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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

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Abstract *Portia* is a behaviourally complex and aberrant salticid genus. The genus is of unusual importance because it is morphologically primitive. Five species were studied in nature (Australia, Kenya, Malaysia, Sri Lanka) and in the laboratory in an effort to clarify the origins of the salticids and of their unique, complex eyes. All the species of *Portia* studied were both web builders and cursorial. *Portia* was also an araneophagic web invader, and it was a highly effective predator on diverse types of alien webs. *Portia* was an aggressive mimic, using a complex repertoire of vibratory behaviour to deceive the host spiders on which it fed. The venom of *Portia* was unusually potent to other spiders; its easily autotomised legs may have helped *Portia* escape if attacked by its frequently dangerous prey. *Portia* was also kleptoparasitic and oophagic when occupying alien webs. *P. fimbriata* from Queensland, where cursorial salticids were superabundant, used a unique manner of stalking and capturing other salticids. The display repertoires used during intraspecific interactions were complex and varied between species. Both visual (typical of other salticids) and vibratory (typical of other web spiders) displays were used. *Portia* copulated both on and away from webs and frequently with the female hanging from a dragline. Males cohabited with subadult females on webs, mating after the female matured. Adult and subadult females sometimes used specialised predatory attacks against courting or mating males. Sperm induction in *Portia* was similar to that in other cursorial spiders. *Portia* mimicked detritus in shape and colour, and its slow, mechanical locomotion preserved concealment. *Portia* occasionally used a special defensive behaviour (wild leaping) if disturbed by a potential predator. Two types of webs were spun by all species (Type 1, small resting platforms; Type 2, large prey-capture webs). Two types of egg sacs were made, both of which were highly aberrant for a salticid. Responses of different species and both sexes of *Portia* were quantitatively compared for different types of prey. Many of the trends in behaviour within the genus, including quantitative differences in predatory behaviour, seemed to be related to differences in the effectiveness of the cryptic morphology of *Portia* in concealing the spider in its natural habitat ('effective crypsis'). The results of the study supported, in general, Jackson & Blest's (1982a) hypothesis of salticid evolution which, in part, proposes that salticid ancestors were web builders with poorly developed vision and that acute vision evolved in conjunction with the ancestral spiders becoming proficient as araneophagic invaders of diverse types of webs.

Keywords Araneae; Salticidae; spiders; evolution; predation; aggressive mimicry; behavioural complexity; displays; communication

INTRODUCTION

Unlike most spiders, jumping spiders (Salticidae) have complex eyes and well developed, acute vision (Homann 1928; 1969a, b; Williams & McIntyre 1980). They are the classic examples of cursorial hunting spiders which, instead of building webs to ensnare their prey, use vision to stalk, chase, and leap on active insects (Drees 1952; Land 1974; Forster 1977, 1982a, b). Many species have complex repertoires of courtship and threat displays (Crane 1949; Jackson 1982a; Jackson & Harding 1982), and much of the communicatory behaviour of these spiders relies on vision.

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Salticids have a pair of large anterior median or principal eyes and six smaller secondary eyes. The secondary eyes detect movement and control the orientation of the spider to objects in its field of vision, bringing images onto the retinae of the principal eyes. The principal eyes discriminate between classes of objects such as prey, mates, and conspecifics of same sex. Typically, the posterior median eyes are very much smaller than the other secondary eyes and they have no known function (Land 1972).

The Salticidae is a large (c. 4000 described species) and diverse family with members on every continent (except Antarctica) and on most oceanic islands. They live in habitats ranging from rain forests to deserts and from 80 m below sea level in Death Valley to 6400 m above sea level on Mt Everest. These spiders are a major component of most terrestrial faunas and are one of the major animal groups in which acute vision has evolved, but the evolutionary origins of the salticids and their unique eyes are poorly understood.

Recent studies of *Portia fimbriata* (Coleman 1978, 1980; Jackson 1982b, 1985, 1986a; Jackson & Blest 1982a, b; Blest 1983; Blest & Price 1984), a highly unusual salticid from Queensland, Australia, suggest that questions about salticid evolution may not be as intractable as they formerly seemed. Although it moves easily across open ground and is a cursorial predator, *P. fimbriata* also spins a large web — an extraordinarily aberrant behaviour for a salticid — and uses it to capture both insects and other spiders. *P. fimbriata* also invades alien webs and preys on the host spider, the eggs of the host spider, and on insects ensnared in the web of the host spider. Typical web-building spiders lack acute vision and detect and locate their prey by web-borne vibrations. When *P. fimbriata* enters alien webs it is an aggressive mimic, generating silk vibrations that deceive the host spider.

Webs of highly varied shapes and designs have evolved in spiders — from the 2-dimensional orb webs of many araneids to the sparsely spun 3-dimensional space webs of many theridiids to the thickly woven sheet webs of many agelenids (Foelix 1982). Some enhance the adhesiveness of their webs by adding special substances to the threads. Cribellate spiders build sticky webs by coating webs with very fine threads from the cribellum, a specialised spinning plate with minute spigots. Non-cribellate spiders which build sticky webs secrete adhesive fluid from spigots on the spinnerets and form droplets of 'glue' along the threads. Webs with neither form of 'glue' added are referred to as 'non-sticky', although all spider silk may be adhesive to some extent.

Generally, cursorial spiders have difficulty moving about on webs, and web-building spiders tend to have difficulty negotiating webs of shapes and designs that are markedly different from the webs they spin themselves (see Foelix 1982). Cursorial spiders, and those that spin non-sticky webs, tend to adhere to sticky webs. Furthermore, spiders that spin non-cribellate sticky webs tend to adhere to cribellate webs and vice versa. *P. fimbriata,* however, is exceptional in being able to move about and capture prey on webs of diverse shapes and designs, and in failing to adhere to either cribellate or non-cribellate sticky webs.

Although *P. fimbriata* is obviously specialised and complex, it belongs to a genus which is considered to be primitive within the Salticidae because it has important morphological characters that are probably primitive (or plesiomorphic) features (Wanless 1978, 1984). The large, functional posterior median eyes of *Portia* are particularly noteworthy. In this context, 'complex' and 'specialised' are not antithetical to 'primitive'.

The primitive morphological traits in *Portia* raised the question of whether some of the behaviours of *P. fimbriata* are also primitive. This possibility led to a hypothesis, presented in detail elsewhere (Jackson & Blest 1982a), that the Salticidae evolved from web-building spiders with poor vision. If so, acute vision may have evolved originally in a spider like *P. fimbriata* that became an araneophagic predator proficient at invading diverse types of webs.

The hypothesis of Jackson & Blest about salticid evolution should be amenable to testing by comparative analysis of behaviour. Comparative information about spiders in the genus *Portia* is particularly important. In his recent review of the subfamily Spartaeinae, Wanless (1984) limited *Portia* to eight species which are found mainly in tropical Africa (*P. africana, P. alboguttata, P. schultzi*) and Asia (*P. albimana, P. assamensis, P. crassipalpis, P. fimbriata, P. labiata*). *P. fimbriata* is also found in New Guinea, the Solomon Islands, and tropical Australia. Reports of web-building, web-invasion, and predation on web-building spiders by *P. schultzi, P. labiata,* and *Portia* sp. in India (Graveley 1921; Sherriffs 1931; Bristowe 1941; Wanless 1978; Forster 1982b; Murphy & Murphy 1983), although lacking in detail, suggest that the unusual behaviours exhibited by *P. fimbriata* are widespread in the genus; however, detailed behavioural studies are only published for *P. fimbriata* in Queensland.

To extend this information, comparative studies were made on five species of *Portia: P. africana* and *P. schultzi* from Kenya; *P. albimana* from Sri Lanka; *P. labiata* from Malaysia and Sri Lanka; and *P. fimbriata* from Malaysia, Sri Lanka, and the Northern Territory of Australia; and more information was obtained on the biology of *P. fimbriata* from Queensland. Silk utilisation and predatory behaviour, intraspecific behaviour, reproductive biology, and the spiders' natural history were studied.

The salticids are one of the major groups of animals to have evolved complex, visually mediated courtship and threat displays. These include special postures and movements of the legs, palps, and abdomen. In contrast, typical web-building spiders from other families, which have poor vision, have evolved specialised vibratory displays (Robinson 1982), which involve special plucking and drumming movements of palps and legs on the web strands.

This dichotomy between the communicatory behaviour of salticids and other families of web-building spiders is not, however, straightforward. In many species, multichannel communication is segregated into phases within the normal courtship sequence. The male employs visual displays at first; but, on mounting the female, he engages in specialised tapping and stroking behaviour during which tactile and chemotactic stimuli seem to be important. Salticids often build silk nests in which they moult, oviposit, and sometimes mate; they also generally stay in their nests at night and during other periods of inactivity. Salticid nests (or 'retreats') are usually tubular and densely woven (Jackson 1979a). In some salticids, the segregation of communication into different sensory channels is related to the nest (Jackson 1977a,1982c, d; Edwards 1981; Jackson & Harding 1982). Each male may use any of three distinct mating tactics, depending on the type of female he encounters and whether she is inside or outside her nest ('courtship versatility'). If he encounters an adult female outside her nest, he performs vision-dependent displays (Type 1 courtship) in front of the facing female. If he encounters an adult female inside her nest, he employs a different type of courtship (Type 2), which consists of various tugging, probing, and vibrating movements on the silk of the nest, and which are not vision-dependent. A male encountering a subadult female inside her nest initially performs Type 2 courtship and then spins a second chamber on the female's nest and cohabits until she moults and matures.

Vibratory communication was unexpected in this family and it was suggested (Jackson 1977a) that part of the explanation for its evolution is historical; i.e., it evolved from ancestors which had poor vision and used vibratory displays. This hypothesis did not, however, presume web-building ancestors for the Salticidae; males of certain spiders with poor vision, such as clubionids and dysderids, court females in nests using silk-borne vibratory displays (Jackson & Pollard 1982; Pollard & Jackson 1982). However, the hypothesis that *Portia* has retained web building from pre-salticid ancestors has heightened interest in the possibility that vibratory courtship by salticids is plesiomorphic. The existence of vibratory displays was predicted, but no evidence of this was found in the earlier study of *Portia fimbriata* (Jackson 1982b), only a few mature males being available at the time. In the present study, the intraspecific interactions of other species of *Portia* are examined, and *P. fimbriata* is re-examined, with larger sample sizes.

Although the testes of male spiders open at a gonopore on the anterior ventral abdomen, the copulatory structures are on the palps. During sperm induction the male spins a small sperm web, deposits a drop of sperm from his gonopore on the silk, touches the drop with his palpal organ, and absorbs the sperm. Induction is direct in most web-building species; the male extends his palp around the web to contact the drop and absorb the sperm. Many cursorial species have indirect induction in which the male absorbs the sperm through the silk (Montgomery 1903; Gerhardt & Kaestner 1928). As the method of sperm induction is potentially significant phylogenetically, sperm induction was investigated in *Portia.*

MATERIALS AND METHODS

Portia

The locations and activities of each of the 480 individual *Portia* (juveniles still in egg cases or aggregated in maternal webs not included) found in nature were noted, and the behaviour of 321 captive adult *Portia* was studied (Table 1) (field studies: RRJ; laboratory studies: RRJ and SEAH). Data from the earlier study (Jackson & Blest 1982a) are pooled with new data on Queensland *P. fimbriata* in this paper.

The population of *P. labiata* in Malaysia is denoted by (M), and that in Sri Lanka by (SL); the populations of *P. fimbriata* in the Northern Territory and Queensland, Australia, are denoted by (NT) and (Q), respectively. This is especially significant for *P. fimbriata,* as the behaviour of this species varied markedly between populations. No differences were found between populations of *P. labiata.* As most of the information on *P. labiata* was derived from Sri Lankan *P. labiata,* (SL) is omitted except when confusion is likely to arise. Some of the spiders currently referred to as *P. fimbriata* are possibly subspecies or new, undescribed species. For ease of expression, the different populations of *P. fimbriata* will often be referred to in the text as if they were different species.

Quantitative behavioural information was obtained for the species studied. In many instances,

Table 1 The species of *Portia* investigated, localities of field work, and the numbers of *Portia* that provided data in nature and in captivity. In captivity: individuals collected in nature and individuals of *P. fimbriata* (Q), *P. labiata* (SL), and *P. schultzi* reared from eggs in the laboratory. Observed in captivity: adults only. Observed in nature: adults and large juveniles. See Table 2 for information about localities.

	Country	Locality	Number observed in nature	Number observed in captivity
P. africana (Simon)	Kenya	Kisumu	10	6
P. albimana (Simon)	Sri Lanka	Badulla, Peradeniya	9	4
P. fimbriata (Doleschall)	Australia	Northern Territory: Katherine	52	24
		Queensland: Cairns	212	117
	Malaysia	Kuala Lumpur	25	5
	Sri Lanka	Badulla, Kaneliya, Ella, Mahiyangana, Peradeniya	37	8
P. labiata (Thorell)	Malaysia	Kuala Lumpur, Pasoh, Tapah	40	10
	Sri Lanka	Badulla, Kaneliya, Peradeniya, Ramboda Falls	65	105
P. schultzi Karsch	Kenya	Malindi, Shimba Hills	30	45

however, there were no marked interspecific differences for certain groups of species. Generally, when this was so, presentation is simplified by using pooled data in tables and statistical tests. Unless stated otherwise, all laboratory data were obtained from observations of adult *Portia.*

Localities

Localities of *Portia* and the arthropods used as prey are given as the names of towns, parks, or field stations that were nearby and which can be readily found on maps of the particular country in question (Table 2, Appendix 1). *Portia* was not, however, studied exclusively, if at all, within the towns themselves. For example, Malindi encompassed, as well as the town of Malindi, wide areas of the neighbouring Sokoke and Midi-Gedi Forests. Pasoh refers to the field station of Institiut Penyelidikan Perhutanan near Kuala Pilah; Tapoh refers to forest along lower stretches of the main road from Tapoh to the Cameron Highlands; Kuala Lumpur refers to the Gombak Forest Reserve and to forest research plots of Universiti Pertanian Malaysia, near Kuala Lumpur. All localities in Malaysia are in the western Malay Peninsula. Kaneliya refers to property of the Ceylon Plywoods Corporation near Galle. Additional information about climate, vegetation, and terminology is provided by Burbidge (1960), Webb (1968), Johnson (1964), Ojany & Ogendo (1973), and Ooi (1976).

Maintenance, analysis, and terminology

Cages were constructed from glass tanks and transparent plastic boxes of various sizes and shapes (see Jackson 1974). Stoppered holes permitted the insertion of prey without damaging webs, and water was continuously available from moist cotton inserted through other holes or from glass vials filled with water, stoppered with cotton, and placed in the cages. Usually, two or three wooden stems were placed in each cage for web attachment. The spiders used as prey were maintained in the same types of cages and fed insects. Cages were kept in rooms with controlled light (13 : 11 L : D or 12 : 12 L : D) and temperature (c. 25°C). Lights were turned on in the laboratory at 0800 h and went off at 2000 h or 2100 h.

Definitions of phasing, amplitude, duration, and site of movement are illustrated with the following example. When two legs were waving (dorso-ventrally) at the same time, they were referred to as being in 'matching phase' if both were at their maximal dorsal positions simultaneously; if one was maximally dorsal when the other was maximally ventral, then their phase difference was 180° and they were 'alternating'. Duration was the period of a complete cycle, as the leg moved from maximally dorsal to maximally ventral and back; amplitude was the distance between these positions. The first major segment distal to the point of articulation was referred to in specifying the site of movement (e.g., femoral movement: coxa-trochanter joint).

Table 2 Major characteristics of the habitats of *Portia*. See Table 1 for the species of *Portia* that occurred at each locality. Three periods of field work at Cairns; one, all other localities.

Country & period of field work	Climate	Locality	Latitude	Altitude	Terrain	Dominant vegetation	Web sites
Sri Lanka							
Jan. 1982	No distinct dry season	Badulla	7°N	1000 m	Gentle hills	Lowland rain-forest	Boulders and trees
		Ella	7°N	1200 m	Steep	Lowland rain-forest	Boulders beside river
		Kaneliya	6°N	100 m	Gentle hills	Lowland rain-forest	Boulders, dirt bank, and trees near river
		Mahiyangana	7°N	100 m	Level	Lowland rain-forest	Trees beside lake
		Peradeniya	7°N	500 m	Level	Lowland rain-forest Botanic Gardens	Buttressed trees
		Ramboda Falls	7°N	1800 m	Steep	High altitude rain-forest	Culvert and boulders beside river
Malaysia							
Dec 1981	Equatorial. No distinct dry season.	Kuala Lumpur	3°N	100 m	Steep	Lowland rain-forest *Dipterocarpus*	Rock and dirt ledges, trees.
		Pasoh	3°N	100 m	Level	Lowland rain-forest *Dipterocarpus*	Trees
		Tapah	4°N	100 m	Steep	Lowland rain-forest *Dipterocarpus*	Trees
Kenya							
Feb–March 1982	Modified equatorial No distinct dry season.	Kisumu	0°	1400 m	Level	Combretacreous savanna	Sisal, *Euphorbia*, and introduced cacti on shore of Lake Victoria
		Malindi	3°S	Sea Level	Level	1. Coastal palm belt 2. Lowland dry forest: *Cynometra — Manilkara* 3. Lowland rain-forest	1. Trees and sisal 2. Short, highly branched trees 3. Buttressed trees and stone walls
		Shimba Hills	4°S	300 m	Gentle hills	Lowland rain-forest	Buttressed trees
Australia							
1 Dec–Jan 1979–80 2 Nov–Jan 1980–81 3 Dec 1982	Monsoonal. Wet season: Dec–Mar.	Cairns	16°S	Sea Level	Precipitous	Mixed closed rain-forest	Rock ledges, boulders, and buttressed trees near creeks and rivers
Dec 1980		Katherine	14°S	200 m	1. Precipitous 2. Level	1. Riverine 2. Sclerophyllous woodland	1. Shallow caves on limestone cliffs 2. Mouths of deep caves

For ease of expression, the terms 'up', 'down', 'forward', 'back', 'to the side', and 'inward' are used sometimes for 'dorsally', 'ventrally', 'anteriorly', 'posteriorly', 'laterally', and 'medially'. The spider's legs were specified as pairs I–IV (anterior to posterior). Life stages were referred to as, for example, egg, postembryo, first instar (see Whitcomb 1978). 'Subadults' were one moult from becoming adults. Unless qualified, 'male' and 'female' referred to adults. 'Juveniles' were at least two moults from being adult. 'Copulation' and 'mating' were used interchangeably. 'Non-salticid web-building spider' is abbreviated to 'web spider', and 'salticid' refers to cursorial salticids other than *Portia.* 'Alien web' refers to a web not spun by *Portia.* Unless stated otherwise, 'web of *Portia*' refers to a Type 2 web (see 'Observations').

A pursuit was defined as beginning when the *Portia* first oriented toward and approached the prey or first vibrated on a web. Pursuit time was the time from then until the prey was captured. If *Portia* ceased vibrating (prey in web), or did not maintain orientation (prey outside web), for 5 min or longer, the observations were discounted.

No individual *Portia* was used in formal observations more than once per day. Whenever spiders had to be moved, they were gently prodded with a camel-hair brush. Video tapes and 16 mm movie films were made during some observations and were analysed by stop motion and frame-by-frame, respectively. Decisions, such as which particular *Portia* was used in a given observation, were made either haphazardly (i.e., with no conscious regard for the identity of the individuals) or randomly (random numbers table).

Normally distributed data are expressed as a mean ± SD; all other data, as medians followed by ranges. The statistical tests are from Sokal & Rohlf (1969). Tests of independence and McNemar tests for significance of changes included Yates' correction when sample sizes were less than 200. When comparing pursuit times, Mann-Whitney U-tests were performed with modifications to approximate the t-distribution.

Expressions such as 'usually' or 'generally', 'sometimes' or 'occasionally', and 'infrequently' or 'rarely' were used to indicate frequencies of occurrence of c.80% or more, 20–80%, and 20% or less, respectively. Frequency of occurrence was expressed with greater precision only if necessary and justified.

Considerable controversy surrounds much of spider taxonomy. Generally, the names adopted in this paper correspond to names preferred by the museums at which most of the voucher specimens were deposited (Queensland Museum for Australian species, British Museum for most others).

Testing with prey

Three types of formal observations of predation were made: Type A tests, in which different types of prey were presented in a predetermined random sequence; similar, but less systematic, Type B tests: and Type C tests, in which the prey-spider was in a web fastened to the web of *Portia.* The tests were described in an earlier study (Jackson & Blest 1982a), except for the differences noted below, and only brief descriptions of methods are given here.

In Type A tests, each *Portia* was presented with a different type of prey each day. Each test began shortly after the lights came on in the laboratory (0800 h). The *Portia* was introduced into the prey's cage and watched continuously until it caught the prey or until 4 h had elapsed. Webs were present in tests with web spiders as prey, but not in tests with other prey types. If the prey was not caught within 4 h, observations were continued intermittently throughout the day. Four types of prey (salticid, amaurobiid, theridiid, housefly) were used. Because individual spiders were tested with each type of prey in random order, allowed 24 h in which to capture it, and then held another 24 h before testing with the next prey in successive tests, responses to different prey types could be compared using McNemar tests for significance of changes. Responses to salticids were compared to responses to one of the two types of web spiders (Amaurobiidae); and in another set of McNemar tests, responses to houseflies were compared to those to the other type of web spider (Theridiidae).

Type B tests were similar to Type A except that there was no routine testing of individual *Portia* on successive days. Sometimes, prey were introduced into cages containing the *Portia* in its own web rather than, as in Type 1 tests, the reverse; and sometimes the *Portia* was dropped onto an alien web, rather than being permitted to enter it spontaneously. Houseflies were either presented on an alien web or introduced to a cage containing *Portia* on its own web. In contrast to the earlier study, observations were sometimes terminated after as little as 2 h when *Portia* ignored the prey, and *Portia* was not always left for 24 h with potential prey it had not caught during the period of observation. There was no evidence that these differences in methodology had important effects on the results.

