

CUES BY WHICH *PORTIA FIMBRIATA*, AN ARANEOPHAGIC JUMPING SPIDER, DISTINGUISHES JUMPING-SPIDER PREY FROM OTHER PREY

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Summary

Portia fimbriata from Queensland, Australia, is an araneophagic jumping spider (Salticidae) that includes in its predatory strategy a tactic (cryptic stalking) enabling it to prey effectively on a wide range of salticids from other genera. Optical cues used by *P. fimbriata* to identify the salticid species on which it most commonly preys, *Jacksonoides queenslandicus*, were investigated experimentally in the laboratory using odourless lures made from dead prey on which various combinations of features were altered. *P. fimbriata* adopted cryptic stalking only against intact salticid lures and modified lures on which the large anterior-median eyes were visible. Ordinary stalking was usually adopted when the lure did

not have the anterior-median eyes visible. There was no evidence that cues from the legs of prey salticids influence the choice of stalking style of *P. fimbriata*, but cues from the legs do appear to influence strongly whether a prey is stalked at all. Cues from the cephalothorax and abdomen also influenced the stalking tendency, but to a lesser degree than cues from the legs. An algorithm to describe the perceptual processes of *P. fimbriata* when visually discriminating between salticid and non-salticid prey is discussed.

Key words: spider, *Portia fimbriata*, jumping spider, stalking, prey, vision.

Introduction

Jumping spiders (Salticidae) have exceptional eyes (Land, 1985a; Blest, 1987). Three pairs positioned along the sides of the cephalothorax (called the secondary eyes) have a combined field-of-view of almost 360° and serve primarily as movement detectors (Land, 1971, 1985b). A pair of forward-facing anterior-median eyes (called the principal eyes) are adapted for colour vision and high spatial acuity (Blest et al., 1981; Blest and Price, 1984).

Salticids also have intricate predatory strategies. Although a minority of species is araneophagic (eat primarily other spiders), motile insects are the primary prey of most salticids. Prey capture tends to be largely, but not entirely (Taylor et al., 1998), guided by vision (Forster, 1982), eyesight alone enabling the salticid to distinguish rapidly between prey, conspecific rivals and potential mates. The use of different prey-capture tactics against different types of prey ('predatory versatility'; Curio, 1976) may be widespread (Edwards and Jackson, 1993) and is especially pronounced in myrmecophagic (ant-eating) and araneophagic (Li and Jackson, 1996a) species. Using vision alone, myrmecophagic and araneophagic salticids are able to discriminate between different types of prey (Li and Jackson, 1996b; Li et al., 1999), but there is little precise information about the optical cues relied upon by these species.

Among the araneophagic salticids, *Portia* spp. display particularly complex predatory strategies. These species are unusual because, in addition to stalking prey away from webs,

they build prey-capture webs of their own and invade the webs of other spiders, against which they adopt predatory tactics based on aggressive mimicry (Jackson and Wilcox, 1998). Among species and populations of *Portia* studied, the Queensland *P. fimbriata* appears to be unique because its preferred prey are other genera of salticids (Li and Jackson, 1996b). Aggressive-mimicry signals are used to entice nesting salticids out of their nests, and a special tactic, cryptic stalking, is used for capturing salticids in the open, away from their nests and webs (Jackson and Blest, 1982).

Portia spp. do not look like typical salticids, but instead resemble a piece of detritus (Wanless, 1978). Dull grey and brown markings have a camouflaging effect, and fringes of hair on the body and legs break up the outline of the spider. When quiescent in a web, *Portia* spp. adopt a special posture, called the 'cryptic rest posture', pulling their legs in close to the body and their palps back beside the chelicerae, thus further obscuring the outlines of these appendages. When walking, *Portia* spp. have a slow, 'choppy' gait that preserves their concealment: pausing at frequent, irregular intervals, all the while waving their legs and palps jerkily up and down, with each appendage tending to move out of synchrony with the other appendages (Jackson and Blest, 1982). This unusual walking style is unlike that of any other spider and gives the impression of a light flickering through the forest canopy and striking a piece of detritus.

When cryptic stalking, the Queensland *P. fimbriata* exaggerates the slowness and 'choppiness' of its normal walking gait and holds its palps retracted beside its chelicerae, as in the cryptic rest posture. If faced by its salticid prey, *P. fimbriata* freezes until the prey turns away. Cryptic stalking can be easily distinguished from 'ordinary' stalking because, when stalking any type of prey other than a salticid, *P. fimbriata* does not consistently pull its palps back, nor does it consistently freeze when faced. Most salticids fail to recognize a cryptically stalking Queensland *P. fimbriata* as a predator, but they often defend themselves when stalked by other species of *Portia* or by *P. fimbriata* from sites other than Queensland (Jackson and Hallas, 1986).

Salticids are especially abundant in the rainforest habitat of the Queensland *P. fimbriata*, and cryptic stalking appears to be a local adaptation to these abundant prey (Jackson and Blest, 1982). Although many species of salticids are found in Queensland, one species, *Jacksonoides queenslandicus*, appears to be by far the most abundant on the tree trunks, boulders and rock walls in the microhabitat of *P. fimbriata* (Jackson, 1988). This disproportionate abundance of *J. queenslandicus* within the environment of *P. fimbriata* suggests that *J. queenslandicus*, rather than salticids in general, might have been responsible for the evolution of cryptic stalking by *P. fimbriata*.

The cues that trigger cryptic stalking are not, however, specific to *J. queenslandicus*. Using standardised tests in which only optical cues were available (prey enclosed in small glass vial within large cage), the reactions of *P. fimbriata* to 114 salticid species were investigated in an earlier study (D. P. Harland and R. R. Jackson, unpublished results). Not only sympatric, but also allopatric, salticids were tested, and species with considerably different appearance were also tested, including beetle mimics, species with unusual body shapes and species with a wide variety of camouflaging markings. With the exception of *Myrmarachne*

spp. (ant mimics), all salticids tested triggered cryptic stalking by *P. fimbriata*. This suggests that some features common to most salticids act as cues that elicit cryptic stalking by *P. fimbriata*, but experimental studies are needed to clarify what these cues may be.

Experiments using odourless lures made from dead, dried prey coated with a plastic lacquer (aerosol spray), mounted in life-like postures and presented without movement, have confirmed that information on the movement patterns of different species is not necessary. Static cues from appendages, body shape and other features (called hereafter 'body form' for short) are apparently sufficient to enable Queensland *P. fimbriata* to distinguish salticids from other types of spider and from insects (Jackson and Tarsitano, 1993; Li and Jackson, 1996b).

