

# SPECULATIVE HUNTING BY AN ARANEOPHAGIC SALTICID SPIDER

by

**ROBERT J. CLARK, DUANE P. HARLAND and ROBERT R. JACKSON<sup>1,2)</sup>**

(Department of Zoology, University of Canterbury, Private Bag 4800, Christchurch, New Zealand)

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## Summary

*Portia fimbriata*, an araneophagic jumping spider (Salticidae), makes undirected leaps (erratic leaping with no particular target being evident) in the presence of chemical cues from *Jacksonoides queenslandicus*, another salticid and a common prey of *P. fimbriata*. Whether undirected leaping by *P. fimbriata* functions as hunting by speculation is investigated experimentally. Our first hypothesis, that undirected leaps provoke movement by *J. queenslandicus*, was investigated using living *P. fimbriata* and three types of lures made from dead, dry arthropods (*P. fimbriata*, *J. queenslandicus* and *Musca domestica*). When a living *P. fimbriata* made undirected leaps or a spring-driven device made the lures suddenly move up and down, simulating undirected leaping, *J. queenslandicus* responded by waving its palps and starting to walk. There was no statistical evidence that the species from which the lure was made influenced *J. queenslandicus* response in these tests. Our second hypothesis, that *J. queenslandicus* reveals its location to *P. fimbriata* by moving, was investigated by recording *P. fimbriata*'s reaction to *J. queenslandicus* when *J. queenslandicus* reacted to lures simulating undirected leaping. In these tests, *P. fimbriata* responded by turning toward *J. queenslandicus* and waving its palps.

**Keywords:** *Portia fimbriata*, *Jacksonoides queenslandicus*, jumping spiders, predation, speculative hunting.

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<sup>1)</sup> Corresponding author; e-mail address: r.jackson@zool.canterbury.ac.nz

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## Introduction

A general problem facing predators is how to locate prey (Curio, 1976). When vision is relied on, being out of the predator's line of sight or being camouflaged will interfere with detection (Edmunds, 1974). 'Hunting by speculation' (directing attacks at refuges where prey tend to be found or probing areas in which prey normally hide) is a potential solution (Curio, 1976). Envisaged not as prey-capture behaviour, but instead as a tactic for locating prey, hunting by speculation might function for a predator by provoking a response that reveals the prey's location. Woodstorks, for example, may probe submerged vegetation even when no prey is visible (Kahl & Peacock, 1963), *Octopus cyanea* Gray attacks holes in coral even in the absence of prey (Yarnell, 1969) and lions may run to the top of hills, apparently in anticipation of startling unwary prey on the other side (Schaller, 1972). However, examples from arthropods, and experimental studies on any predator, have been scarce.

In the present paper, we investigate hunting by speculation in *Portia fimbriata* (Doleschall) from Queensland, Australia, an araneophagic jumping spider (Salticidae) that preys especially often on other salticids (Jackson & Blest, 1982). *Jacksonoides queenslandicus* Wanless (Salticidae) is especially abundant in the same habitat as *P. fimbriata* (Jackson, 1988) and is probably the salticid species on which *P. fimbriata* most often preys. Preliminary studies show that chemical cues from *J. queenslandicus*, even in the absence of *J. queenslandicus*, prepare *P. fimbriata* for predation by stimulating the adoption of a special palp posture (retracted palps) characteristic of stalking sequences against salticids as prey and by heightening *P. fimbriata*'s attention to visual cues from *J. queenslandicus*. Preliminary studies indicate that chemical cues from *J. queenslandicus* also elicit intermittent undirected leaping (erratic leaping with no particular target being evident) by *P. fimbriata*. The absence of an apparent target suggests that this behaviour functions as speculative hunting. Two hypotheses are considered here: (1) undirected leaps by *P. fimbriata* stimulate *J. queenslandicus* to move; (2) by moving, *J. queenslandicus* gives away its location to *P. fimbriata*.

## Methods

### General

Standard maintenance procedures in a controlled-environment laboratory (light-dark cycle, 12L:12D; lights on at 0800 h) were adopted, as detailed elsewhere (Jackson & Hallas, 1986).

Adult females of *P. fimbriata* and *J. queenslandicus* (body length: *P. fimbriata* 10–11 mm; *J. queenslandicus* 5–6 mm), from laboratory cultures, were used.

