Responses of jumping spiders to motionless prey

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Summary

Responses of eleven salticid species to motionless lures were investigated under controlled conditions in the laboratory. We provide evidence that, for each of these species, a lure does not have to move for the salticid to recognise it as prey. By testing species with known prey preferences and with different prey-specific prey-catching behaviours for different prey, we provide evidence that prey movement is not necessary in order for salticids to discriminate between types of prey. We also provide evidence that *Portia*, a salticid that is known to prey especially often,on quiescent prey in nature, is especially prone to respond to motionless lures.

Introduction

The jumping spiders (Salticidae) are one of the few groups of spiders whose major mode of locomotion is, as the name implies, jumping. The most distinguishing characteristic of these spiders, however, is their highly developed vision. Visual acuity and jumping ability have enabled these spiders to hunt their prey actively, instead of relying on silken snares. Salticids are generally envisaged as predators of motile insects whose movements elicit the spiders' initial responses. The salticid's visual system consists of a pair of large anterior median, or "principal", eyes and six smaller, "secondary" eyes. The salticid uses its secondary eyes to detect movement and control orientation to objects in its field of vision, bringing images on to the retinae of the principal eyes. The salticid then uses its principal eyes to discriminate between classes of objects such as prey, mates and conspecifics of the same sex (Land, 1985).

Although it is clear that much of the predatory behaviour of salticids is governed by vision (Drees, 1952; Forster, 1982), little is known about exactly what visual cues are important in prey recognition and discrimination. In particular, the importance of prey movement is not clear. Although it is known that prey movement can be an important cue in initiating predatory sequences of salticids (Drees, 1952; Dill, 1975) and in permitting salticids to distinguish between different types of prey (Freed, 1984), whether it is necessary is unclear. There is, for example, anecdotal evidence that at least some species of salticids do occasionally stalk and attack motionless prey (see Forster, 1985), but studies under controlled conditions in the laboratory have been lacking.

We address three questions in the present paper:

1. Does prey have to move in order for a salticid to recognise it as prey?
2. Does prey have to move in order for salticids to discriminate between different types of prey?
3. Do species from the genus *Portia*, salticids that are known to feed frequently on quiescent prey in nature, respond to motionless prey more readily than do other salticids?

Salticids typically catch prey by orienting, stalking or chasing, crouching when close, then leaping on motile insects (Forster, 1977, 1982). We included in our study six species of salticids which are known to use this "typical" style of preying primarily on soft-bodied and minimally-defended insects such as flies. Some salticids are known, however, to prey on more highly-defended prey (see Robinson & Valerio, 1977), including ants and spiders. We included in our study a species that is specialised at preying on ants and four species that are specialised at preying on spiders. Previous work on salticid prey preferences and prey-specific prey-catching behaviours enables us to assay the abilities of salticids to discriminate between different types of prey. The key to these assays are the ant-eating and spider-eating salticids.

Salticids generally exclude worker ants from their diets, but *Corythalia canosa* (Walckenaer) prefers ants to other insects and uses different prey-specific prey-catching behaviours depending on whether prey is an ant or another insect (Edwards *et al.*, 1974; Jackson & van Olphen, 1991). In a typical ant-catching sequence, *C. canosa* runs in spurts to get head-on to the ant, then lunges or makes a short leap, from about half a body length away, to grab the ant by its dorsal alitrunk. Both during and before attacks on ants, *C. canosa* usually has its body raised and its forelegs arched out to the side. However, when preying on other kinds of insects, *C. canosa*'s behaviour is essentially the same as that typical of other salticids. We examine whether *C. canosa*'s prey-specific predatory behaviours and prey preferences are the same when tested with a dead, motionless lure as they are known to be from tests with a live, motile prey.

We also examine the prey preferences of four species of *Portia*, a genus of behaviourally aberrant salticids (Wanless, 1978) that build webs in addition to hunting cursorially. *Portia* also uses aggressive mimicry to catch other spiders in alien webs, deceiving victim spiders with vibratory signals (Jackson & Blest, 1982; Jackson & Hallas, 1986a). Whether in or away from webs, *Portia* is known to prefer spiders to insects as prey (Jackson & Hallas, 1986b). In this study, we examine whether *Portia* prefers spiders as lures to insects as lures when the lure is motionless.

