Araneophagic jumping spiders discriminate between detour routes that do and do not lead to prey

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Abstract. In a laboratory study, 12 different experimental set-ups were used to examine the ability of *Portia fimbriata*, a web-invading araneophagic jumping spider from Queensland, Australia, to choose between two detour paths, only one of which led to a lure (a dead, dried spider). Regardless of set-up, the spider could see the lure when on the starting platform of the apparatus, but not after leaving the starting platform. The spider consistently chose the 'correct route' (the route that led to the lure) more often than the 'wrong route' (the route that did not lead to the lure). In these tests, the spider was able to make detours that required walking about 180° away from the lure and walking past where the incorrect route began. There was also a pronounced relationship between time of day when tests were carried out and the spider's tendency to choose a route. Furthermore, those spiders that chose the wrong route abandoned the detour more frequently than those that chose the correct route, despite both groups being unable to see the lure when the decision was made to abandon the detour.

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Salticids have unique, complex eyes (Dzimirski 1960; Land 1969a, b; Williams & McIntyre 1980; Blest et al. 1990) with resolution abilities rivalling those of primates (Land 1974; Clark & Uetz 1990; Land & Fernald 1992) and, not surprisingly, most species hunt in the open instead of building webs (Foelix 1982; Richman & Jackson 1992). However, *Portia* is a genus of tropical salticids that not only hunt in the open but also build prey-catching webs and make predatory raids into the webs of other spiders (Jackson & Blest 1982a; Jackson & Hallas 1986a, b). In order to reach an advantageous position to attack a web spider, *Portia* often takes circuitous routes, called detours (Jackson & Wilcox 1993; Tarsitano & Jackson 1993, 1994). To understand this detouring ability requires an appreciation of the unique salticid visual system.

Salticids have a pair of very large anterior median eyes (known as the 'principal eyes') and, located to either side of these, three pairs of smaller secondary eyes. The secondary eyes are highly proficient motion detectors (Land 1971, 1972; Duelli 1978; Hardie & Duelli 1978), but the principal eyes are responsible for acute vision (Homann 1928; Land 1969a, b; Forster 1982), allowing the salticid to identify motionless mates, rivals and predators from as far as 30 body lengths away (Jackson & Blest 1982b; Jackson & Tarsitano 1993). The acuteness of their vision means that salticids can begin predatory sequences while still distant from the prey. Many salticids live in complex, three dimensional habitats of stones and vegetation, where direct access to the prey is frequently unavailable, and laboratory studies have shown that the ability to follow indirect routes (detours) to reach prey is probably common among these species (Hill 1979; Tarsitano & Jackson 1993). However, the detours required of the salticids in these experimental studies were simple and short. Hill (1979) emphasized that detouring required no great insight on the salticid's part because, if no straight route towards a prey was available, the salticid detoured merely by heading towards objects ('secondary goals') that would tend to bring them closer to the intended prey.

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However, *Portia fimbriata*, a salticid from Queensland, Australia, has been reported to take long (in excess of 1 m), complicated detours in the field (Jackson & Wilcox 1993), including detours in which the salticid first moved away from the prey before heading towards it and appeared to choose between routes that did and did not lead to the prey.

In a previous laboratory study, we confirmed that *P. fimbriata* can complete detours requiring initial movement away from the prey (Tarsitano & Jackson 1994). In the present study, we examine *P. fimbriata*'s ability to choose between alternative routes.

METHODS

Standard housing and maintenance procedures were used (Jackson & Hallas 1986b), and basics of the testing procedures were as described in Tarsitano & Jackson (1993). Therefore, only the details of testing methods specific to the present study are described below.

Each test apparatus (Fig. 1) consisted of two routes, each built from an aluminium rod bent into a specified shape and with a plastic dish suspended at the distal end. At the proximal end, each aluminium rod had a forked prong which was inserted into a pair of holes drilled into a base made of polyurethane-coated wood 1000 mm wide × 1000 mm long. The prong was forked to provide stability to the rods. There was a lure at one dish, but not at the other. Before each test, we decided randomly which dish would have the lure.