#### *Experiment 1: J. queenslandicus* viewing *P. fimbriata*

These tests were used to get baseline information on how *J. queenslandicus* reacted when *P. fimbriata* made undirected leaps. For a test chamber, we used a transparent perspex box (length  $\times$  width  $\times$  height: 211  $\times$  144  $\times$  44 mm). Three regions of the box were defined: region 1 extended 50 mm out from one end of the box; region 2 extended 50 mm out from the opposite end; region 3 was the space between the other two regions. There was a 5-mm wide hole (kept plugged with a cork) in the bottom of the box in the centre of region 1 and another in the centre of region 2.

Test spider 1 was put in the box 24–28 h before testing started and had free access to the three regions during this pre-test interval. Testing began between 0800 and 1000 h. When test spider 1 was within 50 mm of one end of the box, a partition (partition 1) was put into place, thereby closing this region (region 1) off from the rest of the box. At the same time, another partition (partition 2) was put into place, closing off region 2. Test spider 2 was introduced 10 min later into region 2 through the hole in the bottom of the cage. For transfer, first test spider 2 was enticed into a plastic tube (diameter 5 mm), then the tube was positioned with one end against the hole in the test chamber. When gently prodded by inserting a soft brush through the other end of the tube, test spider 2 walked slowly out into the test chamber.

Testing began only if *J. queenslandicus* had remained quiescent for the previous 5 s facing region 2. With *J. queenslandicus* quiescent, partition 2 followed by partition 1 was removed. The behaviour of the two spiders was observed for the next 10 min. Control tests were the same as experimental tests except that partition 2 remained in place (*i.e.* *J. queenslandicus* could not see *P. fimbriata* during these tests).

Being interested specifically in how *J. queenslandicus* reacted to undirected leaping by *P. fimbriata*, we consider only those experimental and control tests in which: (1) *P. fimbriata* made a single undirected leap during the 10-min test interval and (2) *J. queenslandicus* remained quiescent for the entire period prior to *P. fimbriata* making its undirected leap. The test was aborted if: (1) *P. fimbriata* moved during an experimental test into region 3 before making an undirected leap or (2) *P. fimbriata* made a second undirected leap before the 10-min test interval elapsed. No individual *J. queenslandicus* or *P. fimbriata* was used in more than one successful test. Different individuals were used in experimental and control tests.

#### *Experiment 2: J. queenslandicus* viewing a lure

Our objective was to test simultaneously how *J. queenslandicus* reacted to a moving lure (a simulation of undirected leaps by *P. fimbriata*) and how *P. fimbriata* reacted to *J. queenslandicus*' reaction to the lure. The test chamber (Fig. 1) was a rectangular perspex box (length  $\times$  width  $\times$  height: 147  $\times$  51  $\times$  51 mm) with two tubes. Its design permitted viewing of a lure by *J. queenslandicus* and viewing of *J. queenslandicus* by *P. fimbriata*.

Tube 1 (internal diameter 13 mm), made of transparent glass, fit inside the box at one end. Except when introducing *J. queenslandicus*, the hole opening to the outside was kept stoppered. Initially, a hole at the opposite end of the tube was blocked by an opaque metal screen (partition 1). Partition 1, which fit into a slit in the box, could be moved from side to side (indicated by dotted lines in Fig. 1). Tube 2 (internal diameter 13 mm), situated on