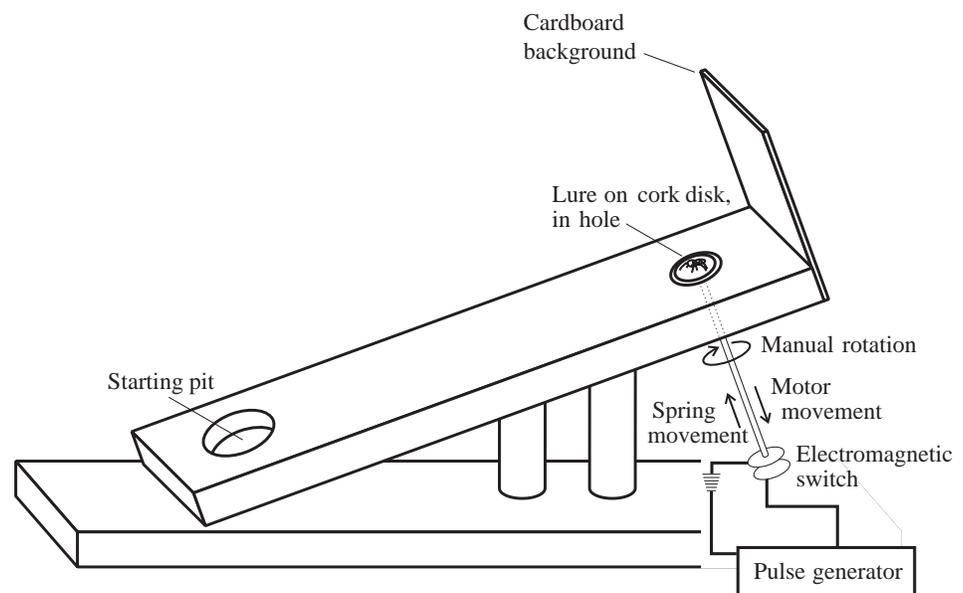
Using lures made from intact females of *J. queenslandicus* as a standard, and systematically altering the appearance of otherwise life-like lures, we have investigated the potential significance that specific features of the salticid body form might have as cues for cryptic stalking.

Materials and methods

The maintenance, testing procedures, cage design, terminology and conventions for describing behaviour were as in earlier spider studies (Jackson and Blest, 1982; Harland et al., 1999). Testing was carried out between 09:00 h and 17:00 h (laboratory photoperiod 12 h:12 h L:D, lights on at 08:00 h).

Each *P. fimbriata* tested was either a juvenile (4–8 mm in body length) or an adult female (8–10 mm body length), and no individual *P. fimbriata* was used in more than one test. Individuals of *P. fimbriata* were chosen at random from the stock culture for each specific test. No adult or subadult (one instar previous to maturity) males were tested. All *P. fimbriata* tested were reared from eggs in the laboratory, and none had prior contact with salticids of any species other than with

Fig. 1. Testing ramp for presenting lures to *Portia fimbriata*. At the beginning of the test, *P. fimbriata* climbs out of the starting pit and walks up the incline. Every 10 s the pulse generator releases an electromagnetic switch that causes the lure to spring above the surface of the ramp by 5 mm. An electric motor pulls the lure slowly back to the level of the ramp surface, resetting the electromagnetic switch. The lure is initially facing 45° away from the starting pit but is turned to face *P. fimbriata* when the spider closes to within 50 mm. The test ends 15 s later.



conspecifics in the egg sac before dispersal. Hunger state was standardized before testing by keeping each *P. fimbriata* without prey for 5 days.

Lures were presented to *P. fimbriata* on a wooden ramp (300 mm long and 70 mm wide, raised at a 20° incline) supported by two wooden poles (diameter 20 mm) glued to a wooden base (400 mm long and 100 mm wide) (Fig. 1). The ramp and the base were both 17 mm thick. The two poles were situated 75 mm and 150 mm, respectively, from the upper end of the base. The entire apparatus was painted with two coats of water-resistant polyurethane. As a precaution against possible chemical traces left by previously tested *P. fimbriata* (see Willey and Jackson, 1993; Clark and Jackson, 1994), the ramp was wiped with 80% ethanol, then allowed to dry for at least 30 min, between each test.

A piece of brown cardboard (80 mm high and 70 mm wide) glued to the top end of the ramp served as a background against which the salticid saw the lure. The lure (on a cork disk) was placed on a spring-loaded platform within a hole drilled through the surface of the ramp (diameter 15 mm) and centred 40 mm from the base of the cardboard. Standardized movement of the lure was generated by a switch-operated device below the platform (Fig. 1) that was activated automatically at 10 s intervals. At rest, the lure sat level with the ramp surface. Activating the switch released a spring, causing the lure to jump 5 mm above the level of the ramp surface, after which a motor slowly pulled the lure back to the rest position (cycle duration approximately 1 s). Movement attracted the attention of *P. fimbriata* to the lure and ensured that the spider remained attentive to the lure while ascending the ramp.

Before each test, an individual *P. fimbriata* was placed in a pit (diameter 32 mm, depth 10 mm, centred 60 mm from the bottom of the ramp) drilled into the top surface of the ramp 200 mm from the lure. The pit was covered with a piece of glass until the spider became quiescent, and was then uncovered to start a test (the test began when *P. fimbriata* walked slowly out of the pit and onto the ramp). *P. fimbriata* tends to walk up inclines and usually ascended towards the lure after leaving the pit. Lighting was from a 100 W tungsten filament lamp bulb 0.75 m above the ramp and fluorescent tube ceiling lights 2 m above the ramp (the light level was approximately 1850 lx at the ramp surface).

At the beginning of a test, the lure faced 45° away from the pit and the emerging *P. fimbriata*. The lure could be rotated by hand. When the spider came to within 50 mm, the orientation of the lure was suddenly rotated to face the spider. After observing the reaction of *P. fimbriata* for the next 15 s, the test ended.