In each apparatus there was also a wooden, polyurethane-coated cylinder platform, 250 mm high × 50 mm in diameter. This platform is referred to as the 'starting platform' (e.g. 'SP' in Fig. 1a) and was placed in the middle of the base of the apparatus. Before the test, a spider was placed in a pit (20 mm in diameter × 20 mm deep) centred at the top of the starting platform. This pit is called the 'starting hole'. The starting hole was covered with a piece of clear plastic until the spider became quiescent. We removed the cover to start the test. The spider would then walk slowly out of the pit and on to the platform, and begin 'scanning' its surroundings. A spider 'scanned' by standing more or less in one place while pivoting about and repeatedly fixating its principal eyes on objects in its environment. ('Scanning', as defined

here, should not be confused with Land's (1969b) use of this word for a specific movement pattern of the principal eye retinae.)

We tested adult females using three different procedures (Fig. 1), each having two variations, one the mirror image of the other. (Compare Fig. 1a and d.) The procedures were numbered 1–3, while the two variations of each procedure were labelled 'sub-procedure A' or 'sub-procedure B'. Each sub-procedure itself had two routes, designated 'A' and 'B'. We decided randomly before each test whether the lure would be placed in the dish at the end of route A or in the dish at the end of route B. We refer to a test with the lure in dish A as a test using 'set-up A'; a test with the lure in dish B is a test using 'set-up B'. Results are referred to according to the set-up, sub-procedure and procedure from which they came. For example, the phrase 'The results from Procedure 2B, lure at A' refers to the results when a spider was tested using procedure 2, sub-procedure B, with the lure placed above the dish at the end of route A.

We could ascertain for each sub-procedure whether the spider's choice of route was influenced by the position of the lure by comparing the numbers of spiders within that sub-procedure that chose route A when the lure was placed in dish A with the numbers that chose route B when the lure was placed at dish B. The 'correct pole' was defined as the first vertical segment of the route that led to the lure and the 'incorrect pole' as the first vertical segment of the route that did not lead to the lure. We considered a spider to have made its choice between routes when it first contacted a pole. If it first contacted the correct pole, then we scored it as having chosen the correct route. If it first contacted the incorrect pole, then we scored it as having chosen the incorrect route. An observed influence of lure position on route choice would suggest that the spider can distinguish between correct and incorrect detour routes.

In all set-ups, the direction in which the spider had to walk after leaving the starting platform in order to reach the correct pole meant that the lure, the dish, the hair supporting the lure and the pole from which the lure was hung could not be seen by the spider's form-seeing principal eyes. Therefore, while walking towards the support pole, the spider could not see these objects.

We used 12 different detour routes (three procedures × two sub-procedures × two set-ups)

to see if we could uncover any simple decision rules the spider may be using for solving a detour problem. To help in this, we categorized routes according to three characteristics: whether they were forward or reverse routes, whether they were crossover or non-crossover routes, and whether they were clockwise or anticlockwise routes. Routes in which the angle made by the lure's position, the starting platform and the correct pole was greater than 90° are called 'reversed routes' (Tarsitano & Jackson 1994): the spider at the starting platform had to walk in a direction away from the lure to reach the correct pole. Routes in which the angle made by the lure's position, the starting platform and the correct pole was less than 90° are called 'forward routes': walking more or less in the direction of the lure would also take the spider towards the pole that led to the lure. Routes in which the spider leaving the starting platform would have to walk past the incorrect pole before reaching the correct pole are called 'crossover' routes. Routes in which the spider would not have to walk past the incorrect pole before reaching correct pole are called 'non-crossover' routes. Routes that ran in a generally clockwise direction away from the lure (as seen from the spider's vantage point on top of the starting platform) were called 'clockwise' detours. Routes that generally ran in the opposite direction away from the lure were called 'anticlockwise' routes. Table I shows how the different detour routes were categorized according to these criteria.

Vertical segments of the route are called 'poles', whereas horizontal segments are called 'rampways'. The beginning of each segment was designated by a number, prefixed by whether the segment was a part of route A or B (e.g. A1–A7; B1–B7; see Fig. 1b for an example of how each route was labelled).