All species of *Portia* that have been studied (Jackson & Hallas, 1986a) have well-developed predatory versatility (i.e., they have repertoires of different prey-specific predatory behaviours that they use against different types of prey). The predatory versatility of *P. fimbriata* (Doleschall) from Queensland (an area in which cursorial salticids are unusually abundant: Jackson, 1988) is especially relevant to the present study.

Queensland *P. fimbriata*, but no other species of *Portia* and no other populations of *P. fimbriata*, use "cryptic stalking", a specialised manner of catching other salticids (Jackson & Blest, 1982). All species of *Portia* are detritus mimics, and they all adopt a slow, "mechanical" mode of walking. However, when cryptically stalking a salticid, a Queensland *P. fimbriata* exaggerates these slow, mechanical aspects of locomotion, hides its palps, by holding them angled alongside the chelicerae, and freezes whenever the salticid faces it.

P. fimbriata pursues other kinds of spiders, and insects, encountered away from webs by performing "normal stalking", the type of stalking other populations of *P. fimbriata* and other species of *Portia* perform against prey encountered away from webs, regardless of whether it is a salticid, some other kind of spider or an insect. Normal stalking is carried out without particular regard to whether the prey is facing or not, is not so extremely slow and "mechanical", and is not carried out with palps retracted alongside the chelicerae. In the present study, we examine whether *P. fimbriata* cryptically stalks when a dead, motionless salticid is used for a lure.

Each species of *Portia* is known readily to prey on quiescent web-building spiders in nature and in the laboratory (Jackson & Hallas, 1986a), suggesting that *Portia* might be more efficient at recognising motionless prey than more typically insectivorous salticids. This possibility is considered in this paper.

Methods

Cages, maintenance procedures, and terminology were the same as in numerous other studies of salticids (see Jackson & Hallas, 1986a). The laboratory was on a 12L:12D light regime, with lights coming on at 0800h. All testing was conducted between 0800 and 1700h.

Salticids were tested with motionless lures on a wooden ramp, 320 mm long and 70 mm wide, raised at a 20° angle from the horizontal (Fig. 1). This ramp was supported by two wooden poles, 20 mm in diameter, glued to a wooden base 400 mm long and 100 mm wide. Both the ramp and the base were 17 mm thick. The two poles were placed at 75 mm and 150 mm, respectively, from the far end of the base. The entire apparatus was painted with two coats of water-resistant polyurethane. The ramp was wiped off with 80% ethanol, then allowed to dry for at least 30 min, between each test to remove possible chemical traces from a previous salticid.

A piece of brown cardboard, 80 mm high and 70 mm wide, was glued to the top end of the ramp. This cardboard served as a background against which the salticid saw the lure. At the start of a test, a lure was placed at the centre of the ramp, 40 mm from the base of the cardboard.

A 200 W incandescent lamp, positioned c.600 mm overhead, lit the entire apparatus; fluorescent ceiling lamps
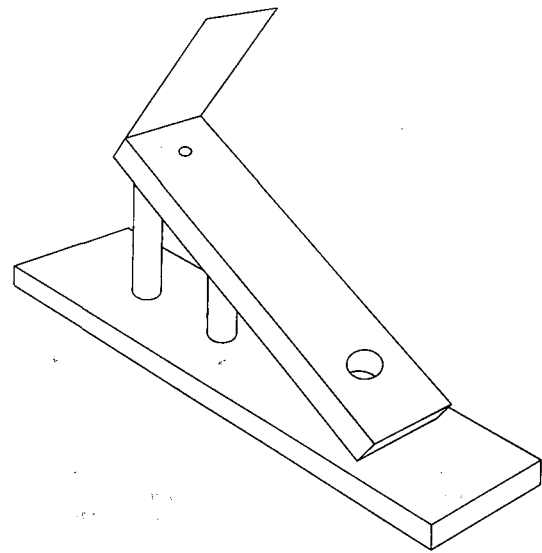

Fig. 1: Apparatus used for testing responses of salticids to motionless prey. Test spider walks out of pit near bottom of ramp (circle on right of diagram) and up ramp towards motionless lure (circle on left in diagram). See text.

provided additional, ambient, lighting. The apparatus was surrounded by a white cardboard screen on three sides, the open side being for the observer. The ramp was positioned so that during the test, the salticid moved away from the open side and the observer.