'Stalking' was defined as a steady head-on movement towards a lure. Three categories were recognized: cryptic stalking (consistent adoption of the retracted-palps posture and freezing when a lure no more than 50 mm away was facing); ordinary stalking (consistent adoption of the posture used during ordinary locomotion, including holding the palps loosely in front of the chelicerae, and failure to freeze when

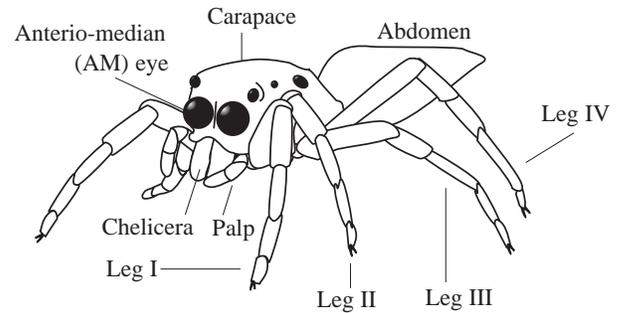


Fig. 2. Conventions for naming the body parts of *Jacksonoides queenslandicus*.

faced by a lure that was 50 mm or closer); ambivalent stalking (test spiders sometimes adopted the retracted-palps posture or sometimes froze when faced by the lure when no more than 50 mm away, but failed to do so consistently). Spiders that reached the top of the ramp without stalking the lure were recorded as not responding. Data on stalking style (cryptic, ordinary and ambivalent) and tendency to stalk (i.e. pursuit tendency) were analysed. Results obtained using different lures were compared using tests of independence with Bonferroni adjustments (see Rice, 1989).

Intact lures (controls) were made, as in previous studies (Jackson and Tarsitano, 1993; Li and Jackson, 1996b), by mounting dead, dried prey on cork disks. Experimental lures were made by systematically modifying the appearance of an intact lure such as that shown in Fig. 2. Eighteen different lures were tested (Fig. 3). Three of these were made from an intact salticid (*J. queenslandicus* Wanless; Fig. 3A), an intact wolf spider (*Lycosa hilaris* Forster; Fig. 3B) and an intact house fly (*Musca domestica* Linnaeus; Fig. 3C) and provided the basis for comparing the reactions of *P. fimbriata* to 15 modified lures (Fig. 3D–R).

Results

Influence of the presence of legs and palps

Eight modified lures were made by removing combinations of legs, palps or both from intact salticid lures: two palps removed (Fig. 3D); one leg I removed (Fig. 3E); both legs I removed (Fig. 3F); four legs (pairs I and II) removed (Fig. 3G); both legs II removed (Fig. 3H); four legs (I and II) and both palps removed (Fig. 3I); all legs removed (Fig. 3J); all appendages (eight legs and both palps) removed (Fig. 3K).

When data from an intact salticid lure were compared with data from each of the modified lures, there were no significant differences in how often different stalking styles were adopted by *P. fimbriata* (Table 1). Pursuit tendencies against the lure with both palps removed, the lure with a single leg I removed and the lure with both legs II removed were not significantly different from the pursuit tendency against the intact salticid lure (Fig. 4A). However, compared with the intact salticid lure, significantly fewer ($P < 0.001$) *P. fimbriata* stalked each of the other modified lures (Fig. 4B,C).