Some organizational features were common to all routes: between positions 1 and 2, the route was vertical and 150 mm long; between positions 2 and 3, the route was horizontal and parallel to one side of the base, S1; between positions 3 and 4, the route was horizontal and parallel to S2 (see Fig. 1a); between positions 4 and 5, the route was vertical and 160 mm long; between positions 5 and 6, the route was horizontal, 190 mm long and parallel to S1; between positions 6 and 7, the route was vertical and 110 mm long. Other distances are given below.

For procedure 1 the distance between positions 2 and 3 was 160 mm, and between positions 3 and 4 100 mm. For procedure 2A set-up A and procedure 2B, set-up B the distance between positions 2 and 3 was 150 mm, and between positions 3 and 4 380 mm. For procedure 2A set-up B and procedure 2B set-up A, the distance between positions 2 and 3 was 150 mm, and between positions 3 and 4 100 mm. For procedure 3A set-up A and procedure 3B set-up B, the distance between positions 2 and 3 was 350 mm, and between positions 3 and 4 440 mm. For procedure 3A set-up B and procedure 3B set-up A, the distance between positions 2 and 3 was 350 mm, and between positions 3 and 4 290 mm.

The vertical segment from position 1 to position 2 supported the rest of the route above the base of the apparatus and is called the 'support pole'. Because the distance from position 1 to 2 was 150 mm, rampways 2–3 and 3–4 were 150 mm above the base. The dish itself had a flat bottom with a radius of 50 mm and was made of an opaque plastic. It had a rim 20 mm high and was fastened at its centre to the base of pole 6–7.