As a preliminary to Type C tests, web spiders were placed in cages containing webs of *Portia* from which the *Portia* had been removed. These spiders spun their own webs and fastened them to the webs of *Portia; Portia* was then returned to the cage. If the *Portia* returned to its own web without first eating the web spider, a Type C test was begun by introducing insects to the cage and observing the spiders according to the time protocol of Type B tests.

Three sizes of prey were defined, by dividing the estimated volume of the prey by the estimated volume of the *Portia*: small (0.1–0.25), medium (0.5–1), large (1.5–2). In Type A and C tests, all prey were medium.

In a given test, failure to capture a potential prey could result from either a failure to pursue the prey or failure to capture a prey that had been pursued. Thus, it was necessary to calculate both pursuit tendencies and capture efficiencies. Pursuit tendency is the percentage of tests during which prey

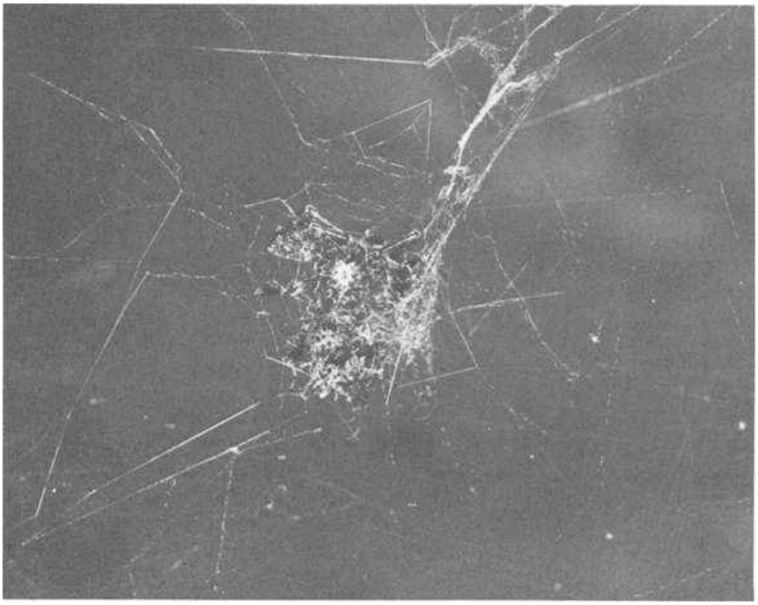


Fig. 1 Female *Portia fimbriata* (Q) (ventral view) hanging beneath a Type 1 web (horizontal platform, about 2× spider size) suspended in Type 2 web.

was pursued; capture efficiency is the percentage of prey pursued that were captured.

In addition, several hundred informal tests were carried out, but the results are not included in the quantitative summaries. Informal tests were like Type B tests except that the period of continuous observation and the total period during which the predator and prey were left together varied widely between tests. The informal tests were carried out in the laboratory and in other settings (such as hotel rooms) in Queensland, the Northern Territory, Asia, and Africa. Some informal tests were staged by dropping a captive *Portia* onto an alien web in nature.

Reproduction and intraspecific behaviour

For tests in the laboratory, spiders were placed together in cages and their behaviour observed. Eight types of interactions were staged: male introduced to cage with female (1, no web; 2, female in her own web; 3, female in alien web); male introduced to cage with another male (4, no web; 5, male in alien web); female introduced to cage with another female (6, no web; 7, female in her own web; 8, female in alien web). For *P. fimbriata* (Q), *P. labiata* (SL), and *P. schultzi*, a minimum of 20 interactions were observed of each of the eight types. For *P. fimbriata* (NT) and *P. labiata* (M), a minimum of five of each type was observed. No interactions were observed for *P. africana*, and only males of *P. albimana* and females of *P. fimbriata* (SL) were available. Six female-female interactions of *P. fimbriata* (SL) were observed.

In these tests, some females had unknown reproductive histories because they were taken from the field as adults. Other females, which matured in the laboratory, had known reproductive histories, and tests were made with both virgin and non-virgin females.

With virgin females, 23 interspecific male-female interactions were staged: 4 were of male *P. albimana* with female *P. labiata*; 4, male *P. labiata* with female *P. fimbriata* (SL); 5, male *P. fimbriata* (Q) with female *P. fimbriata* (SL); 6, male *P. fimbriata* (Q) with female *P. labiata*; 4, male *P. labiata* with female *P. fimbriata* (Q).

OBSERVATIONS

Webs spun by *Portia*

Portia spun two types of webs. Females spun both types of webs; males, Type 1 only. Type 1 webs were silken platforms, 1–3× the body length of the spider, suspended approximately horizontally and were more or less square in outline (Fig. 1). Type 2 webs were larger (c. 4000 cm^3), 3-dimensional silken networks. Although structure varied and was often difficult to discern, the web was basically funnel-like, a result of three loosely woven, inclined sheets converging more or less at the bottom of the web (Fig. 2, 3). The sheets often had considerable curvature and the individual sheets merged at their edges without distinct seams. Also at the top and bottom of the web, the threads were spaced more widely, and the sheets dissipated indistinctly. The

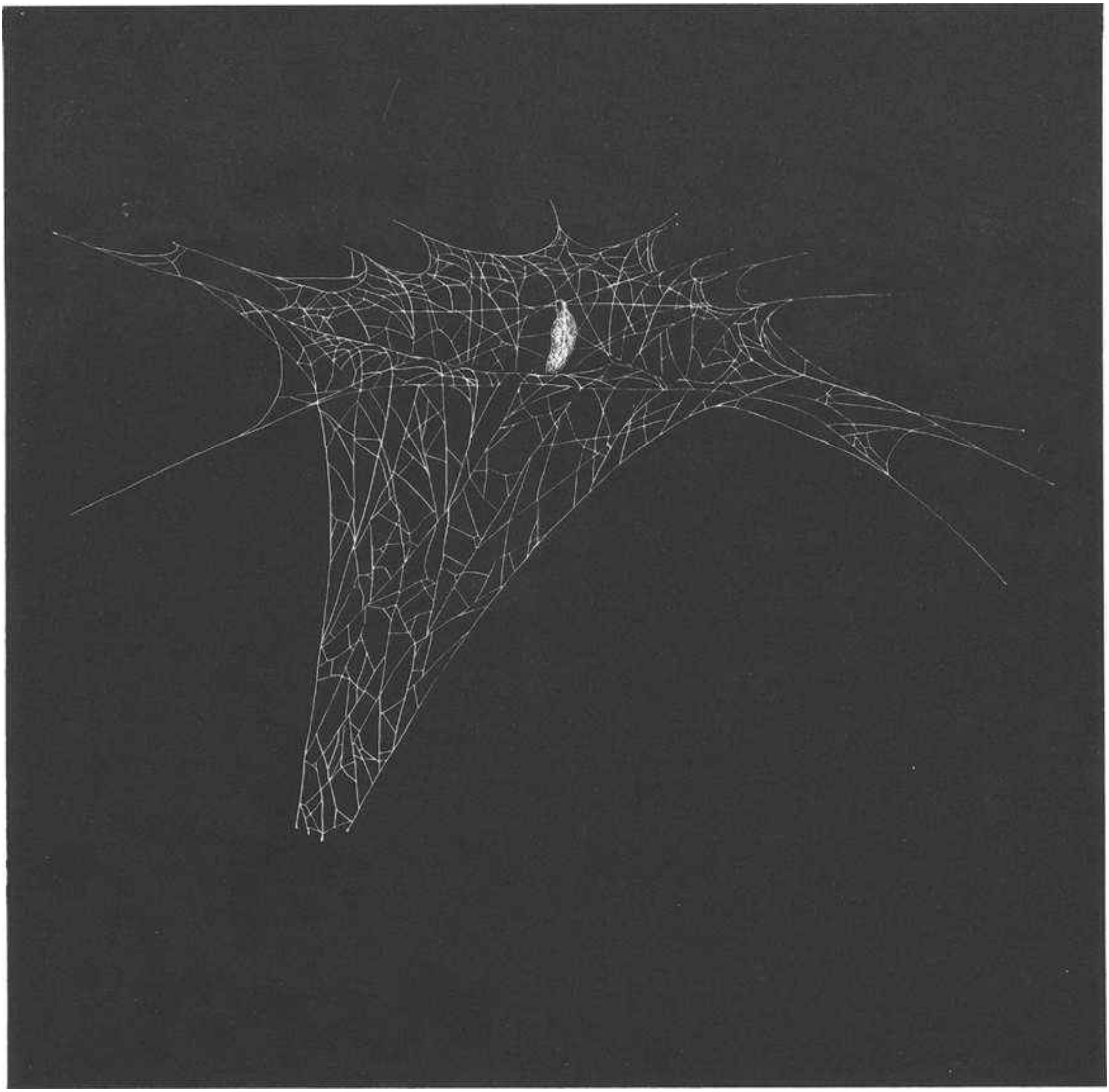


Fig. 2 Simplified diagram of a Type 2 web of *Portia labiata*. See text for details.

interior of the funnel and, to a lesser extent, the immediate exterior, were filled with 3-dimensional arrays of threads.

Usually, a dead leaf (c.20 × 10 mm) or other detritus, such as a clump of dirt or a piece of bark, was suspended near the top centre of the Type 2 web, or a Type 1 web was incorporated near the top centre of the Type 2 web. Additional detritus was often scattered elsewhere in the web.

The behaviour of web construction, observed from each species except *P. albimana*, was essentially as described earlier for *P. fimbriata* (Q) (Jackson & Blest 1982a). Webs were sometimes considerably redesigned, and new sheets were often spun partly into old sheets. As a result, larger, more complex webs enveloped the initial funnel-like structure. In nature, webs of *Portia* (all species) were often built into, within, or around webs of other

Fig. 3 Upper third of a Type 2 web of *Portia labiata* built within an indentation on a dirt bank at Kaneliya in Sri Lanka; a detrital egg sac is suspended near the top centre of the web; this egg sac is unusual in that it incorporates two leaves. The *Portia* is out of view, standing on the opposite side of the egg sac. Pieces of dirt and other detritus are scattered through the web.

species. The compound web that resulted, consisting of both alien silk and the silk of the *Portia*, was exceedingly difficult to characterise.

Habitats and web sites

All *P. fimbriata* (Q) were found within 100 m of permanent running water (creek or river) in rain forests on rugged, precipitous terrain (Table 2). Because of the terrain and the enveloping canopy (Fig. 4), ambient light levels in these habitats were consistently low (Table 3). In contrast, the habitats of the other *Portia* (Fig. 5, 6) were often, but not always, on less sculptured terrain or in less dense forest where ambient light levels tended to be higher. Ambient light levels were extremely low for *P. fimbriata* (NT) living deep within caves; but *P. fimbriata* (NT) also occurred frequently at or near cave mouths, in much brighter light than was typical for *P. fimbriata* (Q). The caves were in woodland with open canopy (Fig. 5). *P. africana* and *P. schultzi* occurred in forests that were generally more open than the forests in Queensland, Malaysia, and Sri Lanka (Fig. 6), but not consistently as open as the forests in the Northern Territory (for *P. schultzi*, also see Murphy & Murphy 1983). Generally, ambient light levels were higher at web sites of *Portia* in the rain forests of Malaysia and Sri Lanka than for *Portia* in Queensland. *P. labiata* (M) also occurred in highly disturbed areas such as oil palm plantations (W. Corley pers. comm.; see also Murphy & Murphy 1983). Occasionally, all species of *Portia* except *P. fimbriata* (Q) were found in webs exposed to direct sunlight for part of the day.

Web-building spiders, which were numerous in each habitat of *Portia*, were extremely abundant in the Queensland habitat of *P. fimbriata* and the habitat of *P. africana* in Kenya on the shore of Lake Victoria. These two habitats, unlike others, were close to permanent water, and insects were very numerous. Uniquely, on Lake Victoria, web spiders occurred in very large and dense, but very localised, interspecific complexes of interconnected webs. Carpenter (1920) described similar, enormous aggregations from islands in Lake Victoria.

Fig. 4 Rain forest in Queensland. *Portia fimbriata* occurred in webs on overhanging boulders in foreground, between buttresses of tree (centre), and on rock ledges (background).

Fig. 5 Katherine Gorge National Park, Northern Territory, Australia. *Portia fimbriata* occurred in caves on the limestone cliffs.

Two species of *Portia* were found in habitats where salticids were extremely abundant; salticids were much less abundant in the other habitats. *P. africana* was found in habitats that contained very large and dense, but very localised, aggregations of three small (< 5 mm body length) species of salticids that nested within the localised aggregations of web spiders (Jackson 1986). However, widespread and dense populations of web spiders and salticids (especially) were unique to Queensland.

Most of the 480 *Portia* observed in nature were clearly in either webs spun by *Portia* (47%) or in alien webs (31%); 12% were in compound webs; 5% were in webs of undertermined origin; and 5% were not in webs. Disproportionately more males than either juveniles or females were found out of webs: 20% of 93 males as against 1% of the 387 juveniles and females ($\chi^2=57.817$, $P<0.0001$). Of the 224 non-compound webs spun by *Portia*, 50% were fastened to, but separate from, alien webs; 55% of the alien webs to which webs of *Portia* were fastened were occupied by other spiders. Webs of all species of *Portia* contained exoskeletons, sometimes as many as four of various sizes, suggesting that all species occupied individual webs for prolonged periods, as has been shown for marked *P. fimbriata* (Q) (Jackson & Blest 1982a).

In nature, non-compound webs of *P. fimbriata* (Q), *P. albimana* and *P. fimbriata* (M, NT, SL) were almost always fastened (usually entirely but at least partly) to rigid substrata such as rocks and tree trunks. Webs of *P. africana, P. schultzi*, and especially *P. labiata* were, however, often fastened to pliable stems and leaves on shrubs and lower branches of trees.

Fig. 6 Sokoke Forest near Malindi, Kenya. *Portia schultzi* occurred in webs (arrows) of *Ishnothele karschi* on stems and trunks of trees. Although the vegetation is dense, ambient light levels in this habitat are considerably greater, because of the more level terrain and open canopy, than in the Queensland habitat.

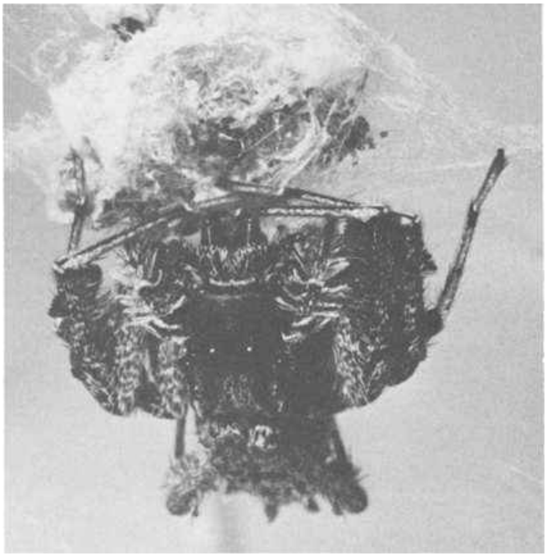


Fig. 7 Female *Portia fimbriata* (NT) in cryptic rest posture, hanging beneath silk egg sac. Legs I-III are held largely ventral to the body, with tarsi angled medially and crossing over the midline of the sternum. Femora IV are angled up and forward, closely following the contour of the carapace, and medially so that the patellae almost meet. The remainder of each leg IV angles back and to the side, with the tarsi contacting the substratum just posterior to the abdomen. Palps are retracted to the sides of the chelicerae in the lateral posture (see Intraspecific interactions).

Cryptic appearance

Adult *Portia* are moderately large salticids. Body lengths were 5-6 mm for males and 7-10 mm for females, except in *P. schultzi* (males 4-6 mm, females 5-7 mm). As a result of their fringes and tufts of hairs on legs and abdomens and their black, white, brown, pale yellow, and pale orange markings, all *Portia* resembled much of the debris present in webs.

Each species adopted a similar cryptic rest posture, when at rest on silk or detritus in webs (Fig. 7), which resulted in outlines of the body and appendages being obscured. All species of *Portia* adopted the cryptic rest posture in response to mild disturbance; *Portia* disturbed while already in this posture often enhanced it by pulling the legs and palps closer to the body. Also, the palps were 'flickered' when *Portia* was mildly disturbed (e.g., if a person lightly touched the web) in the cryptic rest posture; when flickered, palps were held in the lateral posture and were waved smoothly and rapidly (c. 4 Hz, amplitude 1-2 mm) up and down (matching phase) for several seconds without pausing. The legs usually remained flexed and stationary.

Locomotion

Slow, 'mechanical' walking, with asynchronous, 'choppy' palp and leg waving (Jackson & Blest 1982a), occurred in all species of *Portia*, but stepping and waving tended to be about 2-3× faster in the other species of *Portia*, compared to *P. fimbriata* (Q). *P. fimbriata* (Q) was also decidedly more extreme in the bizarre, jerky appearance of its movements (Table 3).

All *Portia* walked with ease on both non-sticky and sticky (cribellate and non-cribellate) webs of varied shapes (Appendix 1: sheet, space, orb). Locomotion on and off webs was basically similar except for the addition of rotary probing (free leg moves in ellipse until catching hold of silk line) when on webs (Fig. 8).

Wild leaping

In wild leaps, the spider suddenly propelled itself, more or less directly, 100–150 mm upward. Wild leaps were often made from the cryptic rest posture. The spider moved on a wide trajectory to the forest floor, onto a tree trunk, to another part of the web, or into the vegetation. Upon landing, *Portia* either froze immediately (i.e., became completely inactive) or ran about 100 mm then froze. Sometimes, additional leaps occurred in rapid succession. Many times, the spider swung out on a dragline during the leap, immediately climbed back to near its point of departure, then froze. Normal leaps were on a more forward trajectory, they were usually shorter, and they occurred less suddenly.

When approached by a threatening object (e.g., a collecting vial), most species of *Portia* usually leapt away; wild leaps were performed by *P. labiata, P. schultzi,* and *P. albimana* (not determined for *P. fimbriata* (M, NT, SL) and *P. africana*). Running and leaping away were only rarely and inconsistently elicited from *P. fimbriata* (Q), and this species could be readily collected in nature by simply placing a vial over the spider and prodding it from behind (Table 3).

Oviposition

Females of each species were observed in nature brooding eggs. The oviposition sites of *P. fimbriata* (Q) and *P. fimbriata* (NT) contrasted sharply. The eggs of *P. fimbriata* (Q) ($n=39$) were always on dead, brown leaves, usually c.20 mm long, suspended near the top centre of the web (see Fig. 3, 9). *P. fimbriata* (NT) ($n=6$) was only once observed with eggs on a similar leaf. Instead, eggs were usually oviposited on the undersides of silk platforms (Fig. 7, 10) which were basically Type 1 webs suspended horizontally in the Type 2 webs, but more densely woven than normal Type 1 webs. In two

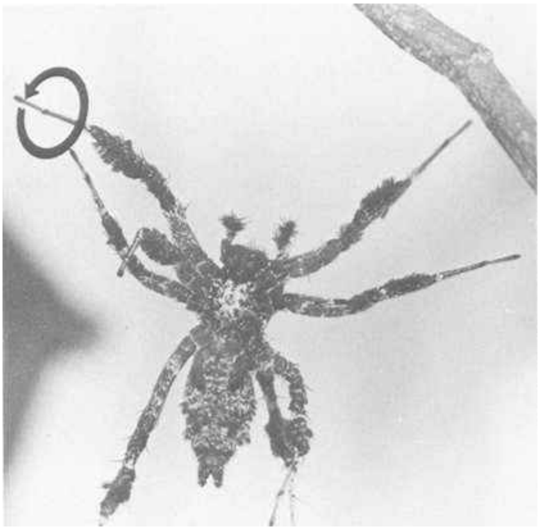


Fig. 8 Female *Portia fimbriata* (Q) (ventral view) making rotary probes (arrow) with right leg I.

Table 3 Summary of major differences between *P. fimbriata* (Q) and the other studied *Portia*.

	Portia fimbriata (Q)	Other *Portia*
Ambient light in habitat	Lesser	Greater
Abundance of web spiders in habitat	Greater	Lesser
Abundance of cursorial salticids in habitat	Greater	Lesser
Slow, mechanical locomotion	More pronounced	Less pronounced
Defensive behaviour when mildly disturbed	Adopts cryptic posture	Performs wild leaps
Predation on web spiders	More efficient. More inclined to use vibratory behaviour. Less inclined to leap	Less efficient. Less inclined to use vibratory behaviour. More inclined to leap
Predation on cursorial salticids	More efficient. Cryptic stalking occurs	Less efficient. Cryptic stalking does not occur
Cursorial predation on insects	Less efficient	More efficient
Intraspecific behaviour	Less cannibalistic. Twist and forward lunging do not occur. Vibratory courtship less pronounced	More cannibalistic. Twist and forward lunging performed by female. Vibratory courtship more pronounced

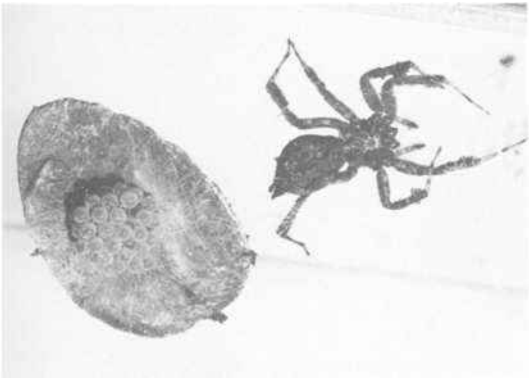


Fig. 9 Detrital egg sac (left) of a *Portia labiata* (right) from Sri Lanka. The *Portia*, with ventral surface in view, is climbing across web to right. Eggs are clustered on a layer of silk at the centre of a concavity on a slightly curled leaf and covered by a fine layer of silk. Note stick visible at the top of the photograph (another stick is out of focus behind the leaf) and insect remains at the far right.