Various lures were made, using dead salticids, amaurobiid spiders, house flies, fruit flies and ants (Table 1). Each salticid species was tested with a set of these lures, but usually not with all of them (Table 3). Generally, each species was tested with the types of lures that corresponded to the species' natural prey. In all cases, the lure was made by killing the spider or insect by asphyxiation with carbon dioxide, then placing it in alcohol for an hour. After mounting the lure on the centre of one side of a disc-shaped piece of cork (diameter c.1.25 times the body length of the animal), the lure plus the cork was sprayed with an aerosol plastic adhesive for preservation and elimination of potential olfactory cues from the dead spider or insect. If the salticid contacted the lure during the test, the lure was washed with 80% ethanol and allowed at least 24 h to dry before being used again.

Before the test, the salticid was placed in a pit drilled through the ramp 200 mm from the lure. The lure was

Species	Description	Use	Collection site
Portia africana (Simon)	Spider-eating salticid	Test spider	Kenya
Portia fimbriata (Doleschall)	Spider-eating salticid	Test spider	Australia (Queensland)
Portia labiata (Thorell)	Spider-eating salticid	Test spider	Sri Lanka
Portia schultzi Karsch	Spider-eating salticid	Test spider	Kenya
Corythalia canosa (Walckenaer)	Ant-eating salticid	Test spider	USA (Florida)
Bavia aericeps Simon	Salticid	Test spider	Australia (Queensland)
Euryattus sp.	Salticid	Test spider	Australia (Queensland)
Trite auricoma (Urquhart)	Salticid	Test spider	New Zealand (South Island)
Trite planiceps Simon	Salticid	Test spider	New Zealand (South Island)
Euophrys parvula Bryant	Salticid	Test spider and lure	New Zealand (South Island)
Marpissa marina (Goyen)	Salticid	Test spider and lure	New Zealand (South Island)
Badumna longinqua (L.Koch)	Amaurobiid spider	Lure	New Zealand (South Island)
Chelaner antarctica (White)	Ant	Lure	New Zealand (South Island)
Drosophila melanogaster (Meigen)	Fruit fly	Lure	Laboratory culture
Musca domestica (L.)	House fly	Lure	Laboratory culture

Table 1: Salticid species tested, and spiders and insects used as lures.

placed so that it was facing 45° away from the pit. The pit was 32 mm in diameter and centred 65 mm from the bottom end of the ramp. A piece of cardboard, covered with plastic, was glued to the pit's bottom.

Tests began when the salticid walked slowly out of the pit and on to the ramp. Tests ended when the salticid either attacked the lure or walked off the top end of the ramp. The test was aborted if the salticid stayed in the pit for 30 min or moved off the ramp at a point below the lure. When tests were aborted, the salticid was re-tested repeatedly, up to four times per day, then on subsequent days, until a successful test was completed or four days of unsuccessful testing elapsed.

When a salticid failed to attack a lure during a test, we needed to be confident that this was not simply because the spider lacked interest in prey (i.e., we had to be sure it was hungry). Therefore, all subjects were deprived of food for 10–14 days before testing. Also, immediately after each test in which the salticid failed to attack the lure, the salticid was given access to a live prey of the salticid's preferred type (spiders for *Portia*, ants for *Corythalia* and flies for all other species). Most salticids attacked the live prey. However, if a salticid which did not attack the lure also failed to attack the live prey, the test was eliminated from the data set and the salticid was not re-tested.

Spiders were chosen for tests at random from the laboratory stock, and no individual spider was tested more than once with a given type of lure, although it might be tested with more than one type of lure. Whenever an individual salticid was used in tests with more than one type of lure, the sequence of lures was random and there was a food-deprivation period between tests.