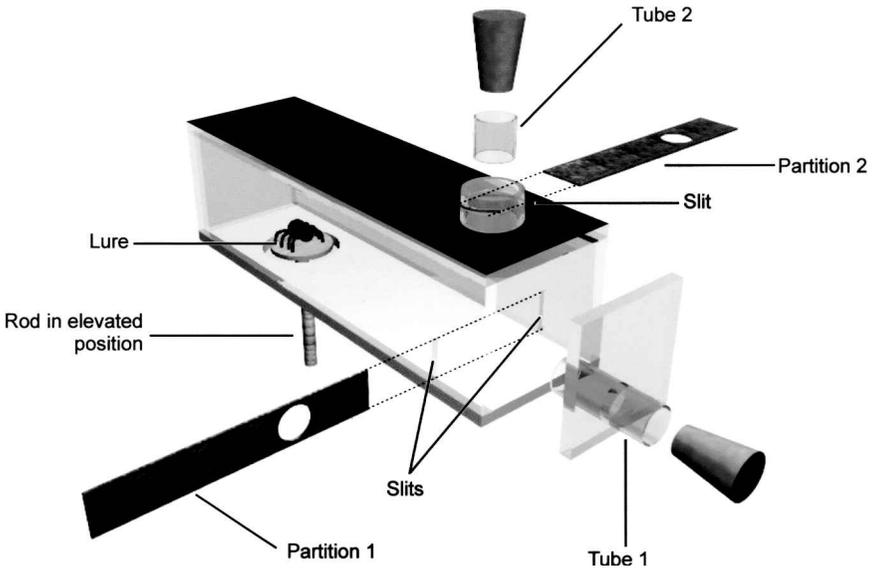


Fig. 1. Apparatus used in experiment 2. *Jacksonoides queenslandicus* (in Tube 1), but not *Portia fimbriata* (in Tube 2), can view the lure. *P. fimbriata* can view the reaction of *J. queenslandicus* to the lure. Top and bottom of the box are opaque perspex and the sides transparent perspex. Tubes are transparent glass. Before testing begins, the opening of each tube into the box is blocked by a sliding partition, as indicated by dotted lines. During testing both tubes are unblocked by aligning the hole in the partition with the tube opening. The lure is on top of a wooden rod connected to an electric motor 'leap generator' (not shown).

the top of the chamber, housed *P. fimbriata*. The distal opening of tube 2 was kept stoppered except when introducing *P. fimbriata*. The proximal opening of tube 2 opened into a wider tube (internal diameter 20 mm) which in turn opened into the box. An opaque metal screen (partition 2) covered the opening between the narrow and wide tube. Partition 2 fit into a slit in the wider tube, and it could be moved from side to side (indicated by dotted lines in Fig. 1).

The wide tube was positioned so that its centre was directly above the opening of tube 1 into the interior of the box. The top of the box was opaque. This meant that the only part of the box's interior visible to *P. fimbriata* during a test was around the opening of tube 1.

At the far end of the box, positioned in front of tube 1, there was a hole in the bottom of the box through which a lure could move. Each lure was made by positioning a dead *J. queenslandicus*, *P. fimbriata* or house fly (*Musca domestica* L.) in a lifelike posture on a cork disk (diameter 17 mm; height 22 mm). The dead arthropod was then sprayed with an aerosol plastic adhesive (Crystal Clear Lacquer, Atsco Australia Pty.) for preservation and to mask chemical traces that might have remained on the dead arthropod.

Undirected leaps were simulated using a 'leap generator' (a metal stylus moved by an electric motor and a spring). When activated, the motor pulled the stylus down 10 mm against an electromagnet, stretching the spring. When a switch was pushed, the electromagnet was temporarily disabled, letting the spring suddenly return the stylus to its original position,

after which the electric motor immediately moved the stylus back against the reactivated electromagnet.

A wooden rod (80 mm long and 1 mm thick) connected the lure to the leap generator. One end of the rod was glued to the centre of the bottom of the cork disk that held the lure (Fig. 1). The other end of the rod was glued at right angles to the distal end of the stylus. Before testing began, the stylus was held in place by the magnet and the lure was positioned just below the hole in the cage. The lure was oriented so that it was facing tube 1. The quiescent lure and the leap generator remained out of the test spiders' view even after tube 1 was uncovered because the bottom of the cage was opaque.

In each partition there was a hole equal in size to the opening of the tube it blocked. Tubes were unblocked by first moving partition 1 slowly to where its hole was aligned with the opening of tube 1, providing *J. queenslandicus* with access to the interior of the box ('partition moved away'). Next, partition 2 was moved away, providing *P. fimbriata* with a clear view of the end of tube 1. Partitions were moved away only when the following criteria were met: (1) *J. queenslandicus* and *P. fimbriata* were both quiescent; (2) neither was standing on the partition; (3) both were facing the proximal opening of the tube (*i.e.*, both were facing into the interior of the box); (4) both had been quiescent for the previous 5 s; (5) *J. queenslandicus* was near the distal end of tube 1 (*i.e.*, far enough back to be out of *P. fimbriata*'s line of sight when partition 2 was moved away). If, after partition 2 was moved away, both test spiders remained quiescent for the next 5 s, testing began by pushing the switch to make the lure spring upward 10 mm into the box. The behaviour of the two test spiders was recorded for the following 30 s.