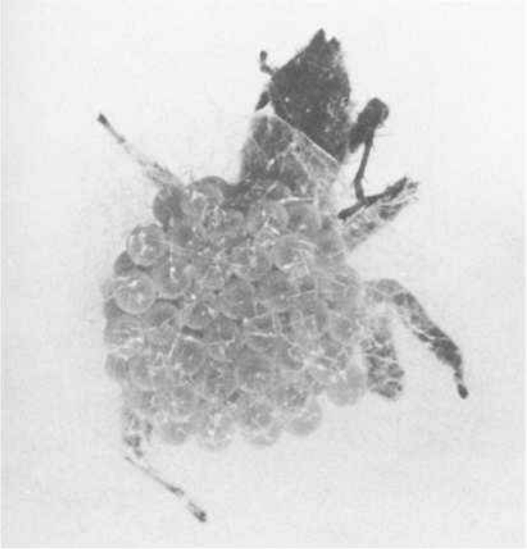


Fig. 10 Silken egg sac of a *Portia fimbriata* from the Northern Territory of Australia. The *Portia* is standing beneath the egg sac, six legs and her posterior, ventral abdomen are visible.

instances, a collection of minute debris was woven into the platform. The only brooding female *P. albimana* observed had her eggs on a silk platform like that of *P. fimbriata* (NT). Egg sacs of this type will be called 'silken egg sacs'. The other species of *Portia* oviposited on: dead leaves, like *P. fimbriata* (Q), and bits of detritus of similar size (18); on pieces of bark (4); clumps of dirt (3); and a seed pod (1). Egg sacs of this type will be called 'detrital egg sacs'.

In the laboratory, 24 female *P. fimbriata* (NT) were given access to leaves. None suspended leaves in its web, but seven made silken egg sacs, as in nature. *P. fimbriata* (Q), *P. labiata*, and *P. schultzi* always made detrital egg sacs if provided with leaves or similar objects (e.g., balls of cotton wool) in the laboratory; but when kept without suitable materials, they occasionally oviposited on silk platforms like *P. fimbriata* (NT).

To make a detrital egg sac, *Portia* spun a thick sheet of silk onto the surface of the leaf (or some other object), covering an area similar to or slightly larger than that of a Type 1 web. Next, the eggs were oviposited on the centre of the sheet and then the eggs and the first layer of silk were covered by a less thickly woven second sheet. Essentially the same procedure was followed on a Type 1 web to make a silken egg sac. The thick first layer of silk, however, completely covered and incorporated the Type 1 web.

Prey

In the laboratory, *Portia* captured and ate each type of arthropod offered (Appendix 1; Fig. 11, 12). Each species of *Portia*, except *P. albimana*, was observed feeding primarily on spiders in nature. More details about the prey of *Portia* in nature will be provided elsewhere (Jackson unpublished data) in conjunction with a comparison with the prey of cursorial salticids.

Pursuit tendencies and capture efficiencies

Female *P. fimbriata* (Q)

Females of *P. fimbriata* (Q) usually pursued, and were very efficient at catching, spiders of all types. Pursuit tendencies and capture efficiencies were 87% or greater for medium spiders in Type A and B tests (Table 4, 5). In contrast, females usually did not pursue, nor were they efficient at capturing, insects (pursuit tendencies and capture efficiencies 41% or less). Pursuit tendencies and capture efficiencies were significantly greater if the prey was a web spider rather than a housefly in Type A tests (Table 4), but were not significantly different when salticids were compared with web spiders.

For Type B tests with webs present, pursuit tendencies and capture efficiencies were greater for the web spiders than for the insects (Table 6). For Type B tests in which insects and salticids were presented to *Portia* in the absence of webs, pursuit tendencies and capture efficiencies were greater for salticids than for insects (Table 7).

Table 4 Results from Type A tests. Each individual spider tested, in random order, with each of the four types of prey. Data for *P. labiata* and *P. schultzi* pooled. McNemar tests for significance of changes used to compare responses of spiders to different types of prey: one type of web-building spider (amaurobiid) compared with salticids and the other type (theridiid) compared with houseflies. Tests of independence: males and females compared separately for *P. fimbriata* (Q) and for *P. labiata* and *P. schultzi*, and *P. fimbriata* (Q) compared with *P. labiata* and *P. schultzi* separately for males and females. Sample sizes for pursuit tendencies: 50 in each case for *P. fimbriata* (Q) and 100 in each case for pooled data of *P. labiata* (50) and *P. schultzi* (50). Sample sizes for capture efficiencies given in table in parentheses. All prey: medium. Salticid and housefly: no web present. Amaurobiid and theridiid: *Portia* introduced to cage with the alien web.

		P. fimbriata (Q)			*P. labiata* and *P. schultzi*			Comparison of species (χ^2)	
Prey		Male	Female	Comparison	Male	Female	Comparison	Male	Female
Salticid	Pursuit tendency	36%	92%	31.641****	20%	68%	46.753****	3.705 NS	9.252**
	Capture efficiency	56%(18)	100%(46)	19.478****	0%(20)	34%(68)	7.490**	12.350***	47.562****
Amaurobiid	Pursuit tendency	30%	90%	35.042****	38%	90%	58.681****	0.616 NS	0.833 NS
	Capture efficiency	67%(15)	96%(45)	6.523**	53%(38)	70%(90)	2.815 NS	0.386 NS	10.150**
Salticid and Amaurobiid Compared (χ^2)	Pursuit tendency	0.211 NS	0.000 NS		7.031**	12.971***			
	Capture efficiency	0.000(7) NS	0.500(42) NS		4.167(14)*	10.240(62)**			
Theridiid	Pursuit tendency	48%	90%	18.700****	33%	87%	60.750****	2.579 NS	0.072 NS
	Capture efficiency	71%(24)	100%(45)	11.583***	76%(33)	83%(87)	0.373 NS	0.013 NS	7.125**
Housefly	Pursuit tendency	24%	40%	2.252 NS	20%	55%	26.133****	0.124 NS	2.430 NS
	Capture efficiency	58%(12)	35%(20)	0.847 NS	50%(20)	65%(55)	0.897 NS	0.008 NS	4.386*
Theridiid and Housefly Compared (χ^2)	Pursuit tendency	6.722**	23.040****		4.364*	26.694****			
	Capture efficiency	0.000(9) NS	11.077**(20)		1.500(10) NS	7.563(53)**			

NS: not significant. *$P < 0.05$; **$P < 0.01$; ***$P < 0.001$; ****$P < 0.0001$.

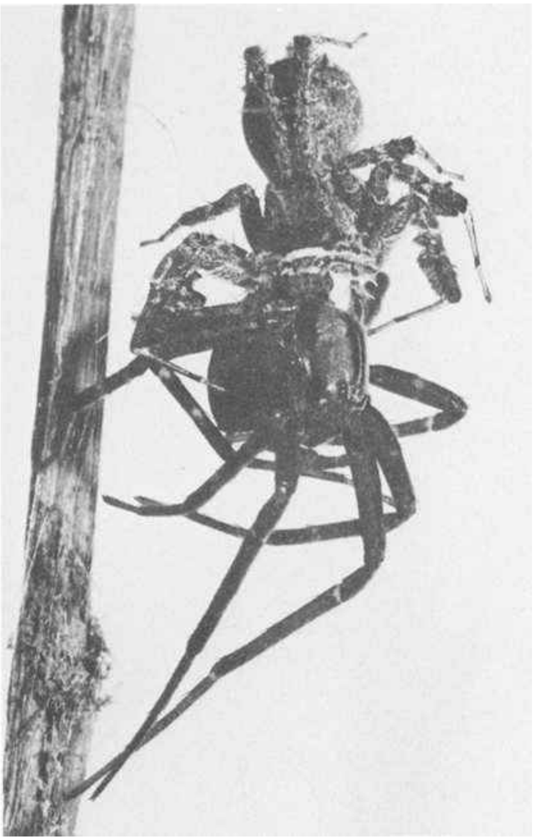


Fig. 11 Female *Portia labiata* feeding on *Badumna longinquus* in sticky (cribellate) web of prey. *Portia* (above) has grasped the dorsal abdomen of the prey near the pedicel. Carapace of prey is visible below and to right of *Portia.*

Size of prey had no significant effect on pursuit tendencies (always 68% or greater) or capture efficiencies (92% or greater) with salticids and web spiders (Table 8). Larger insects were, however, pursued more often than smaller insects by *Portia* on alien webs; the converse was true when *Portia's* own webs were present (Table 9). There was no significant difference when webs were absent. There was also no significant difference in how efficiently larger and smaller insects were captured on alien webs. Sample sizes for tests without an alien web were too small for comparisons to be made. For all sizes of insects, capture efficiencies in the presence of the webs of *Portia* were not significantly different from those when webs were absent, but with small and medium insects, capture efficiencies were greater when alien webs were present (sample size was insufficient for consideration of large insects). Pursuit tendencies for medium and large insects were also greater in the presence of alien webs.

Females of *Portia* other than *P. fimbriata* (Q)

Portia were more likely to pursue and were more efficient at capturing web spiders than either salticids or insects in Type A tests (Table 4) of *P. labiata* and *P. schultzi*, and results from Type B tests on all species other than *P. fimbriata* (Q) showed the same trend (Table 5). Away from webs, salticids were pursued more readily than insects, but they were captured less efficiently (Table 7). Similarly, in the presence of alien webs, spiders were pursued more readily but captured less efficiently than insects (Table 6).

P. labiata and *P. schultzi* pursued smaller prey (both salticids and web spiders) more readily than larger prey (Table 8). Capture effciency was greater on smaller salticids, but prey size did not affect

Table 5 Results from Type B tests (see text) with females of *Portia*. All prey: medium. Salticid and insect: no web present. Web spider: *Portia* introduced to cage with alien web. Sample sizes given in parentheses. Pursuit tendency and capture efficiency are defined in text. Tests of independence: data for *P. fimbriata* (Q) compared with pooled data for all other *Portia*. All comparisons: $P < 0.0001$.

Prey		*P. fimbriata* (Q)	*P. fimbriata* (NT)	*P. fimbriata* (SL)	*P. africana*	*P. labiata*	*P. schultzi*	All *Portia* except *P. fimbriata* (Q)	Tests of independence (χ^2)
Salticid	Pursuit tendency	87%(207)	50%(40)	94%(47)	77%(22)	63%(131)	58%(91)	65%(331)	32.403
	Capture efficiency	93%(181)	10%(20)	45%(44)	29%(17)	40%(82)	36%(53)	37%(216)	132.523
Web-building spider	Pursuit tendency	91%(428)	94%(85)	64%(84)	74%(27)	83%(224)	84%(184)	82%(604)	17.763
	Capture efficiency	92%(390)	81%(80)	83%(54)	65%(20)	79%(185)	72%(155)	77%(494)	34.203
Insect	Pursuit tendency	27%(282)	30%(40)	43%(42)	48%(25)	35%(159)	52%(128)	42%(394)	15.456
	Capture efficiency	41%(76)	83%(12)	78%(18)	67%(12)	71%(55)	69%(67)	71%(164)	20.507

Table 6 Comparison of results from Type B tests with web spiders and insects on alien webs. All prey: medium. Sample sizes given in parentheses. All tests with female *Portia*. Pursuit tendencies and capture efficiencies considered separately. Data for *P. fimbriata* (Q) and pooled data for *P. labiata* and *P. schultzi* considered separately. Tests of independence: spiders and insects as prey compared.

	P. fimbriata (Q)		*P. labiata* and *P. schultzi*	
Prey	Pursuit tendency	Capture efficiency	Pursuit tendency	Capture efficiency
Spider	91%(428)	92%(390)	83%(408)	76%(340)
Insect	49%(65)	78%(32)	67%(82)	93%(55)
Test of independence (χ^2)	80.328****	6.589*	11.551***	7.887**

$^*P < 0.05$; $^{**}P < 0.01$; $^{***}P < 0.001$; $^{****}P < 0.0001$.

Table 7 Comparison of results from Type B tests (see Table 8) with salticids and insects. Pursuit tendencies and capture efficiencies considered separately. Data for *P. fimbriata* (Q) and pooled data for all other *Portia* considered separately. All prey: medium. Sample sizes given in parentheses. All tests with female *Portia*. No webs present during tests. All tests of independence: $P < 0.0001$.

	P. fimbriata (Q)		All *Portia* except *P. fimbriata* (Q)	
Prey	Pursuit tendency	Capture efficiency	Pursuit tendency	Capture efficiency
Salticid	87%(207)	93%(181)	65%(331)	37%(216)
Insect	27%(282)	41%(76)	42%(394)	71%(164)
Test of independence (χ^2)	175.170	82.912	40.280	45.119

Table 8 Results from Type B tests for *P. fimbriata* (Q), *P. labiata*, and *P. schultzi* with three sizes of salticids (no web present) and web spiders (alien web present when *Portia* tested). Male and female *Portia* compared (tests of independence): data for *P. fimbriata* (Q) and pooled data for *P. labiata* and *P. schultzi* considered separately. Responses to small and large salticids compared (tests of independence) separately for males and females.

			P. fimbriata (Q)			*P. labiata* and *P. schultzi*		
Prey			Male	Female	Comparison (χ^2)	Male	Female	Comparison (χ^2)
Salticid	Small	Pursuit tendency	48%(40)	76%(55)	7.186**	42%(81)	54%(83)	1.995 NS
		Capture efficiency	84%(19)	95%(42)	0.903 NS	47%(34)	58%(45)	0.515 NS
	Medium	Pursuit tendency	33%(101)	87%(207)	96.012****	22%(165)	61%(222)	58.353****
		Capture efficiency	48%(33)	93%(181)	45.511****	3%(36)	39%(135)	15.344****
	Large	Pursuit tendency	0%(19)	68%(28)	18.916****	0%(34)	18%(50)	5.101*
		Capture efficiency	—	100%(19)	—	—	11%(9)	—
	Small & Large Compared (χ^2)	Pursuit tendency	11.225***	0.322 NS		18.297****	15.502****	
		Capture efficiency	—	0.036 NS		—	4.800*	
Web spider	Small	Pursuit tendency	84%(44)	94%(50)	1.487 NS	73%(77)	98%(83)	18.108****
		Capture efficiency	92%(37)	100%(47)	1.948 NS	77%(66)	84%(81)	0.663 NS
	Medium	Pursuit tendency	41%(138)	91%(428)	155.971****	35%(262)	83%(408)	164.226****
		Capture efficiency	67%(57)	92%(390)	31.067****	69%(91)	76%(340)	1.671 NS
	Large	Pursuit tendency	7%(30)	91%(44)	48.203****	8%(52)	81%(98)	70.170****
		Capture efficiency	50%(2)	93%(40)	—	25%(4)	82%(79)	4.556*
	Small & Large Compared (χ^2)	Pursuit tendency	39.847****	0.031 NS		6.595*	11.029***	
		Capture efficiency	—	1.746 NS		3.005 NS	0.005 NS	

NS: not significant. $^*P < 0.05$; $^{**}P < 0.01$; $^{***}P < 0.001$; $^{****}P < 0.0001$.

Table 9 Results from Type B tests with insects. Comparison of tests with no web present, web spun by the *Portia* present, and alien web present (host spider absent). All tests with female *Portia*. Data for the three sizes of insects and for each of three species of *Portia* given separately. Tests of independence: **(1)** comparison of results with no web present and results with alien web present; **(2)** comparison of responses to small and large insects.

		P. fimbriata (Q)				*P. labiata* and *P. schultzi*			
		Small	Medium	Large	Small and large compared (χ^2)	Small	Medium	Large	Small and large compared (χ^2)
No web	Pursuit tendency	27%(62)	27%(282)	9%(22)	2.157 NS	41%(169)	43%(287)	12%(58)	16.596****
	Capture efficiency	53%(17)	41%(76)	0%(2)	—	83%(70)	70%(122)	14%(7)	13.096***
Web of *Portia*	Pursuit tendency	35%(75)	32%(120)	0%(20)	7.882**	52%(104)	63%(141)	2%(41)	28.519****
	Capture efficiency	73%(26)	47%(38)	—	—	78%(54)	74%(89)	0%(1)	—
No web and web of *Portia* compared (χ^2)	Pursuit tendency	0.526 NS	0.922 NS	0.431 NS		2.865 NS	16.071****	1.843 NS	
	Capture efficiency	1.055 NS	0.219 NS	—		0.231 NS	1.966 NS	—	
Alien web	Pursuit tendency	43%(51)	49%(65)	70%(40)	5.495*	46%(98)	67%(82)	65%(78)	5.876*
	Capture efficiency	91%(22)	78%(32)	75%(28)	1.172 NS	93%(45)	93%(55)	86%(51)	0.632 NS
No web and alien web compared (χ^2)	Pursuit tendency	2.403 NS	12.233***	18.716****		1.954 NS	15.419****	36.510****	
	Capture efficiency	5.396*	11.122***	—		1.807 NS	10.063**	14.437***	

NS: not significant; *$P < 0.05$; **$P < 0.01$; ***$P < 0.001$; ****$P < 0.0001$.

capture efficiencies with web spiders. In the presence of alien webs, *P. labiata* and *P. schultzi* pursued larger insects more readily than smaller insects, but capture efficiencies were not affected by insect size (Table 9). Both pursuit tendency and capture efficiency were greater with smaller insects in the absence of webs. In the presence of webs of *Portia*, smaller insects were more likely to be pursued; sample size was insufficient for comparison of capture efficiency.

P. labiata and *P. schultzi* pursued medium insects more often in the presence of their own webs than in the absence of webs; for small and large insects, the differences were not significant; capture efficiencies were not significantly affected for any insect size. For medium and large insects, both pursuit tendencies and capture efficiencies were greater in the presence of alien webs than in the absence of webs; no significant effect was evident for small insects.

Comparison of males and females

In Type A tests, females of each species were more likely to pursue each type of prey-spider than were males (Table 4). Also, females of *P. labiata* and *P. schultzi*, but not *P. fimbriata* (Q), had greater pursuit tendencies than males with houseflies as prey. When the prey were salticids, females of all species had greater capture efficiencies than males. Females of *P. fimbriata* (Q), but not *P. labiata* and *P. schultzi*, were more efficient at capturing web spiders than were males. For all species, capture efficiencies were not significantly different for males and females with insects.

Table 10 Pursuit times of *Portia* with different types of prey (see Fig. 13–16). *P. fimbriata* (Q) compared to all other *Portia*.

Prey		*P. fimbriata* (Q)	All *Portia* except *P. fimbriata* (Q)
Salticid	Median	26 min	3 min
	Range	1–318 min	0–41 min
	N	168	79
Web spider	Median	16 min	5 min
	Range	0–583 min	0–465 min
	N	358	381
Insect	Median	3 min	3 min
	Range	0–34 min	0–45 min
	N	31	117

In Type B tests, females of each species were more likely than males to pursue medium or large salticids and web spiders (Table 8). This was true also of *P. fimbriata* (Q), but not of *P. labiata* and *P. schultzi*, with small salticids and of *P. labiata* and *P. schultzi*, but not of *P. fimbriata* (Q), with small web spiders. For all species, females were more efficient than males at capturing medium salticids. There was no difference between the sexes with small salticids as prey, and sample sizes were insufficient for comparison with tests with large salticids. Females of *P. fimbriata* (Q) and of *P. labiata* and *P. schultzi* were more efficient than males at capturing medium (*P. fimbriata* (Q)) and large (*P. labiata* and *P. schultzi*) web spiders.

Comparison of species

In Type A tests, female *P. fimbriata* (Q) were more likely to pursue salticids and were more efficient at capturing salticids and web spiders than were female *P. labiata* and *P. schultzi*. However, female *P. labiata* and *P. schultzi* were more efficient at capturing houseflies than were female *P. fimbriata* (Q) (Table 4). Male *P. fimbriata* (Q) were more likely to pursue and more efficient at capturing salticids than were male *P. labiata* and *P. schultzi*.

A comparison of data from Type B tests of female *P. fimbriata* (Q) with pooled data from Type B tests of females of the other species of *Portia*, showed that *P. fimbriata* (Q) were significantly more likely to pursue, and more efficient at capturing, both salticids and web spiders as prey, and significantly less likely and less efficient with insects as prey (Table 5). *P. fimbriata* (SL) and *P. fimbriata* (NT) were anomalous in that the pursuit tendencies of these two spiders were apparently greater than the pursuit tendency of *P. fimbriata* (Q), with salticids and web spiders, respectively, as prey; however, sample sizes were small.

Pursuit times

Pursuit times of *P. fimbriata* (Q) were longer with salticids ($t = 7.982$, $P < 0.001$) and with web spiders ($t = 8.542$, $P < 0.001$) as prey than with insects (Fig. 13–16, Table 10); pursuit times with salticids and web spiders were not significantly different ($t = 1.848$). Pursuit times of other *Portia* were not significantly different for salticids and insects ($t = 1.798$), but they were longer with web spiders than with insects ($t = 14.591$, $P < 0.001$) or with salticids ($t = 11.018$, $P < 0.001$). Pursuit times for *P. fimbriata* (Q) were longer than for the other *Portia* with salticids ($t = 10.801$, $P < 0.001$) and with web spiders ($t = 6.688$, $P < 0.001$), but not with insects ($t = 0.040$).

Elements of predatory behaviour

All species of *Portia* used a variety of vibratory behaviours when pursuing spiders on webs. All species attacked prey by either seizing or stabbing after leaping, lunging, or picking up. Each element of behaviour, except dropping on prey, has been described previously (Jackson & Blest 1982a), and only brief descriptions will be provided here, although some new terms will be introduced. There were no differences among the species in the form of these behaviours, each of which was performed by all species. The swooping attacks frequently used by *P. fimbriata* (Q) in capturing cursorial salticids were not, however, performed by the other *Portia*. Illustrations of several behaviours will be provided here for the first time.