In previous studies of salticid predatory behaviour (e.g., Jackson & Wilcox, 1990), three prey sizes have been defined by the approximate ratio of prey to predator body volume: small (0.1–0.25), medium (0.5–1.0) and large (1.5–2.0). In most tests in the present study, prey was medium size. However, it was not practicable to use medium ants in tests with *Corythalia canosa* (ants that were sufficiently large or *C. canosa* that were sufficiently small were not readily available). Therefore small ants were used in tests of *C. canosa* and, for comparability, we also used small flies in tests with *C. canosa*. Also, all other salticids that were tested with ants were tested with small ants, and some of the tests of each of these other salticids were with small flies.

In order to gain an impression of whether our conclusions are generally applicable to salticids, we included in this study salticids from a wide geographic and taxonomic range (Tables 1,2) and species that vary considerably in body size, general morphology, habitat preferences, and basic behaviour. However, the subfamily placements in Table 2 should be viewed as only a general guide. Higher order systematics of the salticids is in need of considerable revision, and (for the New Zealand salticids we tested) even generic placements should be viewed with caution.

Comparisons were made using tests of independence, with Bonferroni adjustments for repeated testing of the same data sets (see Rice, 1989).

Results

Pooling of data

To simplify presentation, data from tests using different species of salticids and different types of lures (Table 3) were pooled (Table 4) when there was no evidence (from statistical analysis) of differences between data sets (in all instances, when data were pooled, $p > 0.1$).

There was no evidence that prey size affected how often salticids of any species attacked flies. When a fly was used for a lure, either a house fly or a fruit fly was used, whichever enabled us to obtain the specified prey size. However, because there was no evidence that data for house flies and fruit flies were different, data were pooled and referred to simply as "tests with flies".

Species	Subfamily	Typical body length of adult female (mm)	Behaviour and habitat	Reference
Portia africana	Spartaeinae	7	Web builder and web invader in tropical woodland	Jackson & Hallas (1986a)
Portia fimbriata	Spartaeinae	8	Web builder and web invader in tropical rainforest	Jackson & Hallas (1986a)
Portia labiata	Spartaeinae	8	Web builder and web invader in tropical rainforest	Jackson & Hallas (1986a)
Portia schultzi	Spartaeinae	6	Web builder and web invader in tropical rainforest	Jackson & Hallas (1986a)
Bavia aericeps	Cytaeinae	13	Leaf dweller in tropical rain forest	Jackson (1986)
Euryattus sp.	Cytaeinae	8	Suspends dead rolled-up leaves from tree trunks and rock ledges in tropical rainforest	Jackson (1985)
Trite auricoma	Cytaeinae	8	Ground and vegetation. Wide range of habitats	Forster (1982)
Trite planiceps	Cytaeinae	9	Specialised in habitat of New Zealand flax and cabbage trees	Forster (1982)
Corythalia canosa	Euophryinae	5	Ground dweller in live oak woodland	Edwards *et al.* (1974)
Euophrys parvula	Euophryinae	7	Ground dweller in temperate rainforest	Forster (1982)
Marpissa marina	Marpissinae	7	Coastal ground dweller in upper intertidal region	Jackson *et al.* (1990)

Table 2: Characteristics of salticids tested.

There was no evidence that how often *P. fimbriata* attacked salticids differed from how often *P. fimbriata* attacked amaurobiids. Also, for each type of lure, there was no evidence of differences among the four species of *Portia* in how often the lure was attacked. Therefore, all data from tests of all species of *Portia* with spiders as lures, whether salticids or amaurobiids, were pooled, and all data from tests of all species of *Portia* with flies were pooled.

Only *Corythalia canosa* attacked ant lures; therefore, data from tests of all other salticids with ant lures were pooled.

Only two species of *Portia* were tested with flies. When these two species of *Portia* were excluded, there was no evidence of differences among the remaining salticids in how often they attacked fly lures; therefore, when flies were used as lures, data from tests of all salticids other than the two species of *Portia* were pooled.

Stalking of lures

Data for whether salticids attacked the lure or not are presented (Table 3). In each instance, the salticid's attack was preceded by a distinct stalking sequence. Occasionally, salticids appeared to begin to stalk a lure then moved away and left the ramp. However, it was not always clear whether the salticid was definitely stalking the lure in these instances. Therefore, we do not present data from instances of stalking without attacking. Inclusion of data on instances in which the salticid appeared to have stalked without attacking, however, would change none of the trends evident from the data on attacks alone.