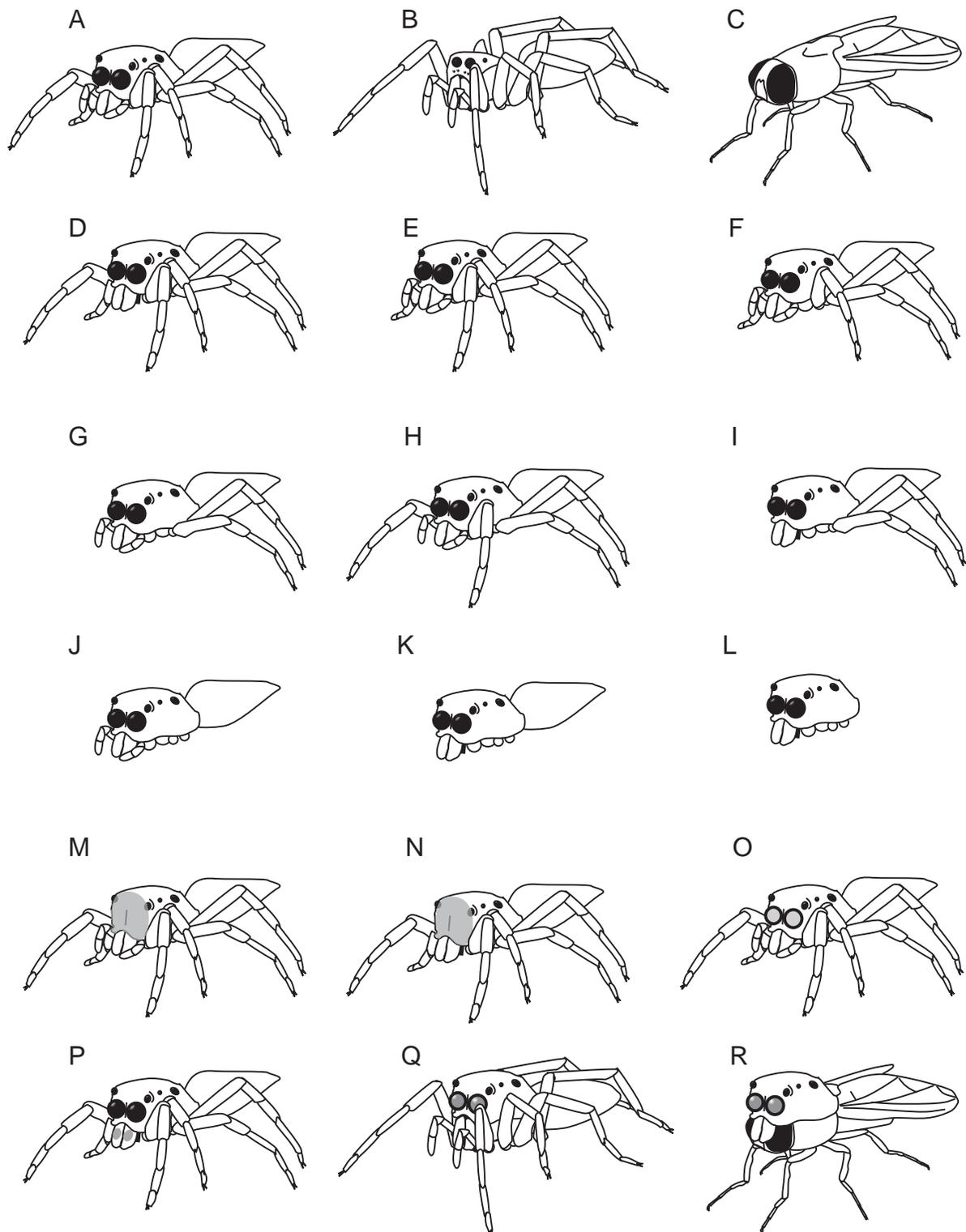


Fig. 3. Lures used to test for optical cues that trigger cryptic stalking by *Portia fimbriata*. Intact lures made from (A) *Jacksonoides queenslandicus* (jumping spider), (B) *Lycosa hiliaris* (wolf spider) and (C) *Musca domestica* (house fly). (D–P) Modified lures made from *J. queenslandicus* with (D) both palps removed, (E) one leg I removed, (F) both legs I removed, (G) legs I and II removed, (H) legs II removed, (I) legs I and II and palps removed, (J) all legs removed, (K) all legs and both palps removed, (L) all legs and both palps and the abdomen removed, (M) anterior-median eyes painted over (outlines obliterated), (N) anterior-median eyes painted over and both palps removed, (O) anterior-median eyes painted over but outlines left intact, (P) both palps removed and circles painted on chelicerae. (Q,R) Two modified non-salticid lures: *J. queenslandicus* carapace (semi-transparent anterior-median eyes) mounted over the anterior dorsal region of *L. hiliaris* (Q) and of *M. domestica* (R).

Table 1. Data for *Portia fimbriata* tested with intact and modified lures

Lure	<i>N</i>	Stalking tendency* (%)	Cryptic stalking‡ (%)	Ambivalent stalking‡ (%)	Ordinary stalking‡ (%)
Intact salticid	224	83	82	14	4
Intact lycosid	70	73	0	16	84
Intact house fly	152	43	0	0	100
Salticid with both palps removed	50	78	97	3	0
Salticid with one leg I removed	49	71	89	11	0
Salticid with both legs I removed	81	67	85	11	4
Salticid with legs I and II removed	74	61	78	18	4
Salticid with both legs II removed	51	80	95	5	0
Salticid with legs I, legs II and both palps removed	96	54	79	19	2
Salticid with all legs removed	131	40	73	21	6
Salticid with all legs and both palps removed	122	46	63	27	11
Salticid with all legs, both palps and abdomen removed	179	27	67	27	6
Salticid with AM eyes painted over (outlines obliterated)	59	69	0	12	88
Salticid with AM eyes painted over (outlines obliterated) and both palps removed	69	61	0	10	90
Salticid with centres of AM eyes painted over (outlines intact)	28	75	57	33	10
Salticid with paint on chelicerae and both palps removed	59	69	90	10	0
Lycosid with salticid carapace atop its own carapace	63	78	92	6	2
House fly with salticid carapace placed on head and thorax	59	54	63	31	6

*Percentage of *N*.

‡Percentage of total number stalking (i.e. cryptic stalking, ambivalent stalking and ordinary stalking sum to 100%).

AM, anterior-median.

Influence of the presence of an abdomen

Two salticid lures were used to test whether the presence of an abdomen is a cue. One lure (Fig. 3K) had all its legs and both its palps removed, but the abdomen was left intact. The other lure was the same except that its abdomen was also removed (Fig. 3L). Removing the legs and palps from both lures ensured that the abdomen (or its absence) was clearly visible, rather than being partly or wholly obscured by appendages.

When data from testing with each of the modified lures and data from testing with the intact lure were compared, there was no significant difference in the frequency with which different stalking styles were adopted by *P. fimbriata*. However, significantly ($P < 0.001$) more *P. fimbriata* (Table 1) stalked the intact lure and the lure with no legs or palps (but the abdomen intact) than stalked the lure with no abdomen (Fig. 4C).

Influence of the presence of a salticid carapace

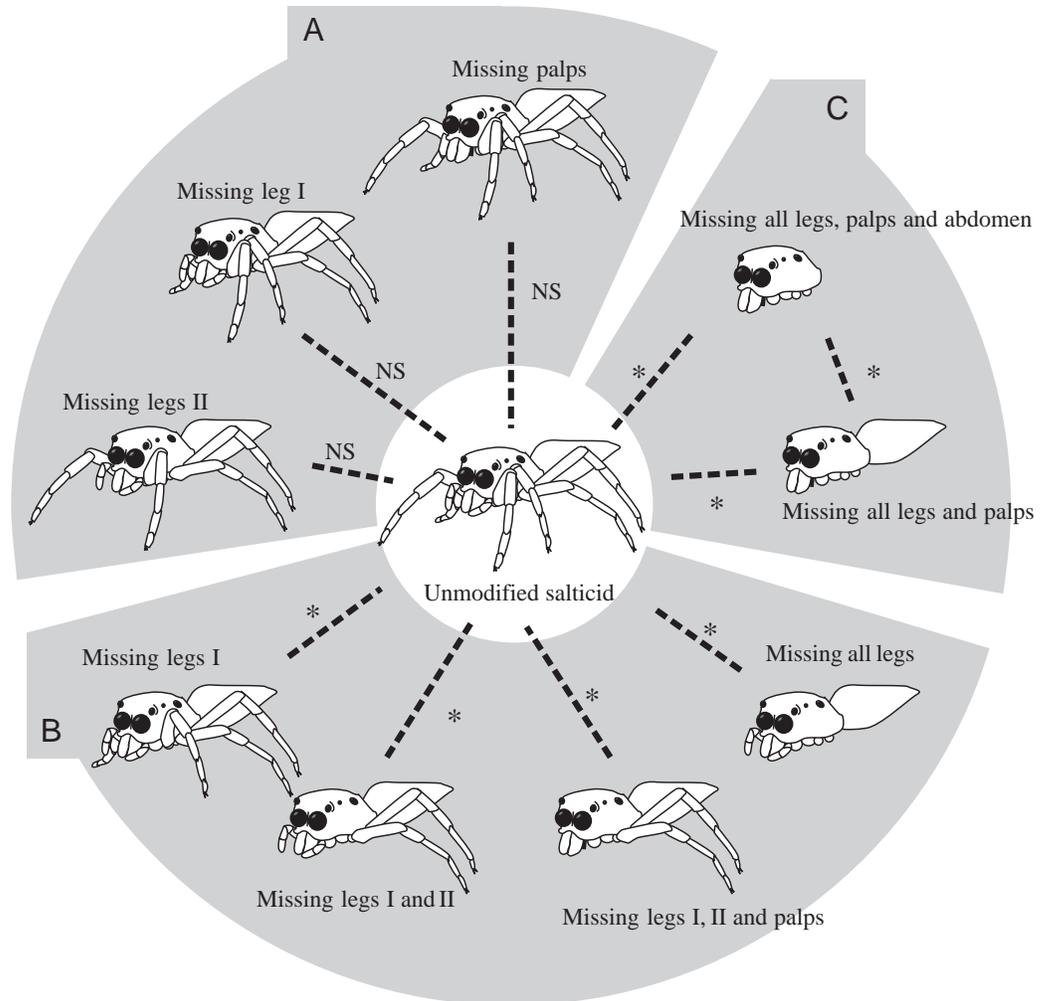
Three intact lures (salticid, lycosid and house fly) and three modified lures were used (Fig. 3). One modified lure had all the legs, both the palps and the abdomen removed (Fig. 3L), leaving only the cephalothorax. The remaining two modified lures were made from an intact lycosid and an intact house fly onto which an excised *J. queenslandicus* carapace, with