Fig. 12 Male *Portia albimana* feeding on *Badumna longinquus* in web of prey. *Portia* (above) has grasped the ventral cephalothorax of its prey, whose legs are visible below the *Portia*.

Vibrate with palps and legs

Flutter. Very rapid oscillations were made against the silk with forward extended palps or forelegs (Fig. 17).

Strike. Palps or forelegs were raised then lowered rapidly and forcefully onto the silk (for details, see 'Intraspecific behaviour').

Pluck. One or more of the legs and palps flexed or extended forcefully one or several times, pulling, pushing, or both on the silk (Fig. 18).

Twitch abdomen

The abdomen moved up and down rapidly.

Lunge and leap

Legs I and II were slowly raised and extended forward (but not 'elevated': see below). After a pause, the fangs were extended, a dragline was fastened, and suddenly legs I and II were extended stiffly forward and the spider was propelled forward by extension of legs III and IV. When lunging, tarsi III and IV remained on the substratum, but when leaping tarsi III and IV left the substratum.

Fig. 13 Pursuit times by *Portia* with web spiders in their webs. 10 min, mid point of 0–19 min; 30 min, mid-point of 20–39 min. All prey: size B. Slashed bars, *P. fimbriata* (Q); plain bars, all *Portia* except *P. fimbriata* (Q).

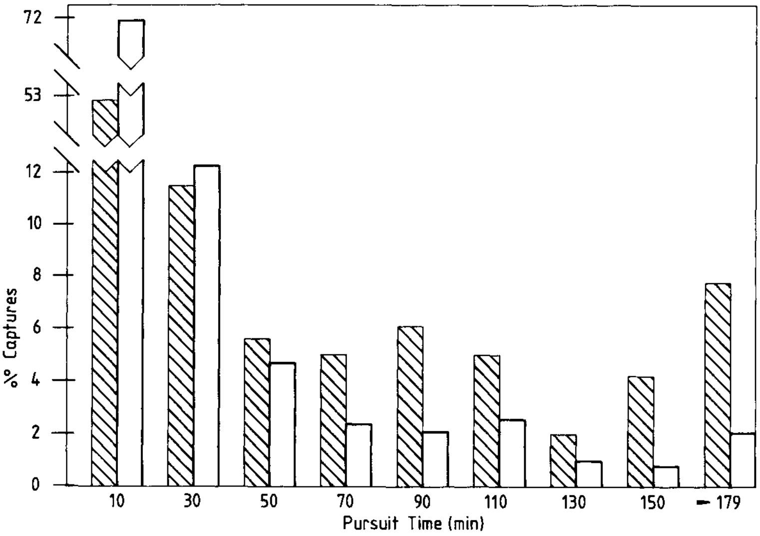
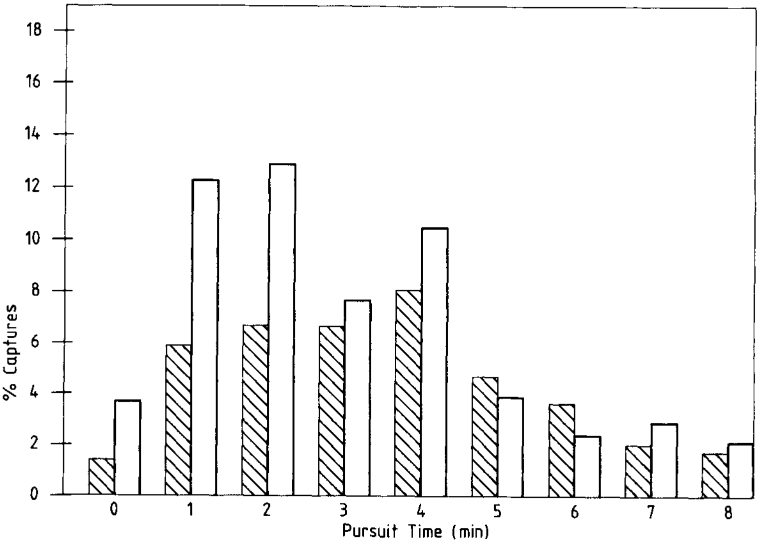


Fig. 14 Pursuit times by *Portia* web spiders in their webs. A subset of the data with web spiders as prey: pursuit times of 8 min or less. See Fig. 13.



Swoop

To swoop, *Portia* slowly positioned its cephalothorax over the prey then moved rapidly down with its chelicerae open.

Pick up

Compared to lunging and swooping, picking up was a slower motion in which the spider moved its chelicerae into contact with and seized the prey. Sometimes *Portia* first used its forelegs to slowly manipulate the prey.

Stab with fangs

Sometimes at the end of a lunge, swoop, or leap a prey-spider was not seized, but was stabbed (fangs punctured the prey then immediately retracted), after which the prey ran away.

The effect of *Portia* venom

When stabbed, Size A and B prey-spiders usually ran 100–200 mm away, went into convulsions, and became paralysed after 10–30 s. As the spider convulsed 10 s–4 min after it was immobilised, *Portia* slowly approached and seized it. Size A and B prey-

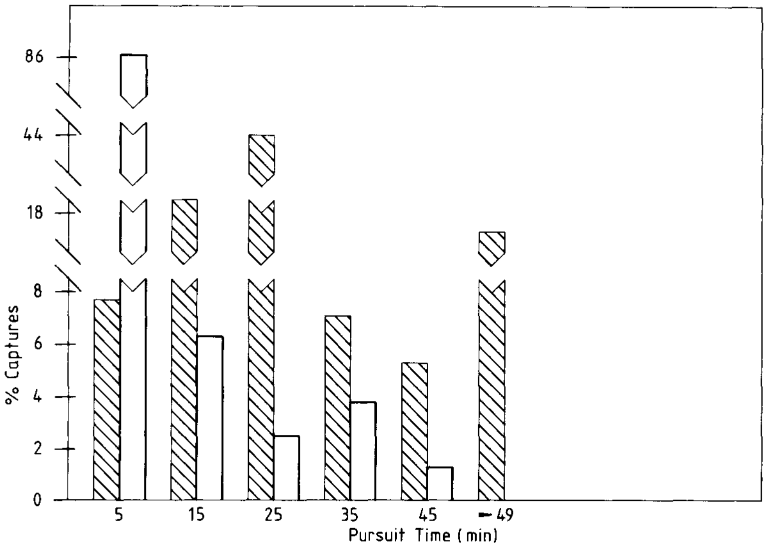


Fig. 15 Pursuit times by *Portia* with cursorial salticids away from webs and nests. 5 min, mid-point of 0-9 min. See Fig. 13.

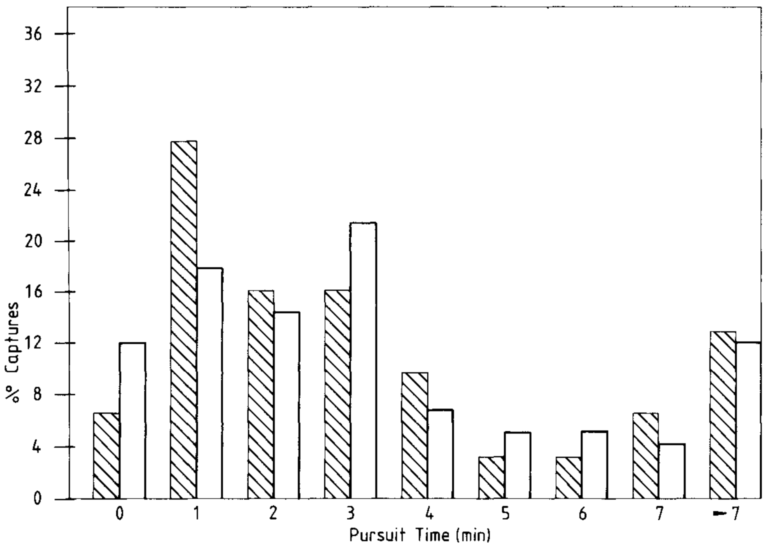


Fig. 16 Pursuit times by *Portia* with insects away from webs. See Fig. 13.

spiders that were seized at the end of leaps, lunges, or swoops were also immobilised, usually within 10-30 s. The venom of *Portia* was also strikingly effective against other *Portia*. Insects, however, generally were not immobilised so quickly, but continued struggling, sometimes for many minutes.

If *Portia* was prevented from making further contact with a stabbed prey or if a seized prey was immediately removed from the *Portia*, the prey usually recovered, although several minutes usually elapsed before it began making sluggish movements, and often up to 1 h elapsed before it began to move about normally.

Multiple stabs

Portia often stabbed Size C spiders several times before they were subdued. A stabbed spider might show no adverse effects or it might become partially or completely disabled for 30 s or more (e.g., become sluggish, undergo brief convulsions, then recover).

Portia continued pursuing and stabbing (sometimes 10-15 times) with the prey eventually becoming completely or almost completely immobilised before being seized and eaten. *Portia* tended to be very slow to retrieve a prey immobilised after multiple stabs, and sometimes faced an immobilised spider, from 20–200 mm away, for 15–30 min before walking over and seizing it.

Drop on prey

Sometimes *Portia* lowered itself very slowly on a dragline toward a prey below it. If *Portia* was in a web, the prey was either lower down in the same web or off, and just below, the web. From a few millimetres above, *Portia* lunged and either seized or stabbed the prey. Propulsion during these lunges came not from sudden extension of legs III and IV but from suddenly dropping the last few millimetres on the dragline.

Cryptic stalking

During cryptic stalking (Fig. 19), palps were held in the lateral posture in the same way as in the cryptic rest posture, but in distinct contrast to how palps were held during normal locomotion. The slow, mechanical characteristics of normal locomotion were exaggerated during cryptic stalking. If the cursorial salticid turned and faced a cryptically stalking *Portia* while they were still 10–50 mm apart, *Portia* usually halted until the salticid again faced away. Locomotion also ceased, but less predictably, when salticids faced from farther away. Cryptic stalking was employed only by *P. fimbriata* (Q) that were pursuing salticids.

Normal stalking

During normal stalking, in contrast to cryptic stalking, palps were in the normal posture and *Portia* did not routinely halt when faced by the prey. Although choppy waving of legs and palps often occurred as *Portia* walked toward the prey, the slow, mechanical characteristics of normal locomotion were not exaggerated. Sometimes, in fact, there was little or no choppy leg- and palp-waving and *Portia* walked faster than during normal locomotion.

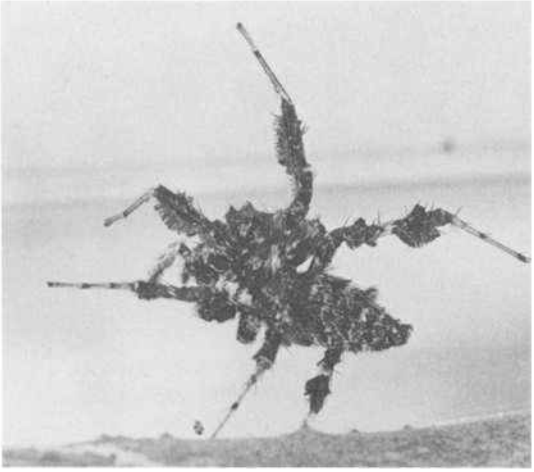


Fig. 17 Female *Portia fimbriata* (Q) (facing left) fluttering legs.

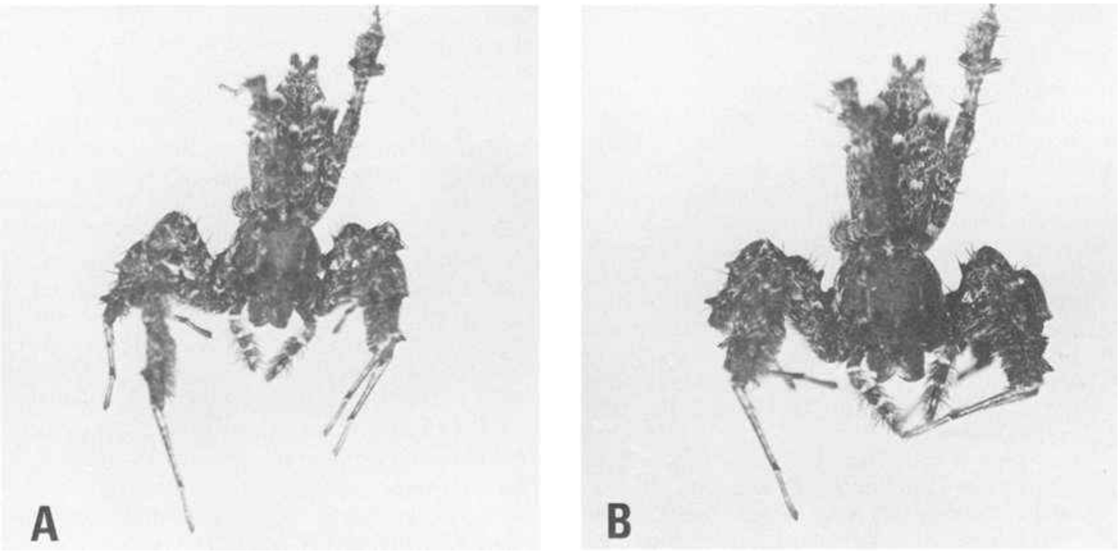


Fig. 18 Female *Portia fimbriata* (Q) plucking by flexing legs I and II (compare A and B).

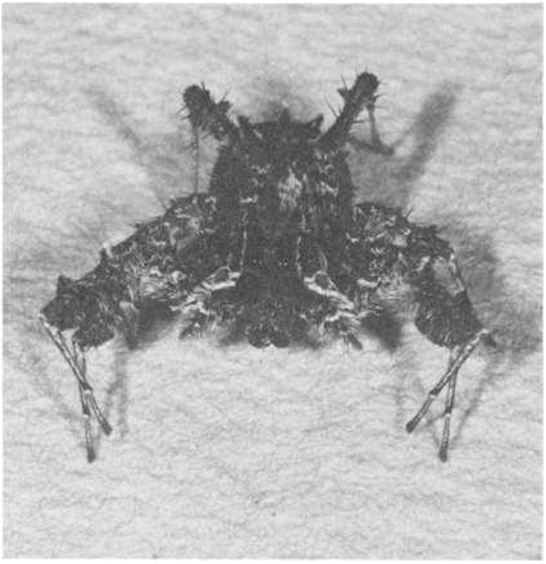


Fig. 19 Female *Portia fimbriata* (Q) (viewed from in front and about 45° above) cryptically stalking a cursorial salticid (not in photograph).

Table 11 Occurrence of vibratory behaviour, leaping into webs, and chasing prey across webs in tests during which female *Portia* pursued small or medium amaurobiids or eresids on densely woven webs. Occurrence of each behaviour expressed as number of tests during which the behaviour occurred divided by the total number of tests during which the amaurobiid or eresid was pursued and multiplied by 100. Tests of independence: data for *P. fimbriata* (Q) and pooled data for *P. labiata* and *P. schultzi* compared.

	Portia fimbriata (Q)	*Portia labiata*	*Portia schultzi*	Test of independence (χ)
No. of pursuits	133	70	39	
Vibratory behaviour	99%	79%	70%	33.777****
Leapt into web	2%	16%	13%	12.779***
Chased prey	8%	21%	31%	13.766***

***$P < 0.001$; ****$P < 0.0001$.

Predatory sequences

The descriptions provided earlier for *P. fimbriata* (Q) (Jackson & Blest 1982a) are broadly applicable to the other species, except for major differences in responses to cursorial salticids. General trends are summarised below and differences among species are detailed (Fig. 20, 21).

Predation on web spiders

Invasion of alien webs. *P. fimbriata* (Q) only rarely leapt onto prey in webs or chased web spiders that decamped (Fig. 20). Instead, *P. fimbriata* (Q) usually vibrated and moved in a consistently slow fashion while in webs. Sometimes the behaviour of each of the other species was comparable to *P. fimbriata* (Q) (vibrating and moving slowly in webs), but *P. labiata* (SL) and *P. schultzi* were more prone to leap into webs from stems or other neighbouring objects and to chase decamping spiders across and out of webs (Table 11). Even when vibrating in webs, these two species sometimes stepped rapidly, compared to *P. fimbriata* (Q), toward the host spider.

From Type B and informal tests, it was evident that *P. africana*, *P. albimana*, *P. fimbriata* (M, NT, SL), and *P. labiata* (M) were similar to *P. labiata* (SL) and *P. schultzi* and different from *P. fimbriata* (Q) in being likely to leap at and chase web spiders instead of consistently using vibratory behaviour. These differences were, however, less pronounced when comparing the different *P. fimbriata* than when comparing *P. fimbriata* (Q) to *P. labiata* and *P. schultzi.*

Rotary probing and breaking lines. *P. labiata* often stood at the edge of the web (e.g., on a stem) and made very slow (2–4 s/Hz) and unusually 'gentle' probes, with the leg stopping as soon as it contacted a thread. Thus, the web was vibrated only a little or not at all, and usually no response was elicited from the host spider. Next, the line was released and *P. labiata* moved slightly away, moved its chelicerae to the thread, and severed it. This continued for variable periods, often for many hours, before *Portia* leapt toward the host spider through the more or less thread-free space it had established. Sometimes *P. labiata* moved out into the web, slowly and gently probing and severing lines, before moving out of the web again to leap.

Use of own web. Type C tests were carried out with *P. fimbriata* (Q, NT, SL), *P. labiata* and *P. schultzi.* In some tests with each species, insects landed in the web of the *Portia*, the spider in the adjoining web entered the web of the *Portia*, and *Portia* pursued and captured the spider that pursued the insect.

Predation on cursorial spiders

Cursorial spider in nest. *P. fimbriata* (Q), in contrast to other *Portia* (Fig. 21), routinely oriented toward and approached nests, then walked onto the nests and began to pluck with legs (Fig. 22). *P. fimbriata* (Q) occasionally chewed by inserting its fangs in the silk then repeatedly opening and closing its

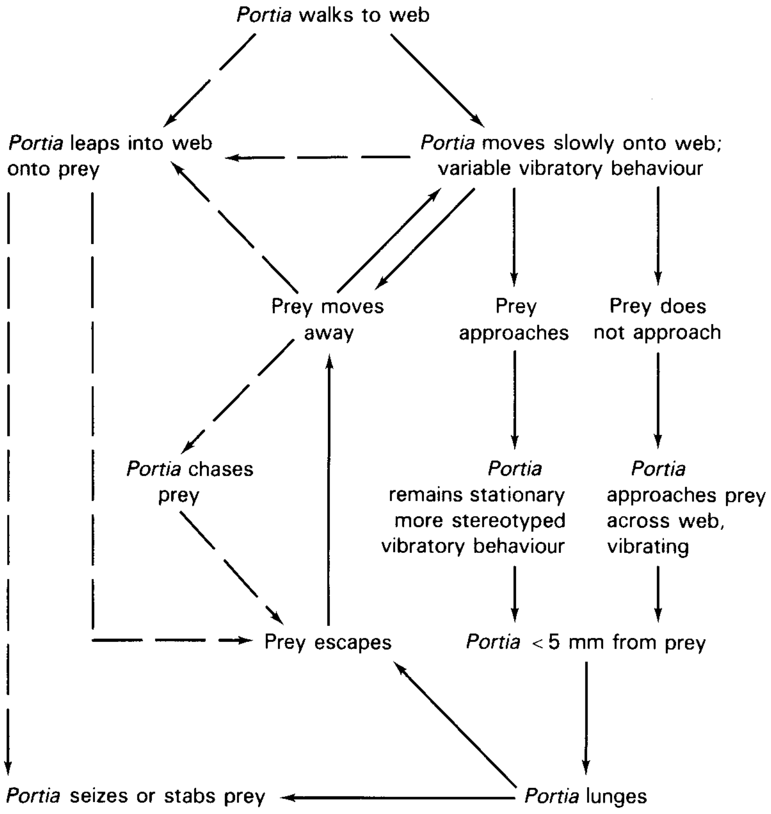


Fig. 20 General trends in predatory sequences. Prey is web spider on its web. Preceding and succeeding events indicated by arrows. Broken line: rare for *Portia fimbriata* (Q) but common for other *Portia*.

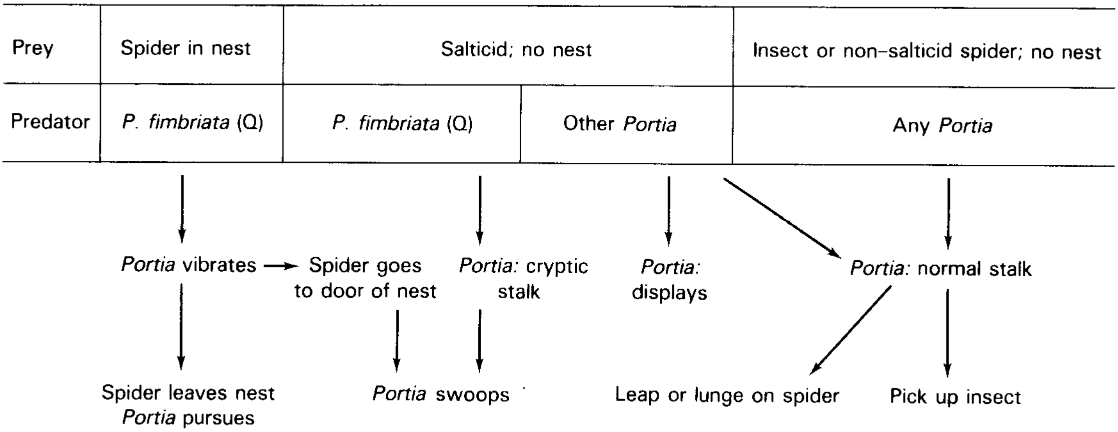


Fig. 21 General trends in predatory sequences in absence of webs.