Each set-up was also surrounded by a white cardboard blind and was lit by a 200-W incandescent lamp placed behind and above the observer's head; additional ambient lighting was provided by overhead fluorescent ceiling lamps.

We made lures from dead *Eriophora pustulosa*, a spider species used in earlier detouring studies (e.g. Tarsitano & Jackson 1994). We used this spider as a lure because *P. fimbriata*'s primary prey in nature is spiders and because *E. pustulosa* is approximately the same size as an adult female *P. fimbriata* (body length 8–10 mm) (Jackson & Hallas 1986b). Although *P. fimbriata* is capable of successfully attacking spiders much larger than itself (Jackson & Hallas 1986a) a medium-sized lure of approximately the same size as *P. fimbriata* was deemed ideal for motivating the test spider to detour because it represented a good meal while also not being very difficult to capture. We made the lure by killing the spider by asphyxiation with carbon dioxide, then placing it in alcohol for 1 h. After gluing it to one side of a disk-shaped piece of cork (diameter ca 1.25 times the body length of the animal), we sprayed the entire lure (cork plus spider) with a mounting adhesive to preserve it and to eliminate any olfactory cues that the dead animal might provide. We glued a magnet to the
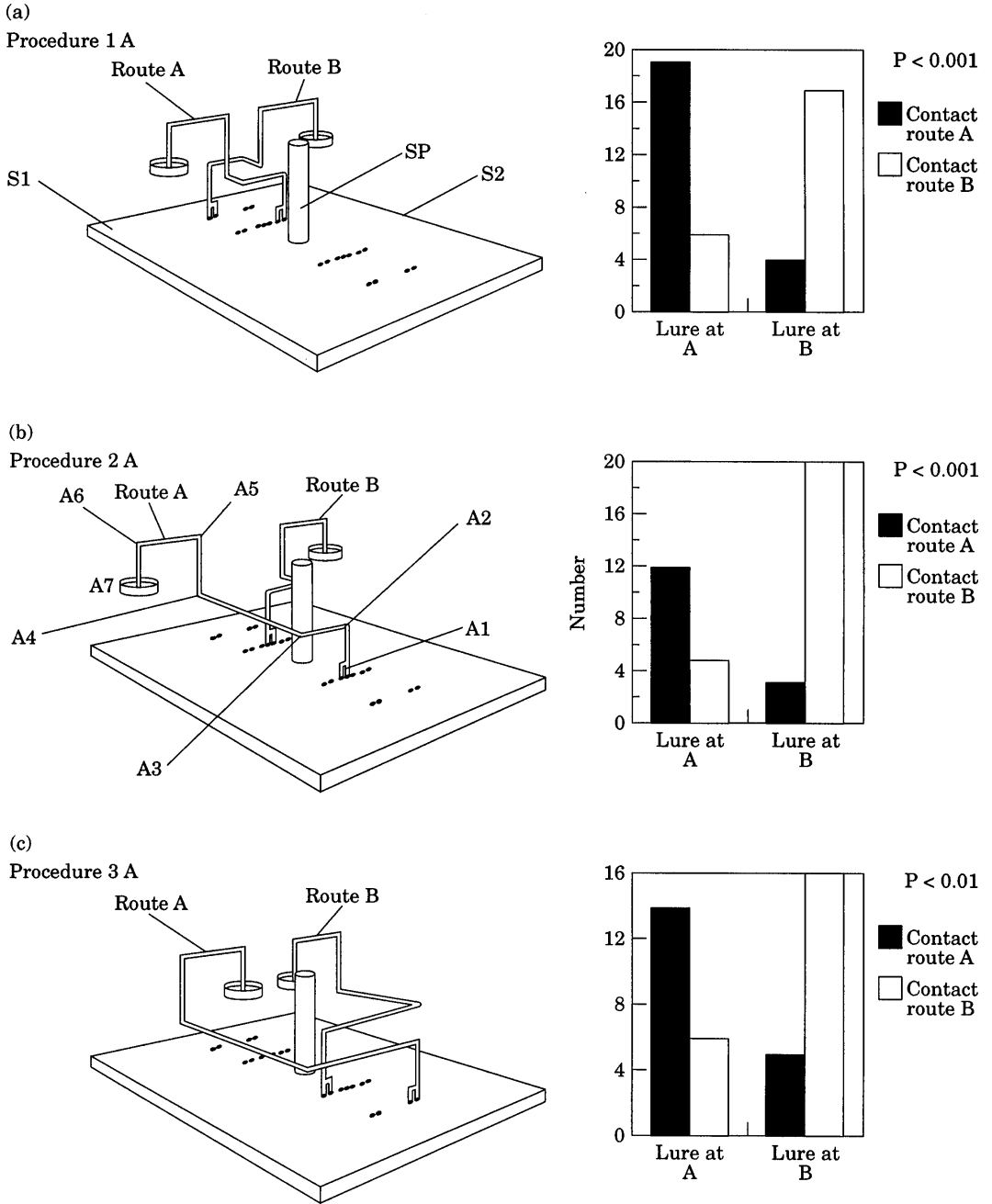
(a)