chelicerae intact, was glued (over the carapace of the lycosid and over the dorsal region of the head and thorax of the fly). These were called the ‘lycosid-salticid’ lure (Fig. 3Q) and ‘fly-salticid’ lure (Fig. 3R). Although the lycosid-salticid and fly-salticid lures had non-salticid legs and body parts, they had salticid carapaces with large anterior-median eyes. The anterior-median eyes, being hollow, were nearly transparent.

When data from an intact salticid lure were compared with data from the three modified lures that retained a salticid carapace (isolated salticid cephalothorax, lycosid-salticid and fly-salticid), there was no significant difference in how often different stalking styles were adopted by *P. fimbriata* (Table 1). However, there was a significant difference in how often different stalking styles were adopted with the intact house-fly lure ($P < 0.001$) and the intact lycosid lure ($P < 0.001$) compared with the intact salticid, the lycosid-salticid and the fly-salticid lures (Fig. 5).

Pursuit tendency against the intact lycosid lure and the lycosid-salticid lure were not significantly different from the pursuit tendency against the intact salticid lure (Fig. 5). Nor was there a significant difference between the pursuit tendency against the fly-salticid lure and the intact house-fly lure, nor against the lycosid-salticid lure and the intact lycosid lure. However, compared with the intact salticid lure,

Fig. 4. Comparisons (χ^2 -tests of independence with Bonferroni adjustments) of the tendency of *Portia fimbriata* to stalk intact and modified *Jacksonoides queenslandicus* lures (different combinations of appendages removed). (A) Three modified lures each compared with the intact lure: no significant differences in stalking tendency were observed. (B,C) For six lures, the stalking tendency was significantly lower than with the intact lure. (C) The influence of the abdomen on the stalking tendency of *P. fimbriata*: lures with all appendages removed, but with the abdomen intact, compared with lures with all legs removed and the abdomen also removed. An asterisk indicates a significant difference ($P < 0.001$). NS, not significant.



significantly fewer ($P < 0.001$) *P. fimbriata* stalked the isolated salticid cephalothorax, the intact house-fly lure and the fly-salticid lure.

Influence of the anterior-median eyes

Four salticid lures were designed for this experiment. Using a fine brush, paint (opaque, red, water-based enamel) was applied to the anterior surfaces of the carapace (face) of two lures (one with both palps removed and the other intact), completely obscuring all details of the anterior-median eyes (Fig. 3M,N). Another two lures were controls for the effects of the paint. One had paint carefully applied to the lens of each anterior-median eye, coating the surface but leaving the outline intact (Fig. 3O). The other control lure (palps removed) had a circle of paint, approximately the same size as an anterior-median eye, applied to the anterior of the basal segment of each chelicera (Fig. 3P).

Paint was applied to each lure shortly after mounting, but before the lure was sprayed with plastic lacquer. The red paint was readily seen by human observers, but salticid photoreceptors are decidedly inefficient at detecting long-wavelength light (i.e. red), being unable to discriminate

wavelengths in the red region from green (Blest et al., 1981). For *P. fimbriata*, red paint would probably appear to be simply an exceptionally dark shading.

When data from an intact salticid lure were compared with data from the two modified control lures (anterior-median eye centres painted only and anterior-median-eye-sized circles painted on the chelicerae), there was no significant difference in how often different stalking styles were adopted by *P. fimbriata* (Table 1). However, there was a significant difference ($P < 0.001$) in how often different stalking styles were adopted with the two lures that had the anterior-median eyes completely obscured by paint compared with the intact salticid lure (Fig. 6). Against none of the modified lures was pursuit tendency significantly different from that against the intact lure.

Discussion

Cryptic stalking was adopted only when lures included a salticid carapace on which the anterior-median eyes were visible. There was no evidence that removal of the palps, the legs or the abdomen from a salticid lure influenced the

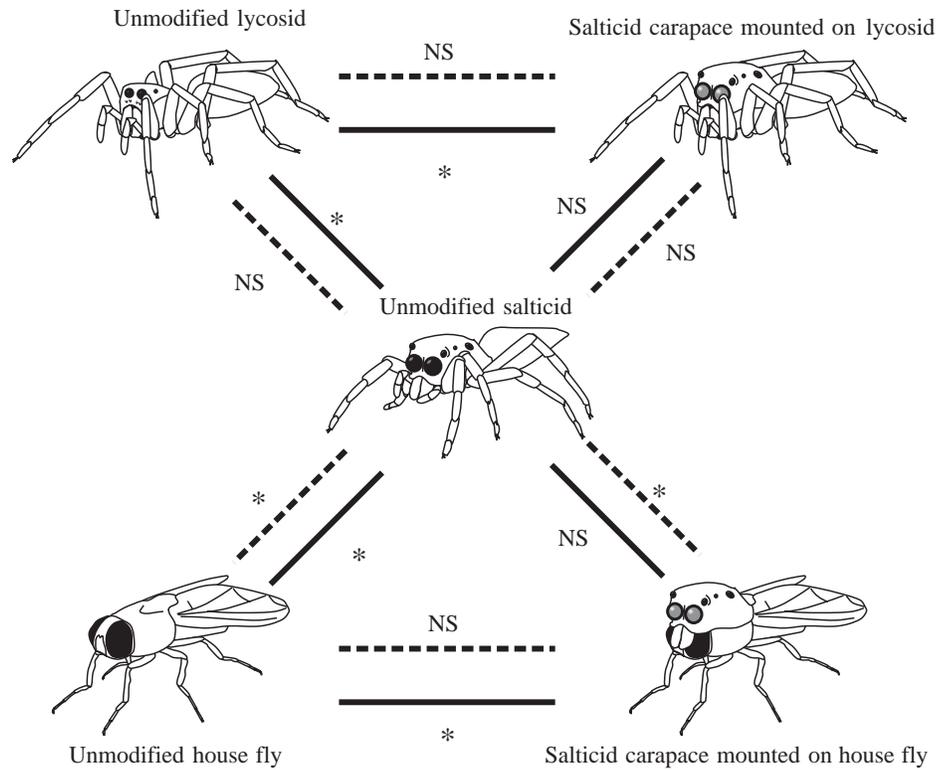


Fig. 5. Comparison (χ^2 -test of independence with Bonferroni adjustment) showing the influence of the salticid carapace on the stalking tendency (dashed lines) and stalking style (solid lines) of *Portia fimbriata*. An asterisk indicates a significant difference ($P < 0.001$). NS, not significant.