Testing was aborted if (1) either spider failed to become quiescent while facing the specified direction within 2 h of being placed into its tube or (2) either spider moved during the interval between moving the partitions (unblocking tubes) and making the lure leap. When tests were aborted, the same two spiders were tested on subsequent days until a successful test was achieved or four successive days of unsuccessful testing elapsed.

These procedures and the design of the apparatus meant that, when a test began, *J. queenslandicus* could see the lure but *P. fimbriata* could not see the lure nor could it see *J. queenslandicus*. *J. queenslandicus* became visible to *P. fimbriata* only after moving to the proximal end of tube 1.

Control tests were identical to tests during which lures were made to leap except that the lure (in controls, always a dead, mounted *P. fimbriata*) was positioned 10 mm further below the hole in the box where it remained below the opaque surface of the box when the switch was pushed. This meant that, in control tests, potential cues that might have come from sound or substrate vibration were still present, but visual cues from the lure were absent. During control tests, the behaviour of both spiders was recorded for 30 s starting 5 s after partition 2 was removed.

No individual *J. queenslandicus* or *P. fimbriata* was used in more than one successful experimental test, and different individuals were used in tests with each of the three types of lures. Another set of individuals was used in the control tests.

## Results

### *Experiment 1. J. queenslandicus viewing P. fimbriata*

There were 14 experimental tests in which *P. fimbriata* made an undirected leap (Table 1). In five of these tests, *J. queenslandicus* remained quiescent for the remainder of the test ('no reaction'). *P. fimbriata* showed no recognisable reaction to these five *J. queenslandicus*. In the other nine tests, *J. queenslandicus* oriented toward *P. fimbriata* and began to wave its palps up and down within 2 s after *P. fimbriata* leapt. Subsequently, eight of these *J. queenslandicus* began to walk about, but the other *J. queenslandicus* remained in place for 145 s, with palps waving intermittently, then became quiescent (*P. fimbriata* oriented toward this *J. queenslandicus*). In one test, *J. queenslandicus* waved its palps, then walked about after the undirected leap, but *P. fimbriata* did not orient toward or otherwise react to *J. queenslandicus*' movement. In the other seven tests, *P. fimbriata* oriented when *J. queenslandicus* became active. In three instances, this was after *J. queenslandicus* began to walk. In the other four instances, it was while *J. queenslandicus* was waving its palps but before beginning to walk. In all instances, *P. fimbriata* retracted its palps after orienting toward *J. queenslandicus*.

TABLE 1. *Results from Experiment 1: Jacksonoides queenslandicus viewing Portia fimbriata in experimental tests but not in controls*

	Experimental	Control
<i>N</i>	14	9
<i>Jacksonoides queenslandicus</i> remained quiescent and <i>Portia fimbriata</i> did not orient toward <i>Jacksonoides queenslandicus</i>	5	9
<i>Jacksonoides queenslandicus</i> became active and <i>Portia fimbriata</i> did not orient toward <i>Jacksonoides queenslandicus</i>	1	0
<i>Jacksonoides queenslandicus</i> became active and <i>Portia fimbriata</i> oriented toward <i>Jacksonoides queenslandicus</i>	8	0

*N*: No. of tests in which *Portia fimbriata* made an undirected leap. Test of independence (Fisher's exact) comparing how many *J. queenslandicus* became active during experimental (9 of 14) and control (0 of 9) tests:  $p = 0.003$ .

There were nine control tests in which *P. fimbriata* (not visible to *J. queenslandicus*) made an undirected leap (Table 1). *Jacksonoides queenslandicus* remained quiescent in each. Compared to when in control cages, *J. queenslandicus* was significantly more likely to begin walking about and waving palps if a leaping *P. fimbriata* was visible (test of independence,  $p < 0.01$ ).

#### *Experiment 2. J. queenslandicus viewing a lure*

Spiders (both *J. queenslandicus* and *P. fimbriata*) rarely left their respective tubes during tests. *J. queenslandicus* became active (walked and waved its palps) in experimental tests (leaping lure of any of the three types visible) significantly more often than in control tests ( $p < 0.001$  for each type of lure, Table 2). How often *J. queenslandicus* and *P. fimbriata* became active during tests did not vary significantly among the experimental tests with different lures.