Procedure 1 A

(b)

Procedure 2 A

(c)

Procedure 3 A

Figure 1 a-c.

back of the lure and dangled it on the end of a human hair from the bend in the rod immediately above the dish. We positioned the lure 10 mm above the dish bottom and jiggled it by passing a current through a hidden magnetic coil every 5 s until the test spider oriented towards it.

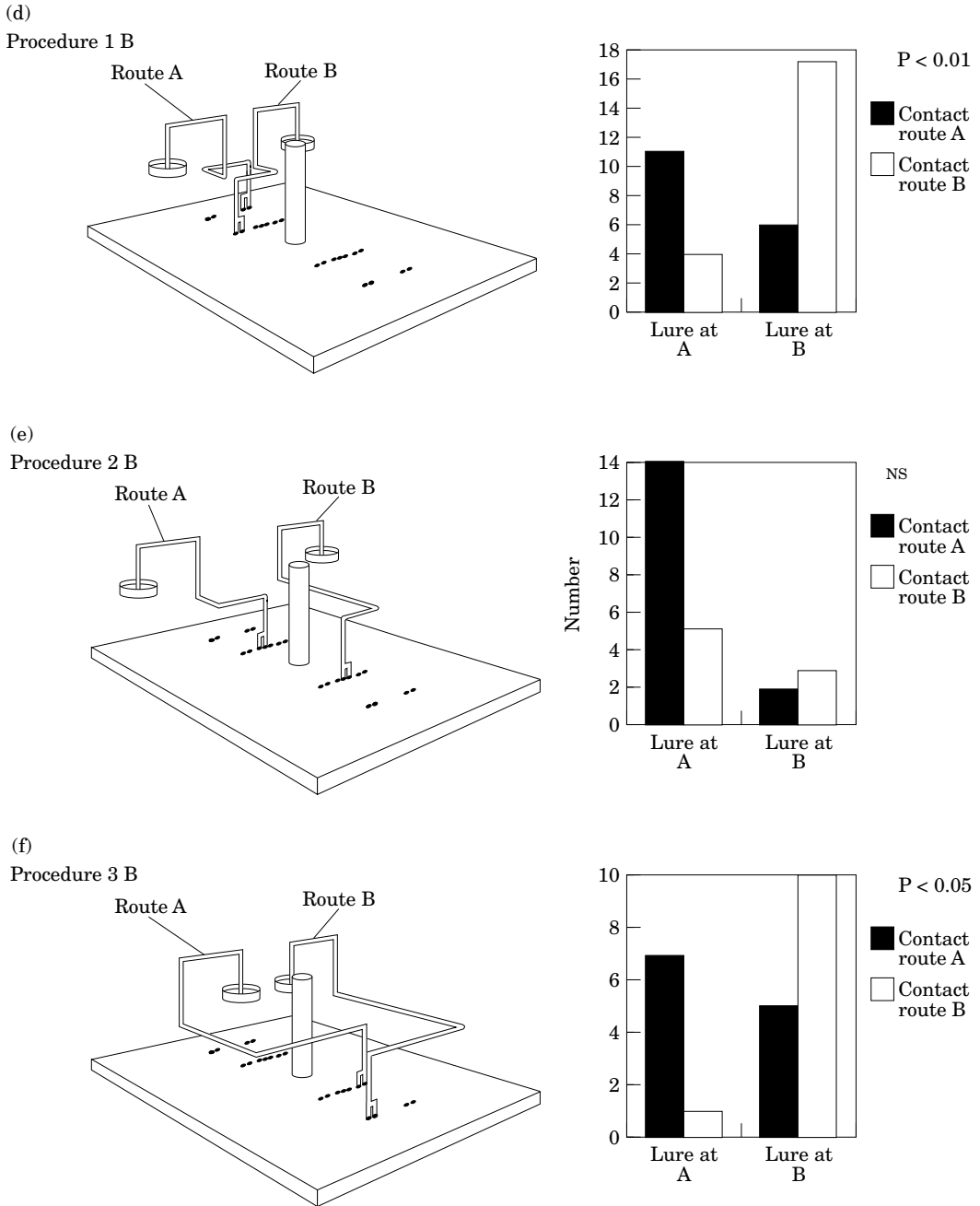Positioning the lure 10 mm above the dish meant that the test spider could see the lure from

(d)
Procedure 1 B

(e)
Procedure 2 B

(f)
Procedure 3 B

Figure 1 d-f.

Figure 1. Diagram of each experimental sub-procedure (see text). For procedure 1A, 'SP'=starting platform. S1, S2 are two sides of the apparatus base. Labelling system for recording *P. fimbriata*'s position is shown for procedure 2A. Each histogram shows the number of spiders, for each set-up of the sub-procedure, that contacted correct and incorrect support poles. *P*-values: chi-square test of independence.

Table I. Categories of detour routes

Procedure	Route A	Route B
1A	Forward route, non-crossover, clockwise	Forward route, crossover, anticlockwise
1B	Forward route, crossover, clockwise	Forward route, non-crossover, anticlockwise
2A	Reversed route, non-crossover, anticlockwise	Forward route, non-crossover, anticlockwise
2B	Forward route, non-crossover, clockwise	Reversed route, non-crossover, clockwise
3A	Reversed route, crossover, anticlockwise	Reversed route, non-crossover, clockwise
3B	Reversed route, non-crossover, anticlockwise	Reversed route, crossover, clockwise

the top of the starting platform, but not from any position along the detour route until it climbed the pole between positions 4 and 5. The rim of the dish hid the lure. Climbing the pole between positions 4 and 5 put the spider above the rim of the dish, from where it could again see the lure.