tendency of *P. fimbriata* to adopt cryptic stalking. Even replacing the appendages, abdomen and body with those of another animal (e.g. a lycosid or house fly) had no apparent influence on this tendency as long as the salticid carapace was left intact and the anterior-median eyes remained visible.

It appears that the anterior-median eyes provide vital cues. The fact that the anterior-median eyes are similar in configuration and appearance across almost all salticid species (Coddington and Levi, 1991) helps explain why the Queensland *P. fimbriata* adopted cryptic stalking against such

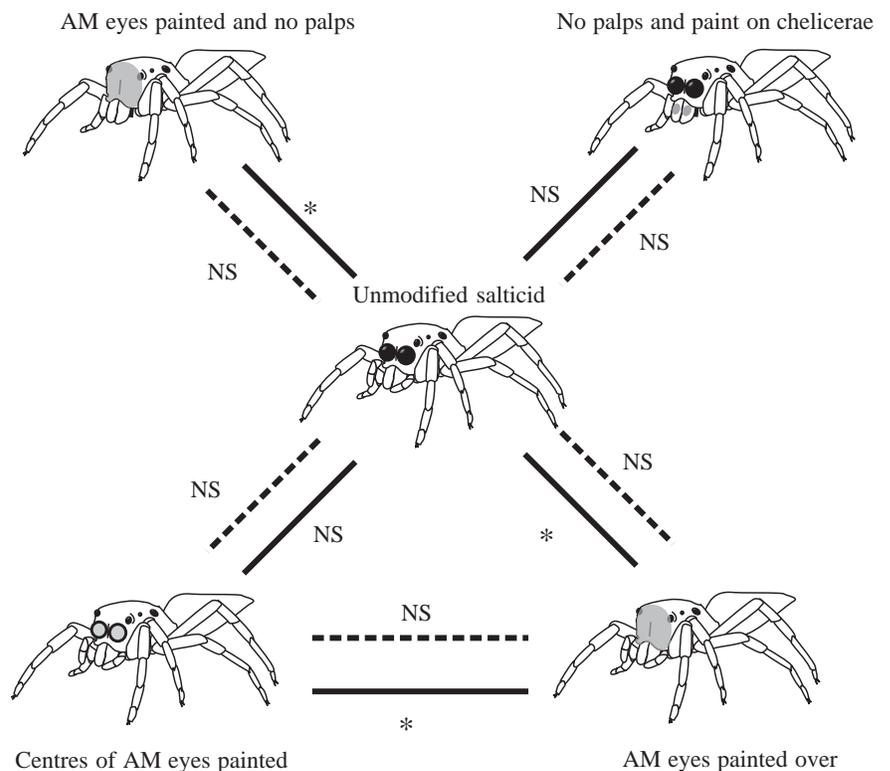


Fig. 6. Comparison (χ^2 -test of independence with Bonferroni adjustment) showing the influence of salticid anterior-median (AM) eyes on the stalking tendency (dashed lines) and stalking style (solid lines) of *Portia fimbriata*. An asterisk indicates a significant difference ($P < 0.001$). NS, not significant.

a wide range of salticids (D. P. Harland and R. R. Jackson, unpublished observations). Salticids from the subfamily Lyssomaninae, which tend to be leaf dwellers, with the females, but not the males, being unusually translucent, elicited some unusual responses (D. P. Harland and R. R. Jackson, unpublished observations). An artefact of the translucent cuticle is that, when viewed head on, the anterior-median eyes of lyssomanine females, unlike those of lyssomanine males, have light and dark regions that flicker in and out of view. *P. fimbriata* sometimes adopted ordinary stalking against lyssomanine females, but never against lyssomanine males, suggesting that the flickering anterior-median eyes may impair the ability of *P. fimbriata* to identify lyssomanine females.

We investigated the cues used by Queensland *P. fimbriata* to identify other salticids in the context of predatory versatility (i.e. cues for distinguishing salticids from other categories of prey), but earlier studies on the prey-recognition cues used by salticids (Homann, 1928; Heil, 1936; Crane, 1949; Drees, 1952) have envisaged salticids facing a simpler problem. In what was arguably the most influential study, Drees (1952) used lures (two-dimensional drawings and three-dimensional models made of Plasticine and wire) to present to males of *Salticus scenicus*, and these established that leg characteristics (angle to the vertical, thickness and positioning around the body) were critical. Drees (1952) envisaged his experiments as asking *S. scenicus* simply to distinguish between two mutually exclusive categories, prey (i.e. insects) and conspecifics (i.e. salticids). When *S. scenicus* attacked a lure, this was taken as evidence that the object had been identified as prey. When *S. scenicus* displayed, this was taken as evidence that the object had been identified as another salticid. The impression from this study is that *S. scenicus* relies on leg characteristics alone (especially thickness, density and a particular angle to the vertical, 25–30°) when identifying salticids, with almost any other object of appropriate size being, by default, accepted as prey. Land (1972) concisely summed up the theory of Drees

by stating that the perceptual decision process used when a salticid identifies an object can be described by an algorithm: ‘if it moves, find out whether it has legs in the right places; if it does, mate or avoid it; if it doesn’t, catch it’.

The algorithm of Drees (1952) is simple. There are only two discrete classes of object (prey and conspecifics), and they are exclusive in terms of both the cues they provide and the responses they elicit. However, the prevalence of predatory versatility in the Salticidae (Jackson, 1992) was not appreciated in the 1950s. That is, in addition to distinguishing between prey and conspecifics, salticids with pronounced predatory versatility also discriminate between different types of prey (e.g. flies, worker ants, caterpillars and spiders), and deploy appropriate tactics against each (Edwards et al., 1975; Cutler, 1980; Jackson and Blest, 1982; Freed, 1984; Jackson and van Olphen, 1991).

