggest that the cues for initiating cryptic stalking differ from the cues for freezing. It seems likely, however, that initiation of cryptic stalking primes *P. fimbriata* (i.e. renders *P. fimbriata* ready to freeze when the appropriate freezing-eliciting cues arrive).

From the perspective of *P. fimbriata*, detecting conditions



Fig. 4. The distance (bar) between the edge of the anterior median (AM) eye and the edge of the visible carapace increases rapidly as *Jacksonoides queenslandicus* turns away. (A) Lure facing  $0^\circ$  (i.e. straight towards the viewer), (B)  $30^\circ$  and (C)  $45^\circ$  from the front. Note how, with increasing angle, the increase in this distance (line) is more rapid than the decrease in each AM eye's apparent width (i.e. the horizontal diameter of the oval).

under which freezing is appropriate (i.e. detecting that a salticid is facing) may be more demanding than detecting conditions under which cryptic stalking is appropriate (i.e. simply detecting the presence of a salticid). The presence of large, round AM eyes alone would not suffice as a freezing-elicitation cue because a salticid's AM eyes are visible over a wide range of orientations, not merely when the salticid prey is face on. For example, the AM eyes are still easily seen when the salticid is facing  $45^\circ$  to the left or the right (Fig. 1), but a salticid at  $45^\circ$  does not elicit freezing (Harland and Jackson, 2000b). Findings from using a lure with one horizontally centred eye suggests that, when *P. fimbriata* is deciding whether to freeze, the horizontal distance between the edge of the AM eye and the visible edge of the carapace may be an especially reliable cue. For example, when an intact prey salticid that is facing *P. fimbriata* is turning away to its left (Fig. 4), the distance between the right edge of the prey's right AM eye and the right edge of its carapace increases rapidly as more of the right side of the carapace comes into view. *P. fimbriata* might measure this distance by first fixing its AM retina on the pattern made by the curved edge of the salticid prey's right AM eye and then moving its retina horizontally (thereby, moving its viewpoint over the image of the salticid) until the edge of the carapace comes into view. Comparing the information gathered in this way with either the distance of the spider from *P. fimbriata* (i.e. its range) or its size (i.e. as established by other cues) would give an accurate measure of how close the salticid is to facing *P. fimbriata* head on.

This hypothesis might explain puzzling findings from a previous study (Harland and Jackson, 2001). *Pachyballus cardiforme* Berland & Millot is, at least to the human eye, an especially convincing beetle mimic (Fig. 5). Almost half of the *P. fimbriata* tested with *Pachyballus cardiforme* classified it as prey (i.e. they stalked it). However, out of the seven *P. fimbriata* that stalked *Pachyballus cardiforme*, only one adopted cryptic stalking. The remaining six *P. fimbriata* that stalked *Pachyballus cardiforme* adopted only some of

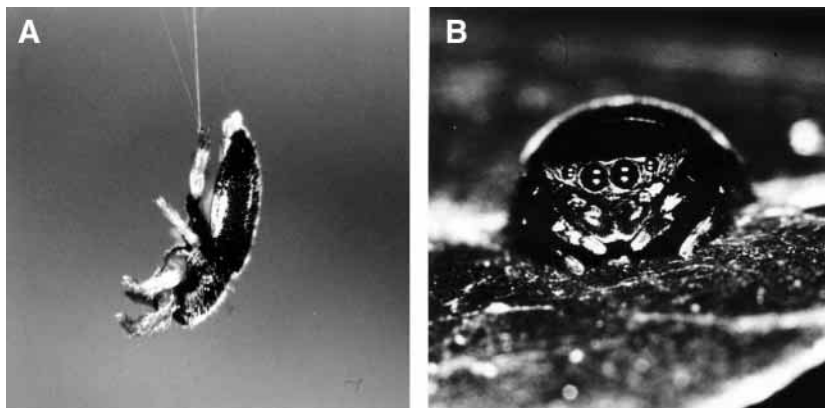


Fig. 5. *Pachyballus cardiforme*, a beetle-mimicking salticid from East Africa. (A) Side view (length ca. 5 mm). (B) Front view. Note the relatively wide distance between the lateral edges of the anterior median eyes and the lateral edges of the carapace (carapace width ca. 3 mm, abdomen width ca. 4 mm).

the components of cryptic stalking and did not consistently freeze when faced. Perhaps, as a consequence of its resemblance to beetles, the AM eyes of *Pachyballus cardiforme* are horizontally centred on a wide face (i.e. the distances between the sides of the AM eyes of *Pachyballus cardiforme* and the edges of the carapace are, compared with other salticids, relatively large even when facing). This may cause problems for the perceptual processes of *P. fimbriata* and account for anomalous reactions to this unusual salticid.

Perhaps the most important conclusion from this exploratory study is that computer-generated virtual lures are applicable in research on visual processes underlying the complex predatory behaviour of araneophagic jumping spiders. Clark and Uetz (1990) established that salticids respond to television (i.e. video tapes). Our study has shown that araneophagic salticids respond to entirely man-made computer-generated special-effects creations.

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