Spiders that did not attack the lure were scored according to how far along the route they reached. For example, a spider that arrived at position A1 (the base of the support pole of route A), but advanced no further, was scored as reaching position A1; one that reached A2 (the top of the support pole of route A), but no further, was scored as reaching A2. We also recorded the spider's heading while it was on the base of the apparatus after leaving the starting platform. The rationale for this was to see if those spiders that chose a pole went there directly (sensu Tarsitano & Jackson 1994) or first went in another direction. Besides its intuitive meaning, 'directly' meant that a spider arrived at the pole without: (1) walking past the pole or (2) pointing its body axis more than about 30° away from the pole (as judged by visual inspection) without immediately re-orienting back towards it.

Tests were concluded when a spider (1) attacked the lure, (2) walked off the apparatus, or (3) 'gave up' a detour route after starting it. 'Giving up' was defined as when, whether the route led to the lure or not, a spider either turned around and went backwards along the route, or leapt off a rampway or pole on to the base of the apparatus. Tests were 'aborted' if a spider stayed in the pit for 30 min or if it left the starting platform without first scanning. When tests were aborted, we re-tested the same spider repeatedly, up to four times per day, either until it scanned or 4 days of unsuccessful testing elapsed. Results from aborted tests were not considered in the analysis. In total, 624 spiders were tested.

We conducted tests between 0800 hours and 1700 hours (laboratory photoperiod: 12:12 h light:dark, lights on 0800 hours) and recorded the time of day for each test. All subjects were deprived of food for 10 days prior to testing. After testing, each spider was provided with a live spider. If this spider was stalked, we assumed that the spider's motivation during the test had been related to attacking the lure. Only spiders that stalked this prey were included in the results.

As *P. fimbriata* is known to leave chemical cues behind with its draglines while walking about (Clark & Jackson 1994), we wiped the apparatus with acetone between each test to remove any traces of a trail that the previous test spider may have left behind. All spiders tested were naive with regard to detour problems: each animal was laboratory-reared and tested only once. We chose subjects for each test at random. All statistical tests and procedures used can be found in Sokal & Rohlf (1981).

RESULTS

Effect of Time of Day

There was a significant relationship (Fig. 2) between the proportion of spiders that chose between routes (contacted a support pole) and the time of day when testing was done (time of day versus number of successful and unsuccessful tests, $\chi^2_7 = 39.74$, $P < 0.001$). When testing was in the early morning, a large proportion of spiders chose a pole, but none did so by late morning. In the mid-afternoon, the proportion choosing a pole began to rise again, reaching a peak around 1600 hours.

The spider's time-dependent tendency to choose a pole represented a hitherto unknown variable influencing its detour behaviour that needed to be
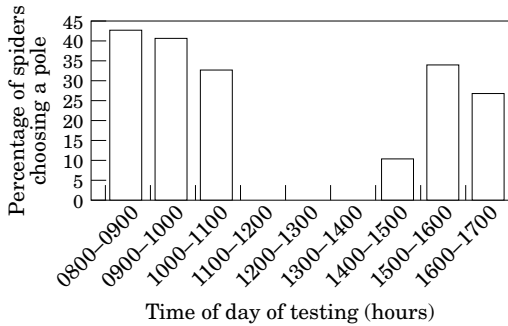
Figure 2. Percentage of successful tests according to test time during the day. Data are pooled across all set-ups. There are no tests between 1200 and 1300 hours.

Figure 3. Percentage of *P. fimbriata* that chose neither route (bar graph). Data are ordered highest to lowest, with set-up listed on the *X*-axis (e.g. Procedure 1A, lure at A). The graph shows, out of those spiders that made a choice between routes (i.e. contacted a support pole), the percentage of spiders from each set-up that chose the correct route.

controlled for post hoc. To find which data from different times of day were compatible, we ordered the data according to the percentage of tests each hour in which a spider chose a pole. We then removed the hour with the lowest percentage and performed a chi-square test on the remaining data. If the result was significant, we then removed the hour with the next lowest percentage and repeated the test. This was done until the chi-square test statistic fell to where $P>0.05$. In this way, we decided to eliminate from further analysis all test results between 1100 and 1500 hours. In all, only five out of 64 spiders tested during this time period contacted a support pole. Including their results does not change whether any of the statistical tests presented elsewhere in the results gave a significance value of $P<0.05$.

Choice of Routes

In the majority of successful tests, regardless of set-up, the support pole chosen was the support pole at the start of the route to the lure (Fig. 1). This trend was significant for five of the six sub-procedures. The exception was sub-procedure B of procedure 2, where, for reasons discussed below, the sample size was limited by the scarcity of successful tests when the lure was in dish B.