There were 36 successful control tests. *Jacksonoides queenslandicus* and *P. fimbriata* both remained quiescent in 31 (Table 2). In five, *J. queenslandicus* walked to the distal end of tube 1. When this happened, *P. fimbriata* retracted and waved its palps.

The behaviour of both *J. queenslandicus* and *P. fimbriata* differed depending on whether or not a lure was visible to *J. queenslandicus*. There were 32 successful tests using a lure made from a *P. fimbriata* (Table 2). In nine, both test spiders remained quiescent during the 30-s testing interval. In one, *P. fimbriata* became active, but *J. queenslandicus* remained quiescent. This *P. fimbriata* did not retract its palps. In the remaining 22 tests, *J. queenslandicus* became active about 5 s after the lure was made to leap, after which *P. fimbriata* retracted and waved its palps.

There were 34 successful tests using a lure made from a *J. queenslandicus* (Table 2). In 14, both test spiders remained quiescent during the 30-s testing interval. There were 20 tests in which *J. queenslandicus* became active within 5 s after the lure was made to leap, after which *P. fimbriata* retracted and waved its palps.

There were 35 successful tests using a lure made from a house fly (Table 2). In 12, both test spiders remained quiescent during the 30-s testing interval. In one, *P. fimbriata* became active, but *J. queenslandicus* remained quiescent. There were 23 tests in which *J. queenslandicus* waved its palps within 5 s after the lure was made to leap, after which *P. fimbriata* retracted and waved its palps.

TABLE 2. *Experiment 2: Jacksonoides queenslandicus viewing a lure and Portia fimbriata viewing J. queenslandicus*

Type of test	<i>N</i>	No. of tests in which <i>Jacksonoides queenslandicus</i> became active	Comparison with control (test of independence)	No. of tests in which <i>Portia fimbriata</i> became active	Comparison with control (test of independence)
Control tests	36	5		5	
Experimental tests (lure made from dead, mounted <i>Portia fimbriata</i> )	32	22	$\chi^2 = 21.30, p < 0.001$	23	23.52, $p < 0.001$
Experimental tests (lure made from dead, mounted <i>Jacksonoides queenslandicus</i> )	34	20	$\chi^2 = 19.06, p < 0.001$	20	15.38, $p < 0.001$
Experimental tests (lure made from dead, mounted house fly)	35	23	$\chi^2 = 19.96, p < 0.001$	24	21.96, $p < 0.001$

*J. queenslandicus* and *P. fimbriata* became active (walked and waved palps) more often in experimental tests (moving lure visible to *J. queenslandicus*) than in control (moving lure not visible to *J. queenslandicus*). Results from tests of independence are from comparing data from each experimental test (row 2, 3, 4) in each row with control (row 1). *p*-values after Bonferroni corrections.

## Discussion

Salticids can detect motionless prey (Jackson & Tarsitano, 1993), but movement facilitates prey detection and stimulates the salticid to begin predatory sequences earlier (Heil, 1936; Crane, 1949; Drees, 1952; Jackson & Tarsitano, 1993). Our hypothesis is that undirected leaps function to enhance *P. fimbriata*'s ability to locate *J. queenslandicus*: leaps, by attracting attention, elicit palp waving and walking by *J. queenslandicus*, which in turn provides movement cues *P. fimbriata* can use to locate *J. queenslandicus*. Our findings support this hypothesis.

In experiment 1, *J. queenslandicus* more often waved its palps and walked when undirected leaps by *P. fimbriata* could be seen. In control tests, when *P. fimbriata*'s undirected leaps could not be seen, *J. queenslandicus* tended to remain quiescent. Experiment 2 also demonstrated that *J. queenslandicus*' reaction to undirected leaps tends to attract *P. fimbriata*'s attention.

Seeing lures make simulations of undirected leaps in experiment 2 elicited comparable reactions from *J. queenslandicus*, regardless of whether the lures were made from *P. fimbriata*, *J. queenslandicus* or house flies. These findings suggest that *J. queenslandicus*' response is a generalised investigatory behaviour provoked by an unidentified object moving in the neighbourhood and not a reaction specifically to *P. fimbriata*.

*P. fimbriata* appears to test the environment for the presence of *J. queenslandicus* by attempting to provoke, with undirected leaps, a response from its not-yet-seen prey. Undirected leaps differ from how octopuses and woodstorks flush out prey by attacking the prey's microhabitat (Yarnell, 1969; Kahl & Peacock, 1973) because *P. fimbriata* appears not to focus on a target when it leaps. *P. fimbriata*'s undirected leaps appear to be more comparable to a lion running up a hill in anticipation of startling unwary but not-yet-seen prey (Schaller, 1972).