Corythalia canosa responded to ant lures and fly lures in the same way that this species is known to respond to live ants and flies (i.e., it performed its different prey-specific predatory behaviours appropriately against these two types of prey). Likewise, *Portia fimbriata* responded to salticid, amaurobiid and fly lures in the same way that this species is known to respond to live salticids, amaurobiids and flies (i.e., by performing the appropriate prey-specific predatory behaviours).

Salticid	Lure	Size	No. of tests	Attack (%)
Portia fimbriata	Fly	Small	17	24
		Medium	31	29
	Ant	Small	23	0
	Amaurobiid	Medium	51	39
	Salticid	Medium	52	50
Portia africana	Amaurobiid	Medium	23	43
Portia labiata	Fly	Medium	23	30
	Amaurobiid	Medium	29	41
Portia schultzi	Amaurobiid	Medium	24	42
Corythalia canosa	Fly	Small	18	6
	Ant	Small	23	9
Euryattus sp.	Fly	Small	25	8
		Medium	23	17
	Ant	Small	22	0
Bavia aericeps	Fly	Medium	15	7
Euophrys parvula	Fly	Medium	31	16
Marpissa marina	Fly	Medium	33	6
Trite auricoma	Fly	Medium	23	13
Trite planiceps	Fly	Medium	35	17

Table 3: Results from testing salticids with motionless prey.

Salticid	Lure	Size	No. of tests	Attack (%)
Portia	Fly	Small	17	24
		Medium	54	30
		All	71	28
	Spider	Medium	179	44
All salticids other than *Portia*	Fly	Small	43	7
		Medium	160	13
		All	203	12
Corythalia canosa	Ant	Small	23	9
All salticids other than *Corythalia canosa*	Ant	Small	45	0
	Fly	All	256	17

Table 4: Results from testing salticids with motionless prey (results from Table 3 pooled where no statistically significant differences between data sets).

Comparison of attack rates against lures made from more preferred and less preferred prey

Portia attacked lures made from its more preferred prey, spiders, more often than it attacked lures made from its less preferred prey ($p < 0.05$). *Corythalia canosa*'s attack rates on both types of lures with which it was tested (flies and ants) were too low for meaningful comparison. Salticids other than *C. canosa* attacked lures made from flies, their preferred prey, more often than they attacked lures made from ants, a prey they tend not to eat ($p < 0.005$).

Comparison of attack rates of different species of salticids

Corythalia canosa attacked lures made from ants, this species' preferred prey, more often than other salticids attacked lures made from ants ($p < 0.05$). Although *Portia* prefers spiders to flies as prey, *Portia* nevertheless attacked lures made from flies more often than other salticids attacked lures made from flies ($p < 0.005$).

Discussion

Based on this study of eleven species of salticids, we can attempt to answer the three questions we raised.

Does prey have to move in order for a salticid to recognise it as prey? Apparently not. Each species we tested sometimes stalked and attacked motionless lures.

How widely does this conclusion apply within the Salticidae? Probably this conclusion is broadly applicable across the family. Although we tested only eleven species from this large family of about 4,400 described species (Coddington & Levi, 1991), the species we chose come from a wide taxonomic and geographic range and these species vary greatly in body size, general morphology, habitat preferences, and basic behaviour (Tables 1,2). Yet each species tested appears to be capable of recognising a motionless lure as prey.

Does prey have to move in order for salticids to discriminate between different types of prey? Apparently not. We tested salticids with known prey preferences and different prey-specific prey-catching behaviours for different prey. These salticids showed these same prey preferences and used the same prey-specific prey-catching behaviours in tests with motionless lures.

Does *Portia*, a salticid that is known to prey frequently on quiescent prey in nature, respond to motionless prey more readily than do other salticids? The data we obtained are consistent with this hypothesis. Each species of *Portia*, with each type of lure, attacked the lure in 24–50% of the tests, but no other salticid species attacked lures in more than 17% of the tests with any type of lure. Even when a motionless fly was used for a lure, *Portia* attacked more often than the other salticid species did, despite flies not being *Portia*'s preferred prey. Proximate mechanisms that might account for how *Portia* can more efficiently recognise motionless prey are discussed elsewhere (Tarsitano & Jackson, in press).

Acknowledgements

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