Fig. 22 Female *Portia fimbriata* (Q) (left) standing on nest of Sp. 1 (Astianae), a cursorial salticid, and plucking with legs. Outline of the salticid is visible through the silk. Salticid facing to the left and slightly downward; *Portia* facing up and slightly to the right. Nest built on a leaf.

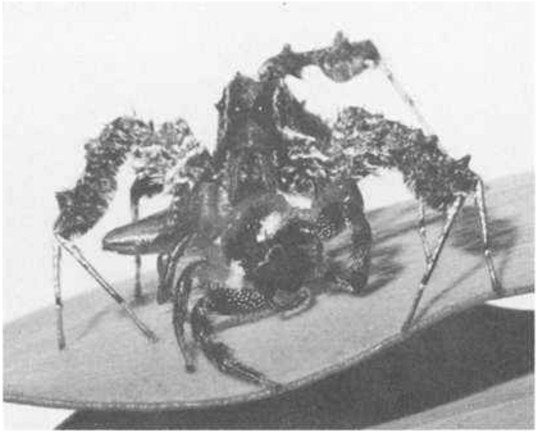


Fig. 23 Female *Portia fimbriata* from Queensland feeding on a cursorial salticid (male *Mopsus mormon*). *Portia* has grasped the salticid's carapace near the pedicel. The cephalothorax of the prey extends forward and slightly to the right and is slightly rotated anticlockwise. The prey's abdomen extends rearward and to the left. The two spiders are on a leaf; a second leaf is in view below.

chelicerae. The resident spider responded by becoming active (turning about, pulling on the silk, spinning, or biting at the silk), and sometimes it left the nest after a few seconds or minutes. More often, the resident spider remained in its nest and became inactive, with the *P. fimbriata* (Q) becoming inactive also. *P. fimbriata* (Q) then waited, on the nest, sometimes for many hours, until the prey-spider came out of the nest, seemingly spontaneously. Sometimes *P. fimbriata* (Q) swooped or lunged onto the prey-spider during its departure from the nest. Otherwise, *P. fimbriata* (Q) left the nest and stalked the spider.

Spiders sometimes responded to *P. fimbriata* (Q) on their nests by reaching out with their legs and cephalothoraxes and lunging or striking at *Portia*, then rapidly backing into the nest again. When the resident spider was a salticid, *P. fimbriata* (Q) sometimes responded by pulling its palps back into the lateral posture. Otherwise, *Portia* on a nest held its palps either in the normal or, less often, raised

Table 12 Occurrence of raised legs displays in Type B tests of *Portia* with salticids (no web present). Occurrence expressed as number of tests during which displays were performed by *Portia* divided by the total number of tests and multiplied by 100. Total number of tests given in parentheses. Data for *P. labiata* and *P. schultzi* pooled. *Portia* compared: tests of independence comparing data for *P. fimbriata* (Q) and pooled data for *P. labiata* and *P. schultzi*. Medium and large salticids compared: tests of independence, carried out separately on data for *P. fimbriata* (Q) and pooled data for all other *Portia*, comparing occurrence of display with different size salticids.

	P. fimbriata (Q)			*P. labiata* and *P. schultzi*			*Portia* compared (χ^2)	
	Male	Female	Comparison	Male	Female	Comparison	Male	Female
Displayed to medium salticid	25%(101)	6%(207)	22.994****	72%(165)	32%(222)	60.576****	55.112****	45.885****
Displayed to large salticid	63%(19)	14%(28)	9.962**	85%(34)	56%(50)	6.676**	2.263 NS	11.242***
Medium and large salticids compared (χ^2)	11.060***	2.801 NS		2.105 NS	10.601**			

NS: not significant; $*P < 0.05$; $**P < 0.01$; $***P < 0.001$; $****P < 0.0001$.

posture. Sometimes *P. fimbriata* (Q) swooped or lunged onto spiders that reached out of their nests to lunge or strike at the *Portia*.

At the end of swoops or lunges, the resident spider was either seized or stabbed. Stabbed spiders usually ran away from nests, but occasionally they backed into their nests and became immobilised inside. *P. fimbriata* (Q) never retrieved its victim from inside a nest. Usually, the stabbed spider recovered after a time and was seized later outside the nest.

Portia labiata and *P. schultzi* sometimes approached translucent occupied nests and stood on or beside the nest while facing the spider inside for variable periods of up to several hours. Occasionally, they leapt at spiders inside nests, but they did not vibrate on nests or capture the resident spiders.

Salticid outside nest. *P. fimbriata* (Q) responded to salticids outside nests with cryptic stalking, at the end of which they occasionally attacked by leaping or lunging (Fig. 21), but swooping was the prevalent mode of attack. *Portia* normally swooped while the salticid was facing away, and usually inserted its fangs near the pedicel of the salticid (Fig. 23). Other species of *Portia* responded to salticids outside nests with normal stalking and attacked by leaping or lunging.

Portia other than *P. fimbriata* (Q) did not consistently use cryptic stalking and swooping against salticids or any other prey, although isolated elements of cryptic stalking sometimes occurred briefly. For example, palps were sometimes held in the lateral posture briefly while stalking, or the *Portia* might halt temporarily when faced by a salticid at close quarters.

When they faced cursorial salticids, all species of *Portia* sometimes performed raised legs displays of the types that typically occurred during intraspecific interactions, usually alternating several times between displaying and stalking. Displays were most usual when *Portia* faced a salticid only a few centimetres away, although *Portia* sometimes displayed with the spiders as much as 300 mm apart. The size of the salticid and the species and sex of *Portia* influenced the frequencies with which raised legs displays occurred (Table 12). *Portia* of all species only rarely displayed to Size A salticids (pooled data: 1% of interactions). Female *P. fimbriata* (Q) displayed infrequently to Size B and C salticids, and frequencies of display to the two sizes of salticids were not significantly different. Compared to *P. fimbriata* (Q), females of *P. labiata* and *P. schultzi* more often displayed to both Size B and C salticids. Male *P. fimbriata* (Q) more frequently displayed to Size C than to Size B salticids. Compared to *P. fimbriata* (Q), males of *P. labiata* and *P. schultzi* more often displayed to Size B salticids, but the difference was not significant with Size C salticids. Unlike *P. fimbriata* (Q), males of *P. labiata* and *P. schultzi* failed to display significantly more often to Size C than to Size B salticids. Males displayed more frequently than females to both Size B and Size C salticids.

In summary, three groups of *Portia* were evident on the basis of the frequency of display to Size B and C salticids: female *P. fimbriata* (Q) displayed infrequently (6–14% of the tests); male *P. fimbriata* (Q) and female *P. labiata* and *P. schultzi* displayed more often (25–32% to Size B salticids and frequently (56–63%) to Size C salticids; and male *P. labiata* and *P. schultzi* frequently (72–85%) displayed to Size B and C salticids. Less information was obtained on other species of *Portia*, but all seemed to be more likely than *P. fimbriata* (Q) to display to salticids.

Responses of cursorial salticids to *Portia*. *P. fimbriata* (Q) did not elicit distinctive responses from the cursorial salticids it cryptically stalked. Generally, salticids gave no indication that they recognised the *P. fimbriata* (Q) as another salticid, a potential predator, or even another animal. Salticids facing away from *Portia* often failed to show any response to the slowly approaching *Portia*. Sometimes, apparently detecting slight movement from behind, the salticid pivoted around and faced the advancing *P. fimbriata* but then behaved in a manner strikingly inappropriate for its perilous circumstances. For instance, the salticid might wipe its eyes with its palps then turn and casually walk directly toward and even under or over *P. fimbriata* (Q). The salticid occasionally remained underneath the predator, grooming or calmly peering out, as if the patiently waiting predator were a harmless clump of detritus.

In contrast, salticids tended to respond to normally stalking *Portia* by repeatedly turning around and facing them and then displaying or running away. Cursorial salticids evidently recognised these *Portia* as other salticids and potential threats. Cursorial salticids also tended to respond distinctively to displaying *Portia*. If not already facing, they turned and faced *Portia*; next they watched, ran away, or reciprocated with their own displays (i.e., the displays typical for each species in intraspecific interactions).

Non-salticid spider outside nest. All species of *Portia* used normal stalking to pursue non-salticid cursorial spiders and attacked by lunging or leaping; *P. fimbriata* (Q) occasionally swooped. All species, however, sometimes briefly showed isolated elements of cryptic stalking. For example, when faced by a non-salticid cursorial spider, and especially if it was large, *P. fimbriata* (Q) sometimes retracted its palps and temporarily halted; but the palps were not held consistently in this posture, and *P. fimbriata* (Q) generally resumed stalking even if the spider remained facing. *Portia* only rarely displayed to non-salticid spiders.

Predation on insects

Away from webs, on alien webs, and on their own webs, all species of *Portia* responded to insects with normal stalking and usually attacked by lunging or picking up. *Portia*, especially *P. labiata* and *P. schultzi*, sometimes leapt on insects away from webs. *P. labiata* and *P. schultzi*, but not *P. fimbriata* (Q), sometimes leapt into webs onto insects. *Portia* only rarely (and briefly) vibrated when pursuing insects on webs.

Generally, *Portia* did not attempt to seize large, vigorously moving insects in webs, even if they were thoroughly stuck; but *Portia* did sometimes remain within a few centimetres of the prey for as long as 24 h, seizing the insect after its struggling had subsided (Fig. 24).

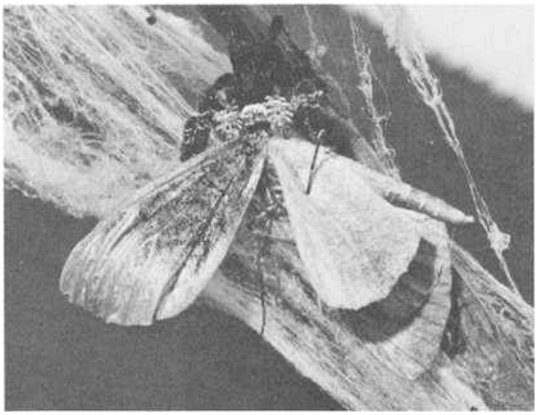


Fig. 24 Female *Portia schultzi* from Kenya feeding kleptoparasitically on moth in a highly adhesive communal web of a colony of cribellate social spiders (*Stegodyphus mimosarum*). *Portia* has grasped the moth by its head. Abdomen of the moth extends to right; wings extend downward.

Scavenging

Webs of species on which *Portia* preyed in nature often contained carcasses of insects and other arthropods that were uneaten or only partially eaten. This was true especially of webs of cribellate social spiders. In the laboratory, *P. fimbriata* (Q), *P. labiata* and *P. schultzi* sometimes oriented toward and walked directly to dead insects and spiders in webs, usually without vibrating, then lunged or, more often, picked up the carcass. Previously eaten carcasses were usually soon released, but dead and uneaten or only partially eaten arthropods were usually consumed, if they had not been dead for more than a few days and did not show obvious signs of decay.

Table 13 Occurrence of Type B tests in which web spiders killed or injured *Portia*. Data for male and female *Portia* and for medium and large prey pooled. *Portia* killed: number of tests during which the spider killed the *Portia* divided by the total number of tests and multiplied by 100. *Portia* killed or injured: as for previous category except includes test during which the *Portia* was bitten by the web spider and bled or lost one or more legs, but was not killed.

	Portia fimbriata (Q)	*Portia labiata*	*Portia schultzi*	Tests of independence (χ^2)
No. of pursuits	491	285	231	
Portia killed	0.6%	2.1%	1.7%	3.477 NS
Portia injured or killed	1.2%	6.0%	7.0%	18.087****

NS: not significant; **** $P < 0.0001$.

Oophagy

All species of *Portia* ate spider eggs, including eggs of conspecifics. Eggs were obtained by opening diverse types of egg sacs, ranging from the flimsy silk wrappings of *Pholcus* to the tough papery cases of *Philoponella* (Appendix 1). Although only *P. fimbriata* (Q) succeeded in capturing cursorial spiders in nests, all species of *Portia* extracted and ate eggs from vacated nests of cursorial spiders.

Egg cases which were not firmly attached to rigid substrata (e.g., the egg cases of pholcids and lycosids, which were carried about by the maternal spider, and the cases of uloborids and theridiids, which were suspended in webs) were picked up by *Portia* and eaten much as *Portia* ate spiders and insects. Holes were made by chewing and by expelling saliva, and then digestive fluids were injected, and finally the liquified contents of the case were extracted.

With attached egg cases, such as the eggs of cursorial spiders (enclosed in nests on the sides of rocks or the cage) or the eggs of *Portia* (fastened to leaves), *Portia* gripped the silk with its chelicerae, chewed intermittently, and eventually made a hole that exposed the eggs. Next the eggs were seized one at a time with the chelicerae and eaten. Eggs not in the immediate vicinity of the hole were raked out with legs I.

There were no evident interspecific differences in tendencies to eat eggs. About equal numbers of tests were carried out with eggs of web spiders and eggs

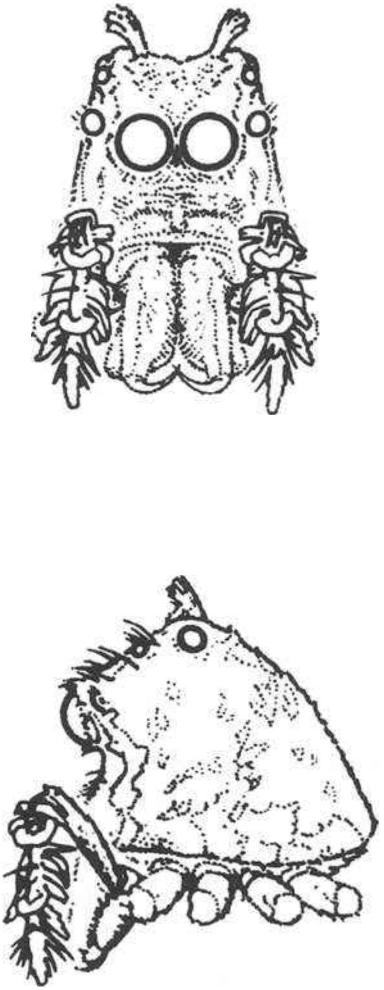


Fig. 25 Female *Portia*. Palps in normal posture. Front and side views.

of cursorial spiders, and there was no tendency for one type to be eaten more readily than the other. Pooling data for the different species of *Portia* and the different types of eggs, there were 78 tests with the maternal female attending her eggs and 84 with the eggs unattended. During the tests, attended eggs were more often (50% of tests) eaten than unattended eggs (29%) ($\chi^2=6.939$, $P<0.01$). Usually the attending spider was also eaten, either before or after its eggs had been consumed.

Observations of predatory behaviour in nature

Once, a female *P. labiata* (SL) was observed to enter an orb web of *Nephilengys malabarensis* (Araneidae), stalk slowly across the sticky spirals while vibrating, and lunge at and capture the host spider at the hub. In total, there have been 20 observations of *P. fimbriata* (Q) in nature vibrating while in alien webs: 17 were reported earlier (Jackson & Blest 1982a); subsequent observations were of a female in a web of a *Psilochorus sphaeroides* (Pholcidae) and two females in webs of *Badumna insignis* (Amaurobiidae). As in the laboratory, pursuit times in nature tended to be long (in the longest, a female *P. fimbriata* (Q) captured a theridiid after remaining in the alien web and vibrating for 3 successive days). On four occasions, *P. fimbriata* (Q) were observed to cryptically stalk salticids. One successful pursuit, observed from start to finish, lasted 90 min (Jackson & Blest 1982a).

Death and injuries of *Portia* during predatory sequences

In nature, *P. fimbriata* (Q) was sometimes killed or injured by its intended prey (Jackson & Blest 1982a). In the laboratory, *Portia* was never killed or injured by Size A web spiders or by insects and

Fig. 26 Male *Portia*. Palps in frontal posture. Front and side views.

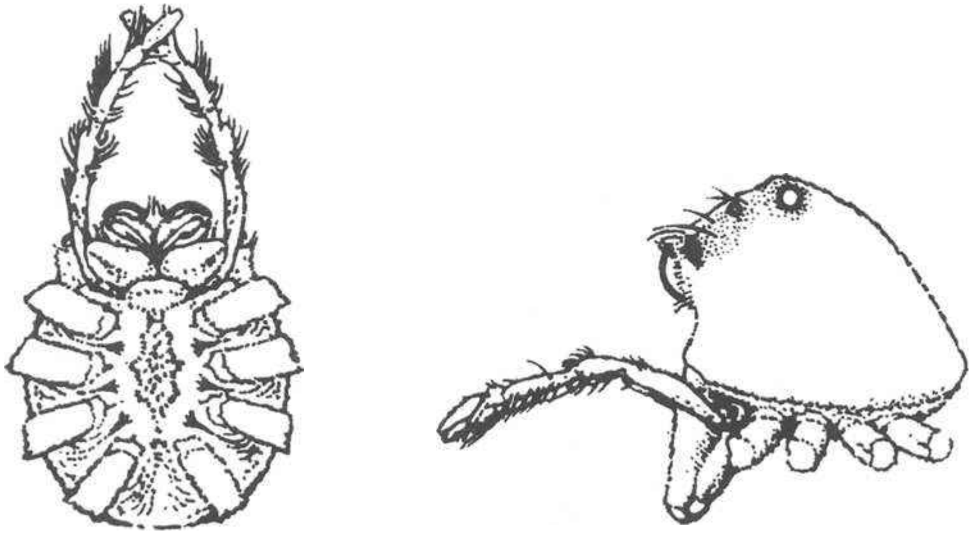


Fig. 27 Female *Portia.* Palps in forward posture. Ventral and side views.

cursorial spiders of any size. Size B and C web spiders, however, sometimes killed *P. fimbriata* (Q), *P. labiata* and *P. schultzi*, although this was rare (1.3% of 1007 tests) and frequencies of occurrence were not significantly greater for *P. labiata* and *P. schultzi* than *P. fimbriata* (Q). During some tests, *Portia* was attacked and injured, but not killed, by the web spider. As a result, the *Portia* bled and sometimes lost one or more legs. *P. labiata* and *P. schultzi* were attacked more often than was *P. fimbriata* (Q) and either killed or injured (Table 13).

Spiders are able to autotomise appendages as a defence mechanism (Bonnet 1930). *Portia*, however, seemed to differ markedly from other salticids and most other spiders that were kept in the laboratory in how readily appendages were autotomised. Furthermore, *Portia* observed in nature, but not other salticids in the same habitats, were often missing legs and palps. The legs and palps of *Portia* were autotomised very readily when seized by another spider during predatory interactions, or when accidentally pressed against, during normal laboratory handling.

The integument of *Portia* seemed to be exceptionally tough. Sometimes, *Portia* were attacked by web spiders but escaped with no evident injury, and in some instances this happened despite the web spider's chelicerae having closed around the body of the *Portia.*

Elements of behaviour in intraspecific interactions

The repertoire of behaviours used in intraspecific interactions of *Portia* was large and complex. Before defining terms and describing behaviours, key terms will be listed alphabetically with index numbers: charge (23); copulation (32); decamp (1); drum with palps (29); elevated legs (6); embrace (18); erect legs (6); follow (3); forward appendages (28); forward legs (27); forward lunge (36); frantic decamp (2); grapple (19); hunched legs (13); hunched posturing (15); hunched waving (14); jerky walking (5); jerky leg waving (10); leg posturing (8); leg shaking (11); leg twitching (7); leg waving (9); long leap (26); mount (32); palp postures (4); palpal pushing (20); postcontact behaviour (34); postmount behaviour (32); premount tapping (12); propulsive displays (21); raised legs (16); ram (24); retract appendages (31); semi-erect leg (6); spin on female (33); strike (22); sway (17); truncated leap (25); tug with legs (30); twist lunge (35); watch (3).

1 Decamp To decamp, one *Portia* walked, ran, or leapt away from the other.

2 Frantic decamp Males decamped frantically from females by very rapidly running or leaping 100–300 mm away, but *Portia* leaping during frantic decamping was not propelled so distinctly upward as during wild leaping (see above).

3 Watch and follow A *Portia* watched another *Portia* by actively orienting so that its anterior median eyes continued to face the other *Portia.* A *Portia* followed another decamping *Portia* by walking or, less often, running or leaping toward the other *Portia.*

4 Palp postures Ten modal palp postures were observed.

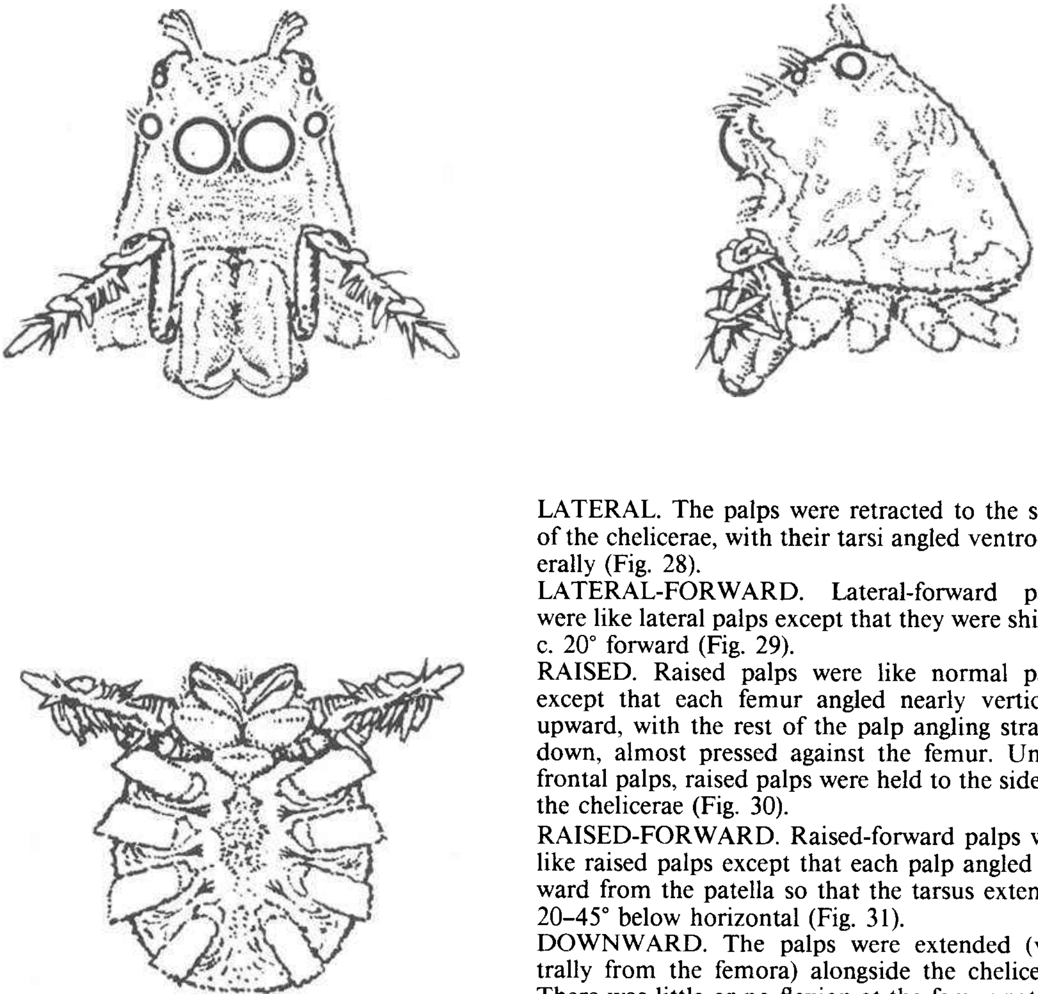


Fig. 28 Female *Portia*. Palps in lateral posture. Front, side, and ventral views.