We might attempt to accommodate predatory versatility into the algorithm of Drees (1952) simply by including a new clause for each type of prey. For the Queensland *P. fimbriata*, we might try an algorithm that reads: ‘find out if the object has large anterior-median eyes; if it does, stalk it using cryptic stalking; if it does not, stalk it using ordinary stalking’. This algorithm, however, is not adequate for *P. fimbriata* because the features that provide cryptic-stalking cues (anterior-median eyes) are present not only on salticid prey but also on conspecifics. A conspecific elicits display behaviour, not cryptic stalking. When displaying, movement is smooth and rapid, rather than slow and choppy. The legs are elevated, the body sways from side to side, the palps are lowered below the chelicerae, and so forth (Jackson, 1982). Although *P. fimbriata* is influenced by pheromones to a degree that is unusual among salticids (Pollard et al., 1987), optical cues alone suffice for eliciting display and distinguishing conspecifics from other salticids, even in the absence of movement. Work in progress suggests that the spindly, fringed legs of *Portia* spp. are critical. Broken outlines of legs may conceal *Portia* spp. from

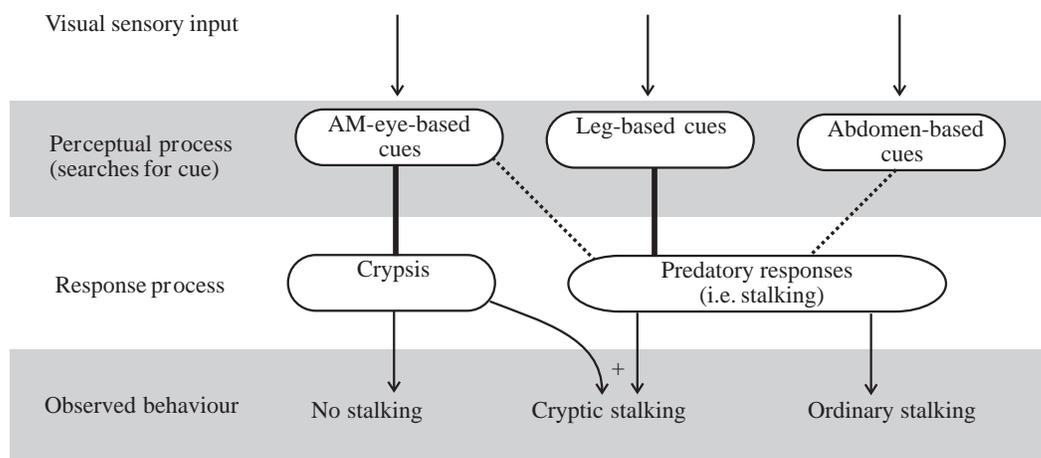


Fig. 7. The proposed decision-structure algorithm for the Queensland *Portia fimbriata* when confronting a lure. Perceptual processes search the visual input for specific cues. When these cues are found, the perceptual processes may ready or activate the response processes. The combination of readied and activated response processes determines the observed behaviour. Perceptual processes can have either a strong (solid lines) or a weak (broken lines) influence on response processes.

other salticids, at the same time serving as conspecific-identifying cues.

Features of the legs of the prey of *P. fimbriata* are also important because they strongly influence stalking tendency (Fig. 4A,B). Having found that removing one or more pairs of legs reduced stalking tendency, it is tempting to suggest an algorithm for *P. fimbriata* phrased in the style of Drees: 'if the object has enough non-fringed legs in the right places, react to it as prey; if it is prey, determine whether it also has anterior-median eyes; if it does, adopt cryptic stalking; if it does not, adopt ordinary stalking'. However, even this is an oversimplification because *P. fimbriata* sometimes stalked salticid lures that had all legs removed. Evidently the cephalothorax (including the anterior-median eyes) and the abdomen also influence the inclination of *P. fimbriata* to begin stalking, but less strongly than cues from salticid legs (Table 1).

Expressing algorithms in terms of a series of 'if' statements joined to form simple discrete decision trees appears to be inadequate for *P. fimbriata*. A more appropriate way of expressing an algorithm for *P. fimbriata* might be to base it on the interactions between a set of independent perceptual processes, each having the task of identifying a specific cue, and a set of response processes, each mediating different predatory tactics. When a perceptual process identifies a relevant cue, it might activate one or more response processes. For stalking lures, there would be only two relevant response processes: (i) a general predatory response (i.e. to stalk or not to stalk) that is activated when the perceptual processes identify some combination of leg-based, anterior-median-eye-based and abdomen-based cues; (ii) a more specific predatory response (i.e. to adopt or not to adopt elements of cryptic stalking: called the 'crypsis response' for short) that is readied (but not necessarily activated) only when the perceptual processes identify anterior-median-eye-based cues. Activating the crypsis response requires that the general predatory response is also activated during the time when the crypsis response is readied. Expressing the algorithm in this way, what we observe when a *P. fimbriata* is confronted with a lure depends on whether one or the other, or both, response process has been activated (Fig. 7). When the crypsis response is activated, but the general predatory response process is not, no stalking is triggered. When the general predatory response process is activated, but the crypsis response process is not, stalking is triggered, but only ordinary stalking. When both the general predatory response process and the crypsis response process are activated, cryptic stalking is triggered.

Each response process might be influenced to different degrees by different cue-identification processes. This might be seen as the probability that a perceptual process, once activated, will in turn activate a particular response process. The crypsis response process appears to be influenced strongly by the perceptual process that identifies the anterior-median-eye-based cues, whereas the general predatory response process appears to be influenced strongly by the perceptual

process that identifies leg-based cues, but only weakly by the perceptual process that identifies abdomen-based cues and the process that identifies anterior-median eye-based cues.