Curio (1976) with the term 'speculative hunting' outlined a general mechanism for how prey might be located. Details about the role of any particular behaviour in a predator's repertoire, or precisely how speculative hunting worked, were not considered. For *P. fimbriata*, we have details concerning the cues that provoke speculative hunting and the manner in which undirected leaping is used by *P. fimbriata* to find its prey.

The stimuli governing speculative hunting by other predators are not well understood, but *P. fimbriata*'s undirected leaping is stimulated by chemical

cues from a specific prey. The leap itself is not prey-capture behaviour, because undirected leaps are not seen after *P. fimbriata* has located its prey. Instead, this tactic can be envisaged as something more akin to setting a trap. Triggered by chemical cues, undirected leaping is still speculative because chemical cues do not guarantee the presence of *J. queenslandicus* in the immediate vicinity. Undirected leaps provide the prey with visual cues and prey in turn provide the predator with visual cues. By soliciting visual cues in response to chemical cues, *P. fimbriata* appears to co-ordinate sensory modalities.

Still other facets of *P. fimbriata*'s predatory strategy may qualify as speculative hunting. Females of *Euryattus* sp., another salticid on which *P. fimbriata* preys, nest in a rolled-up dead leaf suspended by silk guylines from tree trunks, boulders or the vegetation (Jackson, 1985). To catch *Euryattus* females, *P. fimbriata* simulates the courtship signals used by *Euryattus* males (Wilcox & Jackson, 1998). Upon finding a conspecific female's nest, a *Euryattus* male goes down the guylines and signals by suddenly and forcefully flexing his legs, thereby making the leaf rock back and forth. *Euryattus* females react to the male's signal by coming out of the nest and either mating with the male or driving him away. When *P. fimbriata* locates a nest, a similar sequence is seen. *Portia fimbriata* moves to a position above the suspended leaf, then either lowers itself on its own dragline or walks down one of *Euryattus*' guylines. Once on the leaf, *P. fimbriata* uses a special behaviour, 'shuddering', which mimics the courtship of *Euryattus* males and induces the resident to come out (Jackson & Wilcox, 1990). Interestingly, *P. fimbriata* will shudder even when no *Euryattus* is present, suggesting that this behaviour has an investigatory function. When shudders provoke a response from a resident inside a rolled up leaf, *P. fimbriata* continues the predatory sequence. When no reply is forthcoming, *P. fimbriata* desists from signalling (Jackson *et al.*, 1997).

Besides preying on salticids, *P. fimbriata* also preys on web-building spiders from other families. *Portia fimbriata* enters the other spider's web and, instead of simply stalking or chasing down the resident, makes aggressive mimicry signals (Jackson & Wilcox, 1998). For example, by manipulating the web silk with its legs and palps, *P. fimbriata* may lure the resident spider to within striking distance by imitating the struggles of an insect on the web (Jackson & Blest, 1982). However, *P. fimbriata* will initiate signalling even

when a resident is not visible (Jackson, 1995), suggesting that aggressive-mimicry signals may sometimes function as hunting by speculation.

Like undirected leaping, initiating aggressive mimicry signals in another spider's web, or on a suspended leaf of *Euryattus* with no resident visible, may attract the attention of a prey that *P. fimbriata* has not yet seen. By responding with investigatory behaviour to *P. fimbriata*'s aggressive-mimicry signals, the prey may be induced to give away its location. Undirected leaping sends visual cues to potential prey, whereas web signals and shuddering on a leaf send vibratory cues to potential prey, and this may be the primary difference.

Not only might aggressive-mimicry signals sometimes be envisaged as speculative hunting, but undirected leaping might be envisaged as aggressive mimicry because undirected leaping may simulate the kinds of visual cues that normally elicit investigation by *J. queenslandicus*. For example, the initial cues *J. queenslandicus* might normally get from an insect (potential prey) or a conspecific individual (potential mate or rival) may not be so different from the cues provided by *P. fimbriata*'s undirected leaping. In *P. fimbriata*'s predatory strategy, speculative hunting and aggressive mimicry appear to be broadly overlapping topics.

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