NORMAL. The palps were held anterior and slightly lateral to the chelicerae, with the femora angled up and the rest of the palp down (Fig. 25).

FRONTAL. The palps were held anterior to the chelicerae, with the patellae just ventral to the anterior median eyes and the tibiae and tarsi positioned such that the chelicerae were nearly completely obscured from view in front (Fig. 26).

FORWARD. The spider's two palps were extended forward about parallel to the substratum, with c. 20° flexion at the femur-patella joints (femur angled up c. 20°; rest of palp, down c. 20°). Sometimes the two palps were held about parallel to each other or slightly converging (Fig. 27), but they more often converged distinctively such that their tarsi touched at their tips or crossed over by 1–2 mm.

LATERAL. The palps were retracted to the sides of the chelicerae, with their tarsi angled ventro-laterally (Fig. 28).

LATERAL-FORWARD. Lateral-forward palps were like lateral palps except that they were shifted c. 20° forward (Fig. 29).

RAISED. Raised palps were like normal palps except that each femur angled nearly vertically upward, with the rest of the palp angling straight down, almost pressed against the femur. Unlike frontal palps, raised palps were held to the sides of the chelicerae (Fig. 30).

RAISED-FORWARD. Raised-forward palps were like raised palps except that each palp angled forward from the patella so that the tarsus extended 20–45° below horizontal (Fig. 31).

DOWNWARD. The palps were extended (ventrally from the femora) alongside the chelicerae. There was little or no flexion at the femur-patella, and the tarsi angled nearly perpendicularly downward (Fig. 32).

DOWN-FORWARD. Down-forward palps were similar to forward palps except that the femora angled from straight forward to 20° downward, instead of 20° upward (Fig. 33).

ARCHED. The palp femora extended ventro-laterally alongside the chelicerae. The rest of each palp angled ventro-medially so that the tips of the two tarsi were 1–2 mm apart, under the fangs (Fig. 34).

5 Jerky walking Jerky walking was a characteristic gait used by males while they were on webs of females. By making sudden, short steps, and by holding onto the silk during part of the motion, the web was caused to shake conspicuously. The springy nature of these movements was distinctly different from leg plucking. Jerky walking occurred either with or without the male's legs being raised.

6 Elevated legs Erect and semi-erect legs are referred to jointly as 'elevated legs'. Erect legs

Fig. 29 Female *Portia*. Palps in lateral-forward posture. Front, side, and ventral views.

appeared stiff because the joints were more fully extended than in semi-erect legs.

Legs I alone or, more often, legs I and II were elevated. Elevated legs on the same side were about parallel to each other, legs II often being slightly below and to the sides of legs I. When stepping, however, it was not unusual for some of the legs to be lowered to the substratum. For example, right leg I and II sometimes remained elevated while left leg II (or I and II) touched the substratum. It was unusual, however, for leg II but not leg I on the same side to be elevated. Sometimes legs II on one or both sides were semi-erect while legs I were erect, but never the reverse (legs II erect and legs I semi-erect). The tarsi of elevated legs were always off the substratum, and there were three modal positions.

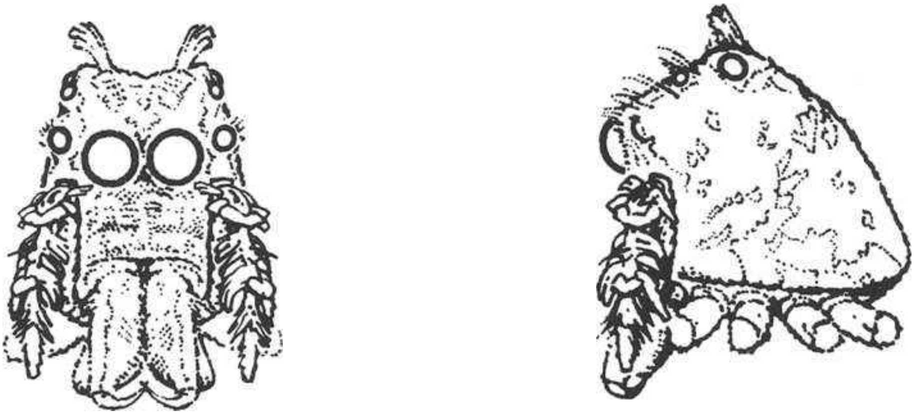


Fig. 30 Female *Portia*. Palps in raised posture. Front and side views.

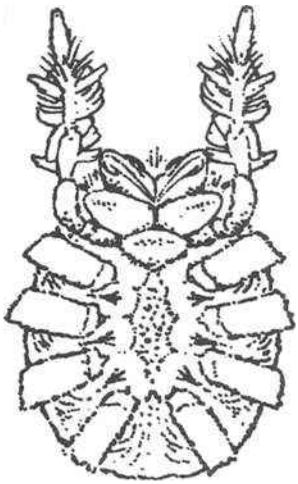
Fig. 31 Female *Portia.* Palps in raised-forward posture. Front, side, and ventral view.

POSITION 1. The femur-patella was fully or almost fully extended. The legs extended about parallel to the substratum, pointing straight forward or converging so that the tarsi almost or actually touched or crossed over by a few millimetres. In Position 1, legs were almost always erect (Fig. 35).
POSITION 2. Legs extended 10–20° to the side with femora angled up. Because of the flexion of the femur-patella, the remainder of the leg extended about parallel to the substratum.
POSITION 3. Legs angled 45–90° out to the side and usually c. 45° upward. The femur-patella was fully, or almost fully, extended.

7 Leg twitching Erect legs I and II in Position 1 twitched by moving, in matching phase, up and down c.1 mm. There were usually about five cycles in a bout lasting c.1 s. Males twitched their legs intermittently during bouts of posturing, usually at 20–50 mm from the female. While leg twitching, the male either remained standing or he stepped toward the female. Sometimes the legs twitched while the male was jerky walking (see above), and occasionally leg twitching was superimposed on leg waving. Only males of *P. schultzi* were observed to perform leg twitching.

8 Leg posturing The spider postured by holding its stationary erect or semi-erect legs in Position 1, 2, or 3 while standing or stepping.

9 Leg waving While standing or stepping (backward or, more often, forward) males waved by moving erect or semi-erect legs (Position 2) up and down 1–3 mm in alternating phase at c. 1 Hz.



10 Jerky leg waving Jerky leg waving was like ordinary waving, with legs semi-erect, except that movement was a sudden, rapid up-then-down motion, similar to movement of legs stepping during jerky walking. There was only one wave at a time, with legs remaining semi-erect during the pause of several seconds between successive waves. The web often vibrated conspicuously as the spider jerky waved.

11 Leg shaking Males shook erect legs I and II (Position 1 or 2) by moving them rapidly down and in, then up and out by 10–45°. Most bouts lasted only 1–2 s. In contrast to waving, shaking appeared forceful. There were two modal forms: Type 1 (Fig. 35) was very rapid (one cycle c. 0.04 s) and of small amplitude (c. 1 mm); Type 2 was less rapid (0.1–0.2 s) and of larger amplitude (c. 3 mm).

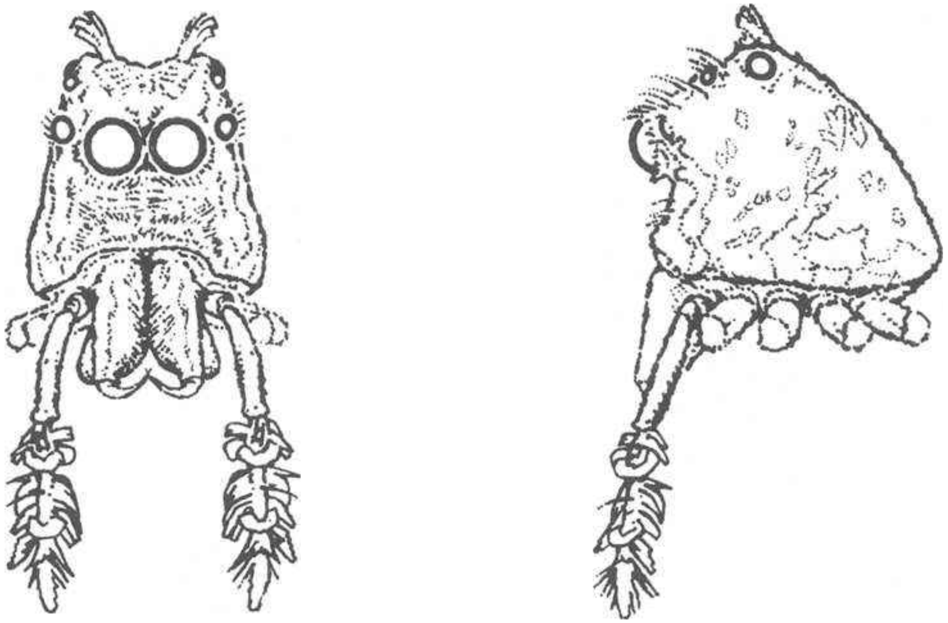


Fig. 32 Female *Portia*. Palps in downward posture. Front and side views.

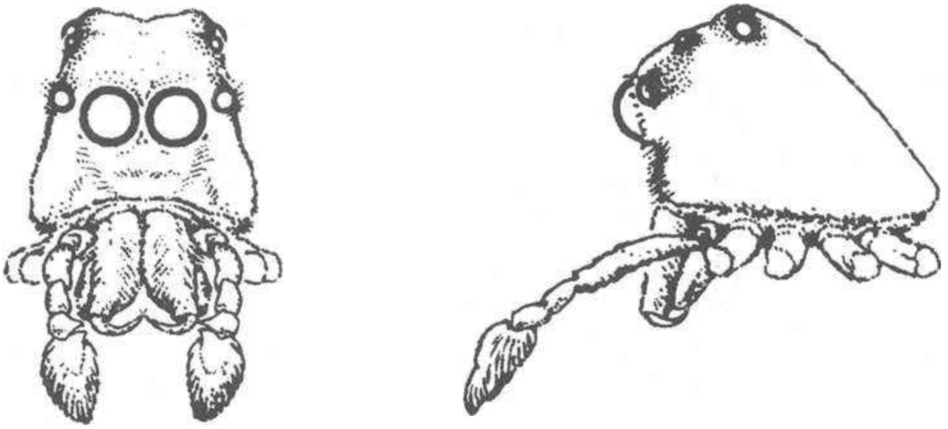


Fig. 33 Male *Portia albimana*. Palps in down-forward posture. Front and side views.

12 Premount tapping With legs I and II over the female, males premount tapped by repeatedly flexing tibia-metatarsus joints, bringing their tarsi into contact with the female's body or legs.

13 Hunched legs Hunched legs were highly flexed at the femur-patella and tibia-metatarsus joints (Fig. 36, 37). Legs I–III were hunched, legs III remaining on the substratum. Tarsi of legs I and usually one or both legs II were held off the substratum. There were two modal positions of hunched legs.

POSITION 1. Legs I and II were held c.45° from forward. Legs III were 45–90° from forward.

POSITION 2. Legs I–III were held c.90° to the side.

14 Hunched waving During hunched waving, hunched legs I and II slowly (1 cycle 0.5–1 s) moved in phase up-and-down (movement primarily fem-

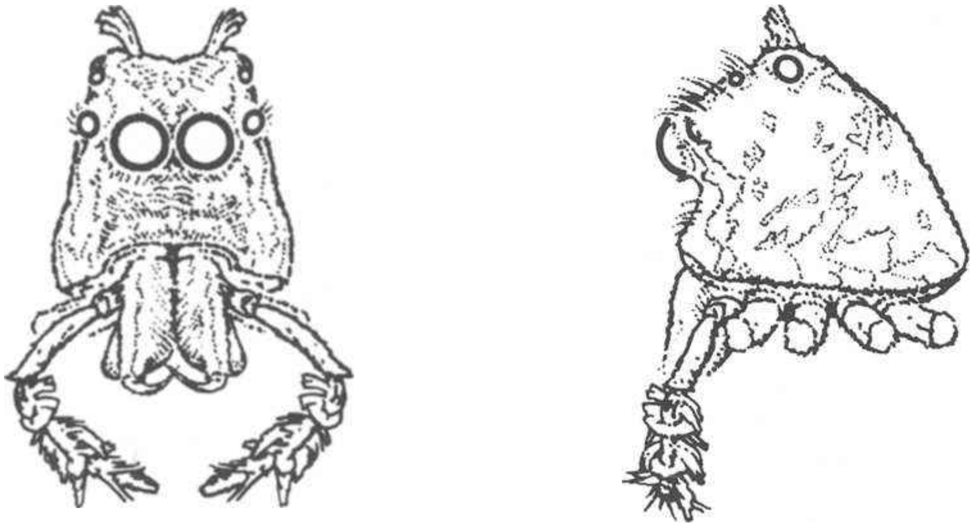


Fig. 34 Female *Portia*. Palps in arched posture. Front and side views.

oral). Most bouts lasted 2–10 s. The spider was either standing or slowly stepping as it hunched waved.

15 Hunched posturing During hunched posturing, the hunched legs were held stationary while the spider was either standing or slowly stepping.

16 Raised legs Elevated and hunched legs are referred to jointly as 'raised legs'.

17 Sway Spiders swayed, while posturing with raised legs (hunched Position 1 or 2 or erect Position 2 or 3), by leaning slowly from side to side. Sometimes the swaying spider slowly extended leg I (less often, I and II) on the side toward which it leaned, moving it from hunched to erect, then brought the leg(s) back to the hunched position as it leaned the other way.

18 Embrace To embrace, spiders approached each other slowly with raised legs. Legs were usually erect (Position 1, 2 or 3) just before contact. If legs were in erect Position 1 when contact was made, the spider continued to advance and moved legs back to elevated Position 2. From embraces with legs in elevated Position 2, spiders often advanced and moved legs back to elevated Position 3. In embraces with legs in Position 3, the chelicerae of the two spiders usually touched, and the fangs were sometimes extended. Erect legs in Position 3 were sometimes moved during an embrace to nearly straight up. Often during the embrace, the spiders' cephalothoraxes were elevated, with abdomens tilting down, and the palps were held in the lateral or, more often, raised posture, unless palpal pushing occurred.

19 Grapple Embracing spiders grappled by moving their legs forward over each other and forcefully flexing them. As a result, one spider sometimes pulled off one or more legs of the other spider.

20 Palpal pushing During embracing, with legs in contact but faces apart, palpal pushing occurred with palps in the lateral-forward or raised-forward posture. Each palp tarsus touched the opposite palp tarsus of the facing spider, then each spider moved, or attempted to move, its palps forward. Sometimes, one spider managed to push one or both palps of its rival back to beside or behind the chelicerae, soon after which the spiders either brought their chelicerae together or stepped apart. Sometimes, too, the palps of the two spiders were simultaneously pushed back to beside the chelicerae as the spiders brought their chelicerae together.

21 Propulsive displays Striking, charging, ramming, truncated leaps, and long leaps, each of which involved sudden rapid forward locomotion of the spider, are termed 'propulsive displays'. Propulsive displays occurred intermittently and, seemingly, unpredictably, except that truncated leaps and strikes were more common when spiders were less than 50 mm apart and the other propulsive displays were more common when the spiders were more than 50 mm apart. Although *Portia* some-

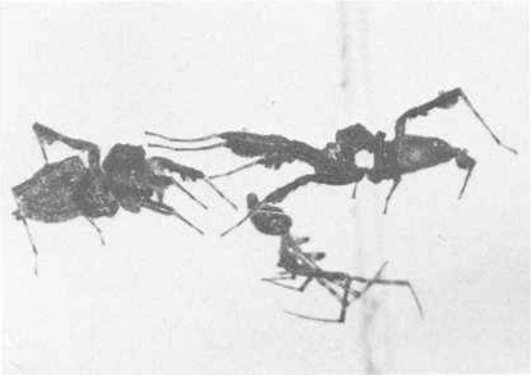


Fig. 35 Male (right) *Portia labiata*, with legs erect (Position 1) and over the female (left), performing Type 1 leg shaking. The two *Portia* are facing each other, dorsal sides up, on a web of a *Badumna longinquus*. Host spider is dead, just below and in front of male in photograph, having been eaten earlier by the female *Portia*. Vertical stick out of focus in background on right.

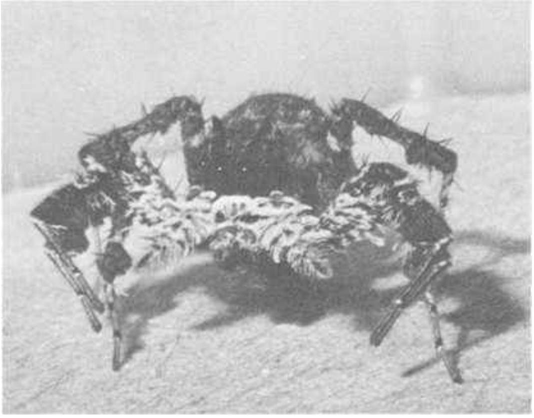


Fig. 36 *Portia schultzi* performing hunched legs displays (Position 2) in female-female interaction. Palps in lateral posture.

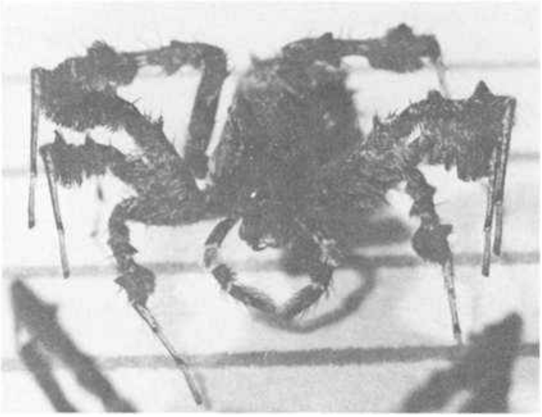


Fig. 37 *Portia fimbriata* (Q) performing hunched legs displays (Position 2) in female-female interaction. Palps in arched posture. Hunched legs I of other female (out of focus) partially in view at bottom of photograph. Spiders standing on lined paper.

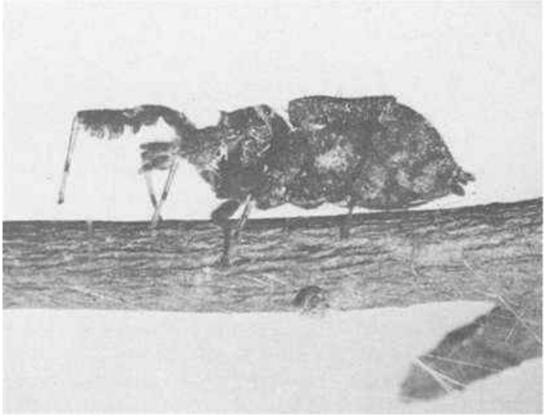


Fig. 38 Female *Portia labiata* on stick at edge of her web, facing left, drumming with palps and tugging with legs. Palps are moving up and down; right palp higher than left palp. Legs I move forward and backward, in alternating phase; female's right leg in front of palps and moving forward, left leg just behind palps and moving rearward. Male out of photograph to left.

times had its legs hunched or erect (Position 3) immediately before performing propulsive displays (especially before striking), propulsive displays were more often preceded by simply watching or standing inactive, with palps normal or lateral. Palps were usually in either the normal or raised posture during propulsive displays.

22 Strike with legs Females struck by slowly raising legs I then rapidly moving them down against the substratum or the other spider, usually stepping rapidly 2–4 mm forward in the process. The tarsi came down c. 2 mm apart, with the legs almost fully extended. *Portia* usually stepped back to its original position, or beyond, immediately after completion of a strike.

23 Charge In charging, spiders suddenly and rapidly ran 20–60 mm then suddenly stopped 10–40 mm in front of the other spider.