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References

- Blest, A. D.** (1987). Comparative aspects of the retinal mosaics of jumping spiders. In *Arthropod Brain: Its Evolution, Development, Structure and Functions* (ed. A. P. Gupta), pp. 203–229. New York, Chichester, Brisbane, Toronto, Singapore: John Wiley and Sons, Inc.
- Blest, A. D., Hardie, R. C., McIntyre, P. and Williams, D. S.** (1981). The spectral sensitivities of identified receptors and the function of retinal tiering in the principal eyes of a jumping spider. *J. Comp. Physiol.* **145**, 227–239.
- Blest, A. D. and Price, G. D.** (1984). Retinal mosaics of the principal eyes of some jumping spiders (Salticidae: Araneae): Adaptations for high visual acuity. *Protoplasma* **120**, 172–184.
- Clark, R. J. and 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**, 371–375.
- Coddington, J. A. and Levi, H. W.** (1991). Systematics and evolution of spiders (Araneae). *Annu. Rev. Ecol. Syst.* **22**, 565–592.
- Crane, J.** (1949). Comparative biology of salticid spiders at Rancho Grande, Venezuela. IV. An analysis of display. *Zoologica* **34**, 159–214.
- Curio, E.** (1976). *The Ethology of Predation*. Berlin: Springer Verlag.
- Cutler, B.** (1980). Ant predation by *Habrocestum pulex* (Hentz) (Araneae: Salticidae). *Zool. Anz.* **204**, 97–101.
- Drees, O.** (1952). Untersuchungen über die angeborenen Verhaltensweisen bei Springspinnen (Salticidae). *Z. Tierpsychol.* **9**, 169–207.
- Edwards, G. B., Carroll, J. F. and Whitcomb, W. H.** (1975). *Stoidis aurata* (Araneae: Salticidae), a spider predator of ants. *Florida Ent.* **57**, 337–346.
- Edwards, G. B. and Jackson, R. R.** (1993). Use of prey-specific behaviour by North American jumping spiders (Araneae, Salticidae) of the genus *Phidippus*. *J. Zool., Lond.* **229**, 709–716.
- Forster, L. M.** (1982). Vision and prey-catching strategies in jumping spiders. *Am. Sci.* **70**, 165–175.
- Freed, A. N.** (1984). Foraging behaviour in the jumping spider *Phidippus audax*: bases for selectivity. *J. Zool., Lond.* **203**, 49–61.
- Harland, D. P., Jackson, R. R. and Macnab, A. M.** (1999). Distances at which jumping spiders (Araneae: Salticidae) distinguish between prey and conspecific rivals. *J. Zool. Lond.* **247**, 357–364.
- Heil, K. H.** (1936). Beiträge zur Physiologie und Psychologie der Springspinnen. *Z. Vergl. Physiol.* **23**, 125–149.
- Homann, H.** (1928). Beiträge zur Physiologie der Spinnenaugen. I. Untersuchungsmethoden. II. Das Sehvermögen der Salticiden. *Z. Vergl. Physiol.* **7**, 201–268.
- Jackson, R. R.** (1982). The biology of *Portia fimbriata*, a web-

- building jumping spider (Araneae, Salticidae) from Queensland: intraspecific interactions. *J. Zool., Lond.* **196**, 295–305.
- Jackson, R. R.** (1988). The biology of *Jacksonoides queenslandica*, a jumping spider (Araneae: Salticidae) from Queensland: intraspecific interactions, web-invasion, predators and prey. *N. Z. J. Zool.* **15**, 1–37.
- Jackson, R. R.** (1992). Eight-legged tricksters: Spiders that specialize in catching other spiders. *Bioscience* **42**, 590–598.
- Jackson, R. R. and 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**, 255–293.
- Jackson, R. R. and Hallas, S. E. A.** (1986). Comparative biology of *Portia africana*, *P. albimana*, *P. fimbriata*, *P. labiata* and *P. shultzi*, araneophagic, web-building jumping spiders (Araneae: Salticidae): utilisation of webs, predatory versatility and intraspecific interactions. *N. Z. J. Zool.* **13**, 423–489.
- Jackson, R. R. and Tarsitano, M. S.** (1993). Responses of jumping spiders to motionless prey. *Bull. Br. Arachnol. Soc.* **9**, 105–109.
- Jackson, R. R. and van Olphen, A.** (1991). Prey-capture techniques and prey preferences of *Corythalia canosa* and *Pystira orbiculata*, ant-eating jumping spiders (Araneae, Salticidae). *J. Zool., Lond.* **223**, 577–591.
- Jackson, R. R. and Wilcox, R. S.** (1998). Spider-eating spiders. *Am. Sci.* **86**, 350–357.
- Land, M. F.** (1971). Orientation by jumping spiders in the absence of visual feedback. *J. Exp. Biol.* **54**, 119–139.
- Land, M. F.** (1972). Mechanisms of orientation and pattern recognition by jumping spiders (Salticidae). In *Information Processing in the Visual Systems of Arthropods* (ed. R. Wehner), pp. 231–247. Berlin, Heidelberg, New York: Springer-Verlag.
- Land, M. F.** (1985a). The morphology and optics of spider eyes. In *Neurobiology of Arachnids* (ed. F. G. Barth), pp. 53–78. Berlin, Heidelberg, New York: Springer-Verlag.
- Land, M. F.** (1985b). Fields of view of the eyes of primitive jumping spiders. *J. Exp. Biol.* **119**, 381–384.
- Li, D. and Jackson R. R.** (1996a). Prey-specific capture behaviour and prey preferences of myrmecophagic and araneophagic jumping spiders (Araneae: Salticidae). *Rev. Suisse Zool. hors série*, 423–436.
- Li, D. and Jackson R. R.** (1996b). Prey preferences of *Portia fimbriata*, an araneophagic, web-building jumping spider (Araneae: Salticidae) from Queensland. *J. Insect Behav.* **9**, 613–642.
- Li, D., Jackson, R. R. and Harland, D. P.** (1999). Prey-capture techniques and prey preferences of *Aelurillus aeruginosus*, *A. cognatus* and *A. kochi*, ant-eating jumping spiders (Araneae: Salticidae) from Israel. *Isr. J. Zool.* **45**, 341–360.
- Pollard, S. D., Macnab, A. M. and Jackson, R. R.** (1987). Communication with chemicals: pheromones and spiders. In *Ecophysiology of Spiders* (ed. W. Nentwig), pp. 133–141. Berlin, Heidelberg, New York: Springer-Verlag.
- Rice, W. R.** (1989). Analyzing tables of statistical tests. *Evolution* **43**, 223–225.
- Taylor, P. W., Jackson, R. R. and Robertson, M. W.** (1998). A case of blind spider's buff?: prey-capture by jumping spiders (Araneae: Salticidae) in the absence of visual cues. *J. Arachnol.* **26**, 369–381.
- Wanless, F. R.** (1978). A revision of the spider genus *Portia* (Araneae: Salticidae). *Bull. Br. Mus. Nat. Hist. Zool.* **34**, 83–124.
- Willey, M. B. and Jackson R. R.** (1993). Olfactory cues from conspecifics inhibit the web-invasion behaviour of *Portia*, a web-invading, araneophagic jumping spider (Araneae, Salticidae). *Can. J. Zool.* **71**, 1415–1420.