Giving-up Points

There was no evidence that the position reached when a spider gave up a route varied between the set-ups (Kruskal–Wallis: NS). Accordingly, we pooled data from the 12 set-ups. Of those spiders that chose the correct pole, 35% abandoned the
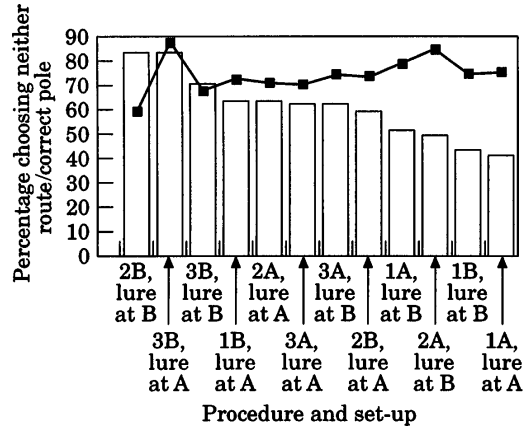
detour before arriving at the dish (Fig. 3). An additional 21% arrived at the dish, but failed to attack the lure. The reason these spiders failed to attack the lure may have been that, when close, the lure's appearance or odour did not correspond closely enough to that of a living prey to trigger the attack sequence. Details such as these may have gone unnoticed by the spider while still distant from the lure, but then became relevant once it got close. From other studies, salticids are known to begin stalking a dead lure or a model of a prey item, only to ignore it once actually close enough to attack (e.g. Drees 1952). All spiders that failed to attack the lure after reaching the dish were counted as having finished the detour.

Spiders tended to give up the route (i.e. not reach the dish) more frequently if the wrong, instead of the correct, route had been chosen (Fig. 4; $\chi^2_1=54.79$, $P<0.001$). This was also true when one considers only the positions on the route where the spiders could not see the lure (i.e. positions 1–5). In other words, at positions on the route where it could not see the lure, a spider was more likely to abandon the detour if it had chosen the incorrect route instead of the correct one ($\chi^2_1=47.95$, $P<0.001$).

The most common point where a spider gave up the detour when it had chosen the wrong route was at the top of the incorrect support pole. Of
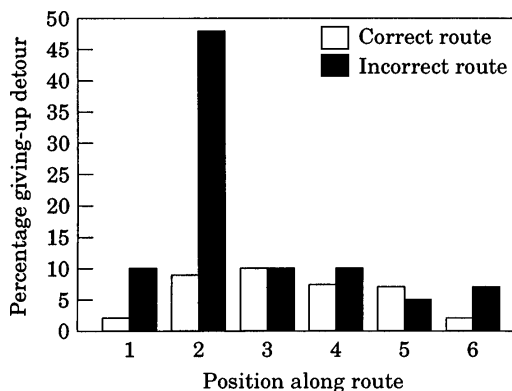
Figure 4. Giving-up points (see text and Fig. 1b) from pooled data across all set-ups. Percentages are calculated independently for spiders that chose the correct and incorrect routes.

the spiders that chose the incorrect route, the number that gave up the detour at this point was almost five times as many as gave up at any other point. Out of those that chose a route, the number that abandoned the route at the top of the support pole was significantly greater when they had chosen the wrong route instead of the correct one ($\chi^2_1 = 40.91$, $P < 0.001$).

Difficulty of Detours

The proportion of spiders that chose a route (i.e. contacted a support pole) varied significantly between set-ups (Fig. 4; $\chi^2_{11} = 39.03$, $P < 0.001$). However, considering only those tests for which the spiders did make a choice of poles, there was no statistical evidence of a relationship between set-ups in the proportion of choices that were correct. Difficulty in detouring for the spider, therefore, seems to be expressed not so much as a failure to choose the correct pole, but as a failure to choose either pole. However, no correlations were found between the failure rates and the different categories of detours described in Table I.

DISCUSSION

Effect of Time of Day

In the laboratory, the proportion of spiders choosing a route peaked in the early morning and again in the mid- to late afternoon. In the field, the spider tends to be most active in the early morning and late afternoon (Jackson & Blest 1982a).