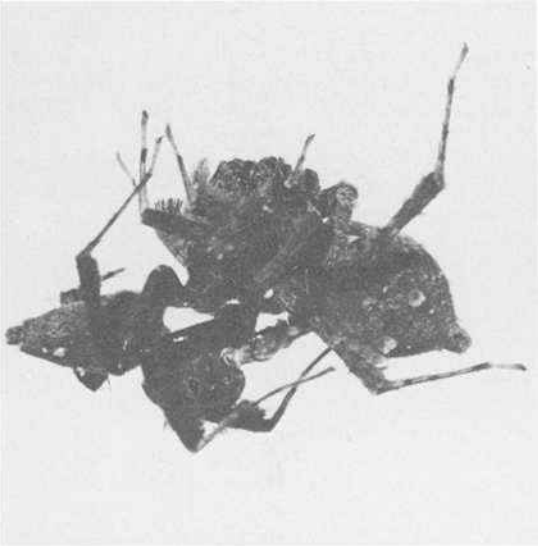


Fig. 39 Male *Portia labiata* (lower) mounting female (upper) and beginning postmount courtship. Female's appendages retracted (except for legs IV). Male and female suspended, ventral sides up, in web.

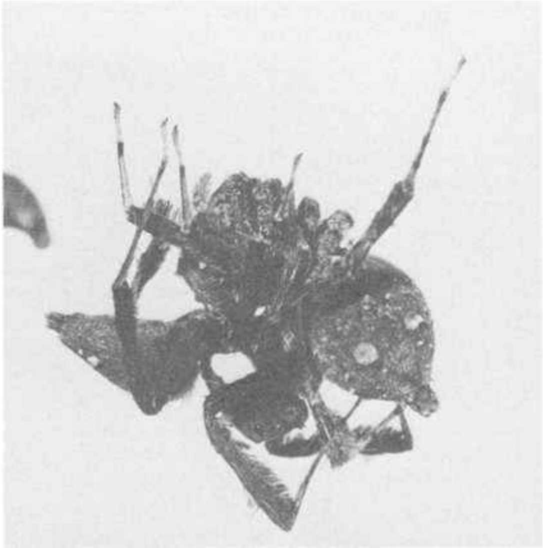


Fig. 40 Male-female pair copulating suspended in webs. Female's abdomen rotated so that dorsal side is in view, male has engaged his left palp. Male facing right, female left.

24 Ram Ramming resembled charging except that the spider failed to stop before forcefully contacting the face of its rival.

25 Truncated leap One spider made a truncated leap by suddenly leaping c. 10 mm forward, barely above the substratum and making no contact with the other spider.

26 Long leap *Portia* made long leaps by suddenly propelling itself forward 30–80 mm and either contacting the other *Portia* or, more often, landing within a few centimetres or millimetres of the other *Portia.* When contact occurred, it was usually face-on.

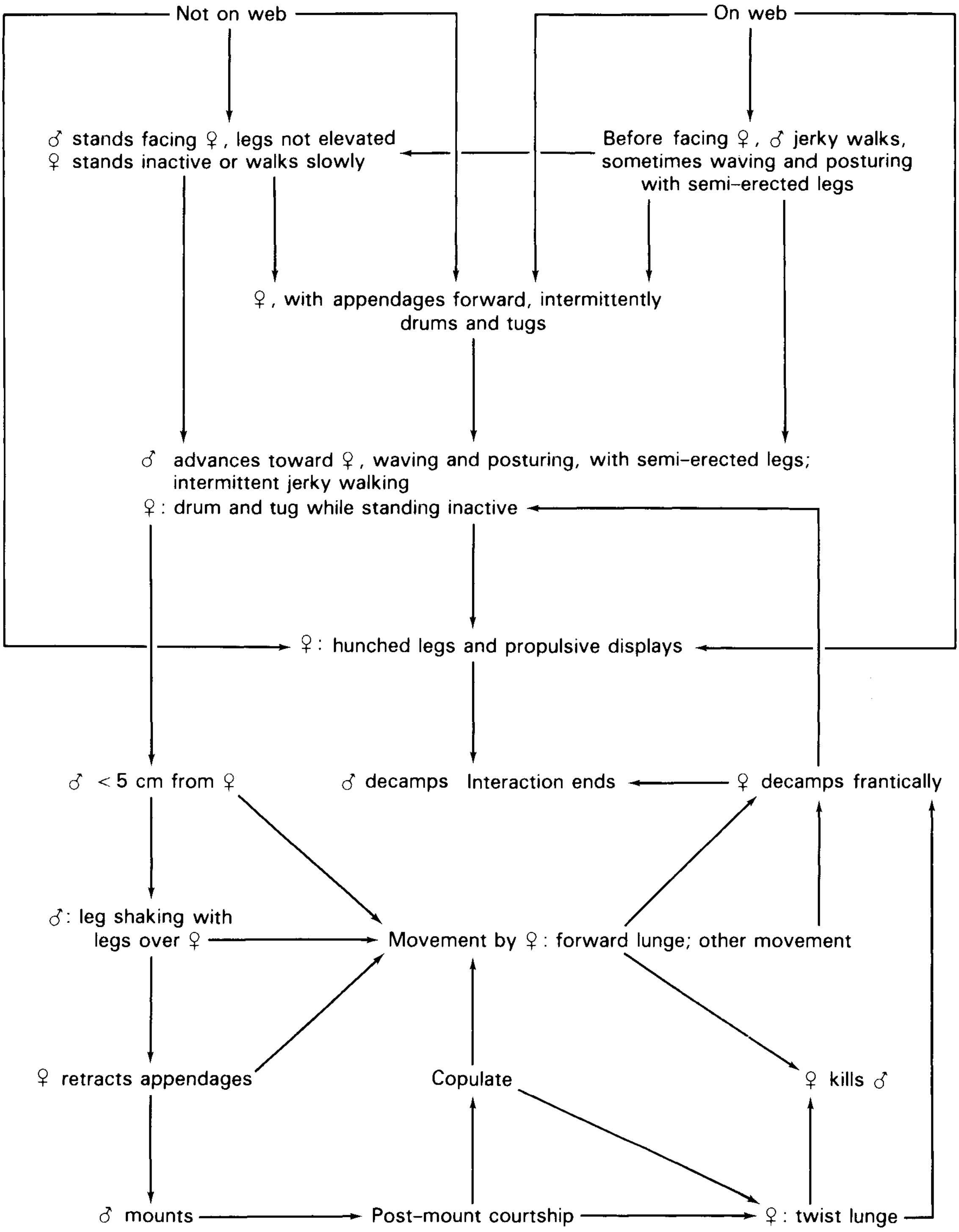
27 Forward legs Forward legs (Fig. 38) were held in a posture similar to forward palps. Legs I alone or, more often, legs I and II extended forward, with tarsi on the substratum. Legs I and II on each side were about parallel. Right and left legs were either about parallel or converging, tarsi sometimes to within 1 mm of each other. Converging legs occasionally touched or even crossed over. The elevation of the femora and flexion of joints varied greatly, from maximally extended (femora barely raised; femur-patella and tibia-metatarsus joints flexed only c. 10°), to maximally retracted (femora almost straight up; c. 90° flexion of femur-patella joints and metatarsus flexed rearward from the tibia; tarsi on substratum only c. 2 mm from chelicerae).

28 Forward appendages Forward legs and forward palps are referred to jointly as forward appendages. Although forward legs was almost never assumed without palps forward (Fig. 38), sometimes palps were held forward while legs were in other postures, including (rarely) hunched.

29 Drum With palps forward, females intermittently drummed with forward-backward rotary movements (Fig. 38). Circles of c. 2 mm diameter were made at 1–4 Hz. Females generally drummed faster when the male was closer. Although a female sometimes drummed a single palp alone, usually both palps were moved in roughly alternate phase. Bout lengths were sometimes as great as 3 min, but c. 5 s was more typical. The initial movement in a bout of drumming was always upward.

Palp drumming appeared to be a smooth, rhythmical stepping-in-place. Drumming palps usually converged, and they often struck each other. If on a web while drumming, the female usually brought her palpal tarsi into contact with the silk; if so, the web was often observed to vibrate.

30 Tug To tug, one or, more often, both legs I flexed at the femur-patella and tibia-metatarsus joints and moved backward (retraction of femora). As a result, the tarsi moved 2–5 mm toward the spider's face; while on webs, tarsi of tugging legs moved the silk conspicuously. Usually legs returned immediately to their original position. Sometimes


Not on web
On web
♂ stands facing ♀, legs not elevated
♀ stands inactive or walks slowly
Before facing ♀, ♂ jerky walks, sometimes waving and posturing with semi-erected legs
♀, with appendages forward, intermittently drums and tugs
♂ advances toward ♀, waving and posturing, with semi-erected legs; intermittent jerky walking
♀: drum and tug while standing inactive
♀: hunched legs and propulsive displays
♂ < 5 cm from ♀
♂ decamps
Interaction ends
♀ decamps frantically
♂: leg shaking with legs over ♀
Movement by ♀: forward lunge; other movement
♀ retracts appendages
Copulate
♀ kills ♂
♂ mounts
Post-mount courtship
♀: twist lunge

the tarsi were lifted slightly during the return movement, but the tarsi remained on the substratum throughout the cycle. Phasing of right and left legs was usually approximately alternate (Fig. 38). When forward legs crossed over, they often stuck each other during tugging.

Drumming accompanied almost every bout of tugging and often occurred alone. The bout of tugging (at 1–2 Hz) usually began before and ended after the simultaneous bout of drumming (at 2–4 Hz). Usually, there were only two or three tugs in a bout. Tugging, like drumming, was smooth and rhythmical; but, because of the minor dorsal component, it was less like stepping in place.

31 Retract appendages The female's apendages were retracted during copulation, with her palps pulled back into the lateral or raised postures and legs drawn in close to the body (Fig. 39, 40). The retraction was either rapid (1–2 s) or slow and intermittent (over many minutes). The female often slid 20–30 mm down on a dragline as she retracted her appendages, and copulation occurred with the pair suspended. If she failed to slide down on a line, the female's ventral cephalothorax lay on the substratum.

32 Mount, postmount behaviour, and copulation Males mounted by walking onto females, usually with the two spiders face-to-face. Males sometimes mounted females that were facing as much as 180° away, then quickly turned to face in the opposite direction.

Once the male had positioned his anterior cephalothorax about over the female's pedicel, with his legs I and II strongly flexed at the femur-patella joints, he began tapping and scraping on the female's legs and dorsal abdomen with his palps and legs. Eventually, the male leaned to one side, moved his leg I across from the opposite side, and began stroking with his leg on the female's abdomen (Fig. 39). When the female's abdomen rotated 45–90° to the side, the male moved his nearer palp back and forth on the female's ventral abdomen for up to 1 min before the palpal organ was engaged and copulation began (Fig. 40). During copulation the female's abdomen usually flexed upward from the cephalothorax as much as 45°. Tapping, scraping, and stroking by the male were referred to as 'postmount courtship'.

33 Spin on female While mounted, the male pivoted and stepped about, periodically touching the female's body and especially her legs and the neighbouring web or substratum with his spinnerets as he fastened threads. Spinning sometimes continued for up to 5 min; a sparsely woven 'basket' could sometimes be seen beneath the female. While the male spun, the female remained inactive on a web, on a non-web substratum, or suspended by a line. Occasionally, the female dropped on a line (or farther down on a line) and rested in the 'basket' spun by the male.

34 Postcontact behaviour In addition to postmount courtship, postcontact courtship included leg shaking in *P. albimana, P. labiata,* and *P. schultzi* and premount tapping in *P. fimbriata* (Q). Embracing, grappling, and palpal pushing were postcontact displays in intrasexual interactions.

35 Twist lunge This usually happened when the female's abdomen was rotated and the male either had his palp engaged or was scraping with his palp. The female then suddenly twist lunged by rotating her cephalothorax toward the male (i.e., moving her cephalothorax into alignment with her abdomen), simultaneously making scooping motions with her legs, and moving her extended fangs toward the male. Twist lunges were completed in c. 0.1 s and looked very violent. The female sometimes grasped the male with her scooping legs and inserted her fangs, then killed and ate the male.

36 Forward lunge To lunge forward, the spider suddenly and rapidly leaned forward, with all or most legs remaining on the substratum; the fangs were sometimes extended. The lunging spider was either on a web or, more often, a rigid substratum. Spiders typically lunged when they were 10 mm or less apart. Sometimes females lunged forward instead of stepping, when they struck. Sudden and forceful lunges forward, while embracing, occasionally knocked rivals over backward. Occasionally, females made forward lunges while males performed leg shaking displays or premount tapping (even when their legs were over the female), while males were mounted, and sometimes while mating.

Male-female interactions of *P. fimbriata* (Q), *P. labiata*, and *P. schultzi*

As male-female interactions of *P. labiata* and *P. schultzi* were similar, they are summarised in a single diagram (Fig. 41). Interactions of *P. fimbriata* (Q) (Fig. 42) differed considerably from those of the other two species. The major behaviours of each species are given in Table 14, and major differences between species are summarised in Tables 15 and 16.

Fig. 41 (*opposite*). General trends in behavioural sequences during intraspecific male-female interactions of *Portia labiata* and *P. schultzi.*

Table 14 Major elements of intraspecific behaviour, the types of interactions in which they occur, and the species that perform them. Male-female: male behaviour. Female-male: female behaviour. The species that routinely perform the indicated behaviours in the indicated interactions are listed. Pf: *P. fimbriata* (Q); Pl: *P. labiata* (SL); Ps: *P. schultzi*. See text for comments on other species. None: performed by none of the species. All: performed by all of the species.

Behaviour		Male-Female	Female-Male	Male-Male	Female-Female
Charge		None	All	None	All
Embrace		None	None	All	All
Drum and tug		None	Pl, Ps	None	None
Erect legs:	Position 1	All	None	Pl, Ps	None
	Position 2	All	None	Pl, Ps	Pl, Ps
	Position 3	None	None	All	All
Frantic decamping		Pl, Ps	None	None	None
Strike		None	All	None	All
Hunched legs:	Position 1	None	Pl, Ps	Pl, Ps	Pl, Ps
	Position 2	None	All	All	All
Jerky walking		All	None	None	None
Leg posturing		Pl, Ps	None	Pl, Ps	All
Leg shaking		All	None	Ps	None
Leg waving		All	None	None	None
Long leap		None	All	Pl, Ps	All
Palp postures adopted while displaying with raised legs (not embracing):	Arched	Ps	All	All	All
	Downward	Pl, Ps	All	All	All
	Frontal	All	None	Pl, Ps	None
	Lateral	None	Pl, Ps	Pl, Ps	Pl, Ps
	Lateral-forward	Pl, Ps	None	Pl, Ps	Pl, Ps
	Normal	None	All	None	None
	Raised	Pl, Ps	All	All	All
	Raised-forward	Pl, Ps	None	Pl, Ps	Pl, Ps
Premount tapping		Pf	None	None	None
Ram		None	All	None	All
Retract appendages		None	All	None	None
Semi-erect legs:	Position 2	Pl, Ps	None	Pl, Ps	Pl, Ps
	Position 3	None	None	All	All
Sway		None	All	All	All
Truncated leap		None	All	Pl, Ps	All
Twitch abdomen:	not mounted	All	None	None	None
	postmount behaviour	Pl, Ps	None	None	None
Twitch legs		Ps	None	None	None
Twist and forward lunge, not embracing		None	Pl, Ps	None	None
Forward lunge while embracing		None	None	None	Pl, Ps
Twitch legs		Ps	None	None	None

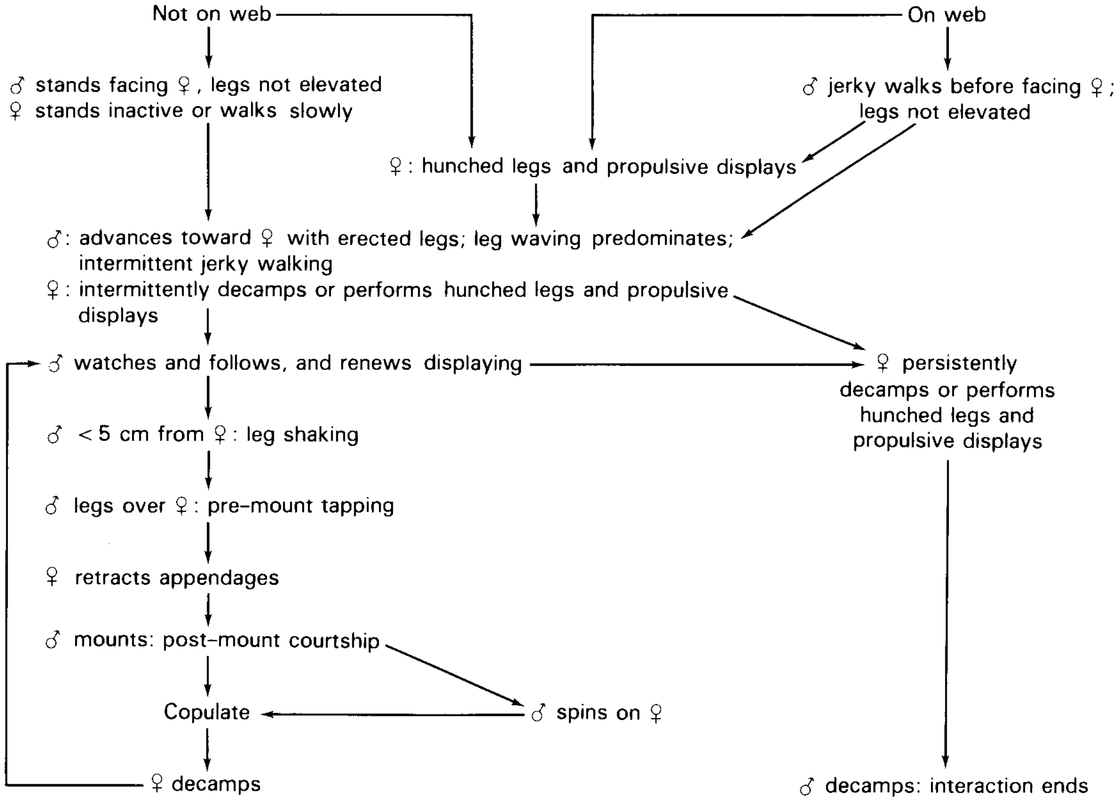


Fig. 42 General trends in behavioural sequences during intraspecific male-female interactions of *P. fimbriata* (Q).

In many interactions of all three species, the male stood watching the female at a distance of 100–300 mm for 2–15 min before displaying. On webs, jerky walking often preceded or followed watching. Sometimes several episodes of watching and jerky walking, not necessarily oriented toward the female, alternated before the male displayed with elevated legs for the first time. Initial displays with elevated legs generally occurred with the spiders 100–300 mm apart, with *P. labiata* and *P. schultzi* not always directly facing the female. Sometimes, the male (all three species) initially displayed with elevated legs while facing a female that was facing as much as 180° away from him.

Often a female displayed (drum and tug,*P. labiata* and *P. schultzi*; hunched legs and propulsive displays, *P. fimbriata* (Q)) before the male gave the initial elevated legs display, but elevated legs displays by males usually soon followed. Females of *P. labiata* and *P. schultzi* on webs sometimes began drumming and tugging before facing the males that were jerky walking.

Both on and off webs, female *P. labiata* and *P. schultzi* that subsequently mated usually stood displaying with forward appendages during most or all of the male's approach. Intermittent drumming and tugging were routine on webs, but were less common off webs. Females of these species often faced away from the male during some or all of the male's approach, but female *P. fimbriata* were more likely to decamp and to perform hunched legs and propulsive displays, eventually becoming more or less inactive during the male's final approach.

Female *P. labiata* and *P. schultzi* that performed hunched legs and propulsive displays rarely mated subsequently (this included females that had and females that had not mated earlier in the interaction). The male usually stopped watching, following, and displaying toward a female, and the interaction ended within 5 min of her beginning hunched legs and propulsive displays.

Males of all three species rarely moved close to females that were performing hunched legs and propulsive displays; however, females, with legs hunched, sometimes slowly approached males. The male usually decamped before the female got closer than 50 mm; occasionally, however, the male briefly stood his ground, posturing with elevated (Position 2 or 3) or, rarely, hunched legs.

Females sometimes switched their legs briefly from hunched to elevated (Position 2 or 3) when they got close to males. Elevated legs by females and hunched or Position 3 elevated legs by males were, however, not routine in male-female interactions.

During the first 5 min after the male began displaying with elevated legs, he sometimes intermittently walked jerkily as he approached the female, with or without his legs elevated; sometimes he walked jerkily as he leg waved. Jerky walking was rare later in the interaction. In all three species, males usually performed leg waving displays when distant from the female and leg shaking displays when close. Only *P. fimbriata* (Q) and *P. schultzi* performed premount tapping and leg twitching, respectively.

Male *P. fimbriata* (Q) displayed with frontal palps and erect legs during most of the approach to the female. Early in the interaction, Position 2 was most common while the male was distant ($>$ 100 mm) from the female; Position 1, when closer. Later in the interaction, Position 1 was common at all distances. Posturing was infrequent.

Semi-erect legs and posturing were common in interactions of *P. labiata* and *P. schultzi* but not *P. fimbriata* (Q). *P. labiata* and *P. schultzi* started displaying with erect legs when the spiders were close. Later in the interaction, legs tended to be erect at greater distances, although semi-erect legs continued to be prevalent. With both erect and semi-erect legs, Position 2 was more usual when the spiders were more distant and Position 1 when they were closer, especially early in interactions. Switching from semi-erect to erect, vice versa, and from one position to the other, became more common later in interactions.

Male *P. labiata* and *P. schultzi*, in contrast to *P. fimbriata* (Q), adopted varied palp postures while displaying with elevated legs. Frontal was the most common, but downward, raised, lateral-forward, and raised-forward were also frequent, especially when the spiders were close (or when they were some distance apart following a lunge or a propulsive display of the female).

Females of all three species usually held their palps arched or downward while their legs were hunched. With legs hunched, female *P. labiata* and *P. schultzi* sometimes held palps in the normal or lateral posture. Female *P. schultzi* occasionally stood with hunched legs and forward palps while intermittently drumming. Normally, after a few seconds, the female either moved her palps to a different position and continued performing hunched legs displays, or she moved her legs into the forward position.