Therefore, its reluctance to detour during the middle of the day is probably a reflection of its crepuscular pattern of activity.

Choice of Routes

In tests with five of the six sub-procedures, spiders consistently chose the route that led to the prey. Evidently, the spider can distinguish a correct route from an incorrect one, even if the correct route is longer, requires movement away from the lure, results in losing visual contact with the lure and requires going past where the incorrect route begins. The ability to choose the correct pole, even when it was on the side of the starting platform opposite the lure (Fig. 1e, f), would appear to require an ability by the spider to see the various relationships between the different components of the route (i.e. how the pole, rampways and mount connect). This suggests that the processes the spider uses when selecting a detour route are more sophisticated than what has been implied by previous studies of salticid detouring (Hill 1979).

Only in procedure 2B was there no statistically significant evidence of route choice by the spider, and this was probably because so few spiders chose any pole when the lure was in dish B. Why so few chose a pole with this detour route is not known.

These results suggest that the spider can make detours on par in complexity with the detours completed by vertebrates (von Frisch 1962; Collett 1982), but most detour tests with naive vertebrates have involved the animal circumnavigating a physical barrier (e.g. Regolin et al. 1994, 1995a, b; for reviews see Chapuis 1987; Rashotte 1987). In contrast, in the detours completed by *P. fimbriata*, there was no barrier to get around before reaching the prey. In our design, a detour was required not because of a barrier but because there was no straight path available to the lure. Whether the spider can perform detours that force it to circumnavigate an impassable barrier has not been investigated, and we are hesitant to draw too close a parallel between our findings and those from the vertebrate research literature.

Giving-up Points

Along the correct detour route, there was a steady rate of attrition as approximately equal

numbers of spiders gave up the detour at points 1–6. Apparently, choosing the correct route is no guarantee that a spider will finish a detour, and once started along a detour route, a spider steadily becomes less and less likely to complete the journey: i.e. on longer detours, *P. fimbriata* seems to be more likely to lose its way, or its interest, before reaching the lure.

Comparing the spiders' giving-up points on incorrect versus correct routes reveals a more interesting finding. First, more spiders gave up the route when they had chosen the wrong route than when they had chosen the correct route. Second, most spiders gave up the route at a position where they could not see the lure. Third, almost 50% of the spiders that chose the wrong route gave up the detour at the top of the support pole. Apparently, the spider can distinguish between when it has taken the correct or the incorrect route, and makes this distinction from the top of the support pole.

In a previous study, the spider almost always re-oriented towards the lure when it reached the position at the top of the first pole climbed (Tarsitano & Jackson 1994). This was interpreted as the spider attempting to verify that continuing the detour is still worthwhile by confirming that the prey was still there (Tarsitano & Jackson 1994). However, in the current study, the lure was not visible from the top of either the correct or incorrect support pole. Therefore, the spider could not have used seeing the lure as a cue for deciding whether to continue the detour. How it decided whether to continue a detour in the absence of direct visual cues from the lure is not known.

Difficulty of Detours

The spiders were clearly able to choose the correct route to a lure in a number of different detouring set-ups. However, there was a striking tendency for the proportions of spiders that chose a route to vary between set-ups. Considering only those that made a choice of routes, however, there was no evidence of variation between set-ups in the proportion of correct versus incorrect route choices. It appears as though *P. fimbriata* tries to reach prey by taking a detour only when the correct route can be discerned with a threshold level of confidence; otherwise, it chooses not to try. Of those that chose neither pole, 85% simply

wandered around the base of the apparatus before walking off (data not shown).

We performed many types of analysis in different permutations in an effort to find a pattern between the type of route used for testing *P. fimbriata* and the proportion choosing a route. None was found, suggesting that the spider does not use any simple decision rules for determining its detour routes. However, the spider's scanning behaviour at the start of a detour is very complicated. Obviously, any decision the spider makes about what route to take while detouring will be dictated to a large extent by the visual information it receives while scanning. Therefore, given the failure to find any simple rules used by the spider to select a detour route, a better research tactic may be to look into the mechanisms that mediate its scanning behaviour. This work is in progress.

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