After a female *P. labiata* or *P. schultzi* had adopted the forward appendage posture, she tended to remain stationary, although she might return her appendages to the normal posture several times and walk a few centimetres to a higher location before standing and adopting the forward posture again.

If the male was moving when females with forward appendages drummed and tugged, he usually stopped and postured, but slight movements of the female (e.g., turning a few degrees, stepping a few millimetres, or slightly lifting a leg) often resulted in the male's decamping frantically. Males became increasingly likely to decamp frantically as they got closer to females.

After decamping frantically, the male usually turned, faced the female, elevated his legs, and began advancing again within 5–10 s, reaching his former location quickly (e.g., 10–20 s to move from 200 mm to 50 mm from the female after decamping from 50 mm, as against 10–20 min to cover this distance originally).

Females almost never performed rapid, forceful movements while they had appendages forward, except that, occasionally (and seemingly unpredictably), females made forward lunges toward males (especially if the male was within 10–20 mm). Sometimes the lunging female inserted her fangs, killed the male, and ate him. Males that escaped frontal lunge decamped frantically, but they often soon displayed and returned.

If the female *P. labiata* and *P. schultzi* remained stationary with forward appendages, usually the male would eventually bring his elevated legs over the female and begin leg shaking. At this stage the male would very likely decamp frantically; if he did not, he normally backed away 10–50 mm then repeatedly advanced again, each time bringing his elevated legs over the female. Males of *P. labiata* and *P. schultzi* rarely stayed still with legs over the female, but either continued to advance and mounted or else backed away again. In contrast, male *P. fimbriata* (Q) stood with legs over females, premount tapping for many seconds at a time.

Sometimes, a male *P. fimbriata* (Q) mounted before the female completely retracted her appendages, sometimes spinning on her for several seconds or minutes, but the female always retracted her appendages before copulation began. In contrast, male *P. labiata* and *P. schultzi* did not fully mount until the female had fully or almost fully retracted her appendages, although retraction and mounting was sometimes almost simultaneous. Females often gradually retracted their legs, with palps remaining forward until the last moment, and

Table 15 General trends in male behaviour during male-female interactions. *Portia fimbriata* (Q), *P. labiata*, and *P. schultzi* compared.

	P. fimbriata (Q)	*P. labiata*	*P. schultzi*
Approach to female	Advances more or less directly, often from below the female. Prolonged periods of remaining stationary and episodes of moving away then advancing again: infrequent.	When possible, makes wide sweeping detours so that final approach is from above the female. Prolonged periods of remaining stationary and episodes of moving away then advancing again: frequent.	Less slow and intermittent than *P. labiata* but more like *P. labiata* than like *P. fimbriata* (Q).
Response to female movement (exclusive of drumming and tugging)	Usually stands. Sometimes backs 20–50 mm away. Rarely moves away rapidly.	Frantic decamping.	
Jerky walking	Occurs less often. When occurs, often of shorter duration and performed less forcefully (web moves less conspicuously).	Occurs more often. When occurs, often of greater duration and performed more forcefully (web moves more conspicuously).	
Semi-erect legs before initially facing female	Does not occur.	Common in conjunction with jerky walking.	
Displays with semi-erect legs	Rare. When occurs, brief and male usually distant from female.	Predominant behaviour during all interactions.	
Displays with erect legs	Predominant behaviour during all interactions.	Rarely occurs when male is > 50 mm from female. First occurrence usually when male first brings legs I over female. Afterward, often occurs at greater distances.	Often occurs when male is > 50 mm from female, but first occurrence is usually when < 50 mm from female, but before legs I are over female.
Leg posturing	Rare	Common	
Leg waving	Usually with erect legs.	Usually with semi-erect legs.	With semi-erect and with erect legs are both common.
Leg shaking	Male usually < 50 mm from female. First occurrence usually as male brings legs I over female.	Male usually < 50 mm from female. First occurrence usually as male first brings legs I over female.	Male often > 50 mm from female. First occurrence usually when < 50 mm from female but before legs I over female.
	Type 1 only. Bout: 3–10. Usually, no contact of legs with female or silk. Usually shakes with legs I and II. Shaking causes female to rock up and down on web less conspicuously compared to *P. labiata* and *P. schultzi*.	Legs over female: Type 1. Legs not over female: Type 2, Bouts: highly variable, up to c. 1000. Male legs contact female's body and legs and the web. Legs II often on substratum, about parallel to legs I, not shaking. Shaking causes female to rock up and down on web conspicuously.	
Palp posture while legs are elevated	Frontal.	Frontal, downward, raised, lateral-forward, and raised forward.	
Behaviour just before mounting	With legs over female, male alternately stands and steps forward c. 1 mm until mounted.	Steps forward, bringing legs and, sometimes, cephalothorax over female, then backs away. Rarely stands with legs over female. Eventually, mounts in one continuous movement.	
Duration of post-mount courtship before first palp engagement	10–60 s	5–10 s	
First palp engagement	Engages first palp that scrapes.	Scrapes 2–5 s with one palp, then scrapes with and engages opposite palp.	

Table 16 General trends in female behaviour during male-female interactions. *Portia fimbriata* (Q), *P. labiata*, and *P. schultzi* compared.

	P. fimbriata (Q)	*P. labiata* and *P. schultzi*
Hunched legs and propulsive displays before male initially elevates legs	Common.	Uncommon.
Relocation during male's approach	Occasionally moves to higher location then remains stationary. More often moves repeatedly in varied directions before eventually mating.	Often, early in interaction, moves to higher location (e.g., leaf in web or stem at top edge of web). Subsequently tends to remain stationary.
Palp posture	Usually normal. Never forward.	Usually forward, especially if mating occurs subsequently.
Drum and tug	Does not occur.	Common, especially if mating occurs subsequently.
Mates after performing hunched legs and propulsive displays	Common.	Rare.
Retracts appendages	Either just before or just after male mounts.	Just before male mounts.
Drop on dragline	Often fails to occur, especially if on web.	Usually occurs unless right-side-up on horizontal surface.
Twist lunge	Does not occur.	Usually occurs if on web or suspended on line.
Lunge forward	Does not occur.	Common, especially if not on web.
Injure male	Rare.	Common.
Cannibalism	Does not occur.	Occurs occasionally.

continued to drum even when the male's legs were over her. Males often performed leg shaking and mounted females that were facing as much as 180° away.

The female *P. labiata* and *P. schultzi* usually slipped down 20–30 mm on a dragline as she retracted her appendages with the male mounted (unless she was right-side-up on a substratum from which this was not possible; e.g., the floor of the cage). Before the male mounted, the female usually moved to a position suitable for fastening a dragline.

On both their own and alien webs, females often managed to drop down, suspended by a dragline fastened to the structural threads of the web. Although female *P. fimbriata* (Q) regularly slipped down on draglines, mating while suspended was not as common in this species as in *P. labiata* and *P. schultzi.*

Female *P. labiata* and *P. schultzi* which mated while suspended almost always twist lunged unpredictably, before, during, or after any palp engagement. Also females resting on webs but not suspended, often twist lunged while the male mounted. Females on non-silk substrata probably could not twist lunge, but they often lunged forward with the male mounted.

Males of all three species normally did not dismount from females until the female became active (usually twist or forward lunge for *P. labiata* and *P. schultzi* and walking for *P. fimbriata* (Q)). Female *P. labiata* and *P. schultzi* sometimes captured, killed, and ate males that had been mounted when they twist lunged, although all males escaped after forward lunges. If the male was not killed when the female became active, he decamped frantically. If two palp engagements had not preceded frantic decamping, the male returned, displaying, and usually he eventually mounted and copulated again. If two or more engagements had occurred, males did not return after frantically decamping, although they might face and briefly display from a distance before walking away. In contrast, female *P. fimbriata* (Q) did not kill males, males did not decamp frantically, and once the female became active and the male dismounted, copulation rarely resumed.

If a palp was engaged when the female lunged, the male often escaped with his life but minus his palp. If his palp was not lost, it was often injured and came off by the end of the day. Males that had lost one palp but had not yet engaged the other, returned displaying and often resumed copulation.

Female *P. fimbriata* (Q) did not lunge when males were mounted, and they were not observed to kill males; but when females began walking, copulating males sometimes lost palps. When observed and collected in nature, males (but not females) of each species of *Portia* (except *P. albimana*; probably because of small sample size) were sometimes missing a palp.

Males of *P. fimbriata* (Q) performed postmount courtship, leaned to the left or right, and engaged their palps when the female's abdomen rotated. Occasionally, if the female's abdomen failed to rotate or it rotated only partially, the male leaned

Table 17 General trends in behaviour during intrasexual interactions. *Portia fimbriata* (Q), *P. labiata,* and *P. schultzi* compared.

	P. fimbriata (Q)	*P. labiata*	*P. schultzi*
Male-male: palp postures while legs are raised (not embracing)	Arched or downward.	Normal, arched, or downward.	Normal, arched, downward, raised-forward, or lateral-forward.
Female-female: palp postures while legs are raised (not embracing)	Arched or downward.	Normal, arched, or downward.	Normal, arched, downward, or lateral.
Hunched legs	Position 1 uncommon. Position 2 common.	Positions 1 and 2 common.	
Sway	Usually faster (2–4 s/cycle) and continuous.	Usually slower and interrupted: 2–5 s to move to one side; extreme position held 2–5 s; 2–5 s to move to other side; etc.	
Erect legs just before embrace	Position 3 (held for a few seconds) common. Position 2 rare. Position 1 absent.	Males: Position 1–3 common; often initial contact in Position 1. Females: Positions 2 and 3 common and often held for several seconds or minutes; Position 1 does not occur.	
Erect legs during embrace	Position 3 common; 2, less common. Rarely raised > 45° above horizontal.	Positions 2 and 3 common. Often raised nearly vertical.	
Female-female embracing	Grappling more common than lunging.	Lunging more common than grappling.	
Female kills female	Does not occur.	Common.	

to the other side. Males of *P. labiata* and *P. schultzi,* however, routinely leaned to the left (or right) just after mounting, with the female's abdomen rotating, scraped their left (or right) palps on the female's abdomen for 2–5 s, then moved across to the right (or left), scraped and engaged the right (or left) palp. This side-switching ritual did not, however, occur between subsequent palp engagements unless the male dismounted, then remounted.

Copulation

Copulation was observed in 88 intraspecific male-female interactions (*P. fimbriata* (NT), 6; *P. fimbriata* (Q), 22; *P. labiata,* 48; and *P. schultzi,* 12). There were no obvious differences between the species. The median duration of courtship (time elapsing between first display and first palpal engagement) was 29.5 min (4–169 min). Median latency to contact (first display to first contact of female by male, ramming excluded) was 19.5 min (1–166 min). Duration of copulation (sum of durations of all palp engagements during the interaction) was 100.5 s (11 s–31 min), individual palp engagements ($n=236$) being 42.5 s long (8 s–8 min). Intervals between successive palp engagements averaged 12 s (3s–8 min) when males remained mounted ($n=117$) and 8 min (2–43 min) when they dismounted between engagements ($n=32$). All copulations seemed to be functional (some of the shortest copulations were with virgin females, and although these females were subsequently kept isolated from males, they all oviposited many fertile eggs).

Female receptivity

Virgin females of each species generally mated with the first male with which they were tested. Previously-mated females frequently remated; females of *P. labiata* and *P. schultzi* were more receptive to remating than were *P. fimbriata* (Q): previously-mated *P. labiata* and *P. schultzi* remated in 24 of 30 tests; *P. fimbriata* (Q) in only 12 of 41 tests ($\chi^2=15.866$, $P<0.001$). In nature, females of all species were found with sperm plugs covering the copulatory pores (see Jackson 1980a); in the laboratory mated females had plugs, but virgins did not.

Interspecific male-female interactions

Copulation was observed between species in seven instances (in *P. albimana* ♂ × *P. labiata* ♀ 1; *P. fimbriata* (Q) ♂ × *P. fimbriata* (SL) ♀ 5; *P. fimbriata* (Q) ♂ × *P. labiata* ♀ 1), but none of the females subsequently oviposited.

During interspecific interactions, *P. fimbriata* (Q) and *P. labiata* behaved similarly to intraspecific interactions. Males of *P. labiata* did not mount females of *P. fimbriata* (Q, SL). *P. fimbriata* (Q) was, in comparison to *P. labiata*, more active, and male *P. labiata* repeatedly decamped frantically and eventually ceased to interact. Although females of *P. fimbriata* (SL) were less active, similar to females of *P. labiata*, males of *P. labiata* failed to approach them closely.

In one interaction between a male *P. fimbriata* (Q) and a female *P. labiata*, the female approached the displaying male and the male decamped. In the other six interactions, the female drummed and tugged, then the male approached and mounted. All females lunged while males were mounted, but no males were killed. Two males approached females again, remounted, and were lunged at again. In five instances, the female's abdomen had rotated before she twist lunged.

Males of *P. albimana* readily courted and mounted females of *P. labiata*, and the female *P. labiata* made twist lunges; in one interaction, the male started copulation before the female lunged.

Intrasexual interactions of *P. fimbriata* (Q), *P. labiata*, and *P. schultzi*

Behaviour sequences during intrasexual interactions did not differ appreciably if a web was present or not. Jerky walking did not occur. Interactions usually began when one spider faced the other from 100–300 mm and displayed; the other soon reciprocated. Long periods of watching were rare before initial displays. Major behaviours in intrasexual interactions are shown in Table 14, and major interspecific differences are summarised in Table 17. Intrasexual interactions usually ended when the first spider decamped.

Both elevated and hunched legs were common in male-male interactions of *P. labiata* and *P. schultzi*. Erect legs were more common than semi-erect legs. Posturing and leg shaking occurred occasionally; leg waving did not. Leg shaking was performed by only one male at a time, with the spiders 20–50 mm apart. Leg shaking with legs over the other male was rare and usually lasted for only c. 1 s. Males tended to shift their legs continually and slowly during the interaction between erect, semi-erect, and hunched, and between the different positions of each. The sequence of switching patterns was highly variable (e.g., hunched Position 2 to hunched 3 to erect 3 to semi-erect 2 to erect 1).

In contrast to male-female interactions, male-male interactions of *P. labiata* and *P. schultzi* included erect legs more commonly than semi-erect legs, and the males interacted at varied distances. Each leg position also occurred at varied distances. Erect legs were usually in Position 1 during the initial display.

Except for the adoption of Positions 2 and 3 during swaying, elevated legs displays were uncommon in intrasexual interactions of *P. fimbriata* (Q). Both hunched and erect (Position 2 and, especially, 3) legs were, however, common in female-female interactions of *P. labiata* and *P. schultzi*. The initial displays of females of *P. labiata* and *P. schultzi* were often Position 3 erect legs. Position 1 erect legs were not seen in intrasexual interactions of *P. fimbriata* (Q) or in female-female interactions of any of the three species.

Swaying was common in intrasexual interactions of each species, especially when spiders were within 50 mm of each other. Embracing (often preceded by swaying) was especially frequent in female-female interactions. To embrace, the spiders approached slowly with hunched legs. In male-male interactions of *P. fimbriata* (Q) and female-female interactions of all species, legs were usually in erect Positions 2 or 3 just before contact was made. Males of *P. labiata* and *P. schultzi* often made initial contact with legs erect in Position 1; as they continued to advance, the males moved their legs back to Position 2 then 3.

In male-male interactions of all three species, embraces usually lasted only 5–10 s, with only legs making contact. In female-female interactions, however, longer embraces (usually 20–60 s, maximum c. 10 min) were common. Although females of *P. fimbriata* (Q) usually grappled during embraces and sometimes lost legs, they rarely made forward lunges. Females of *P. labiata* and *P. schultzi* usually made forward lunges, but grappled less commonly while embracing.

While embracing, palps were generally held raised or (occasionally) lateral, except that males of *P. labiata* and *P. schultzi* often performed palpal pushing with palps raised-forward or lateral-forward. *P. fimbriata* (Q), with raised legs, held palps arched or, less often, downward. Palps were sometimes raised or, rarely, lateral just before embracing. When their legs were raised, *P. labiata* and *P. schultzi* often held palps normal, arched, or downward. Females of *P. schultzi* often held their palps lateral, too. Males of *P. schultzi* often held their palps raised-forward or lateral-forward when close together, especially just before embracing.

Cannibalism was sometimes observed in female-female interactions of *P. labiata* and *P. schultzi*; e.g., during embracing one female might push the other female over backwards by lunging or simply walking forward, after which the up-ended spider usually immediately righted itself and ran away, but occasionally it was killed and eaten when its rival's fangs pierced its ventral cephalothorax or abdomen during the up-ending (Fig. 43). In other instances, the rival walked over the up-ended spider, and the pair grappled wildly, venter-to-venter,

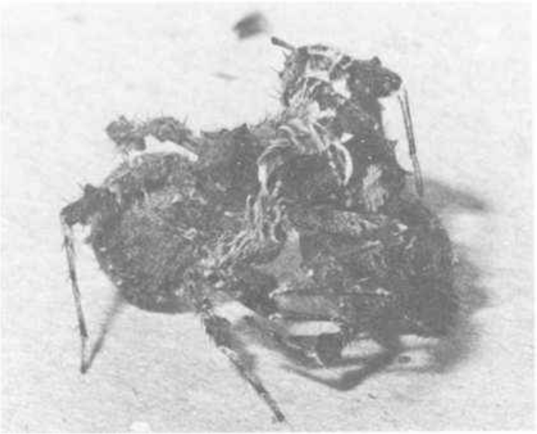


Fig. 43 Cannibalism in female-female interaction of *Portia labiata.* Females had been embracing, with faces pressed together. Female on left has upended female on right and inserted her fangs into ventral cephalothorax of upended rival.

for several seconds before one *Portia* ran away or was killed. Up-ending and cannibalism were not observed when *P. fimbriata* (Q) embraced.

For each species, when females interacted on webs containing the eggs of one female, the intruding female sometimes evicted (or killed: *P. labiata* and *P. schultzi*) the resident then ate the resident's eggs. Afterwards, females sometimes oviposited their own eggs on the leaf that had held the rival's eggs.

Except for occasional truncated leaps by *P. labiata* and *P. schultzi*, male-male interactions did not include propulsive displays. In female-female interactions of all three species, propulsive displays were routine, if intermittent and seemingly unpredictable. Females of all three species sometimes knocked over their rivals by ramming and making long leaps. The up-ended spider always righted itself immediately and ran away.

Intraspecific interactions of other species of *Portia*

Malaysian and Sri Lankan *P. labiata* did not differ in behaviour during intraspecific interactions. Behaviourally, female *P. fimbriata* (NT, SL) resembled *P. labiata* and *P. schultzi* during male-female and female-male interactions, especially by palpal drumming, leg tugging, and twist lunging. Male *P. albimana* and *P. fimbriata* (NT, SL) were more like *P. labiata* and *P. schultzi* than *P. fimbriata* (Q). However, males of *P. albimana* were not observed to frantically decamp.

Walking jerkily by *P. albimana* males was especially pronounced compared to that in other *Portia*; males of this species applied greater force to the silk, making the female rock conspicuously — females 100 mm away were seen to rock up and down 30–40 mm — 10–20 mm was more typical for other *Portia.* During male-female interactions male *P. albimana* also performed jerky leg waving and adopted the down-forward palp posture when within 50 mm of the female. These behaviours were not observed for other *Portia.*

During male-female interactions, males of *P. fimbriata* (Q) (occasionally) and *P. fimbriata* (NT) (usually) spun on females. Males of other species were not observed to spin on females.

Cohabitation

Cohabiting pairs of males and subadult females of *P. africana, P. fimbriata* (Q, NT, SL), *P. labiata* (M, SL), and *P. schultzi* were observed in Type 2 web in nature. Cohabiting pairs of subadult males and subadult females of *P. fimbriata* (Q) were also observed.

In nature, cohabiting spiders were often observed standing within 20–50 mm of each other on the web. Cohabiting pairs of males and subadult females of *P. fimbriata* (Q), *P. labiata,* and *P. schultzi,* set up in the laboratory, also tended to remain close together on the web; however, male-female, male-male or female-female pairs tended to remain at opposite sides of the cage when left together.

Interactions between males and subadult females

Displays and distinctive interactions between the spiders were not observed while pairs cohabited. When males first encountered subadult females on webs, however, the pairs often displayed as in male-female interactions. The male usually soon stopped displaying, then either decamped or remained quietly on the web and started to cohabit. However, in two of the seven tests with *P. labiata* and in one of the five with *P. schultzi* (but none of the six with *P. fimbriata* (Q)), the male continued to approach, displaying as the female drummed and tugged, and eventually mounted. The female's abdomen then rotated and the male scraped his palp on the female's ventral abdomen for several minutes (pseudocopulation). The female eventually made a twist-lunge, but the male escaped in each instance. One subadult *P. schultzi* did kill two males in succession by making forward lunges as the males brought their erect legs over the carapace of the subadult.

Sperm induction

Sperm induction was observed for *P. labiata* and *P. schultzi*: there were no interspecific differences. Several hours after mating, the male began to spin by stepping and pivoting about in a small area and swinging his abdomen from side to side. He groomed intermittently, especially his palps. The horizontal sperm web, completed c. 1.5 h later, was similar to a Type 1 web but smaller (c. 5 × 5 mm) and more sparsely woven. Hanging beneath the web, the male rhythmically moved his abdomen up and down, repeatedly contacting the silk, and deposited a sperm drop after c. 1 min. Almost immediately, the male reached around with one palp and tapped it up and down (0.5–1 mm; 2–6 Hz) over the sperm drop as he hung from the lower surface. The other palp was held stationary beside the chelicerae (Fig. 44). After 20–30 s, the male switched to tapping with the other palp. Each palp tapped about 10 times, with only 1–2 s during each switch-over, then the male stopped, groomed (including wiping his palps across the silk), and walked away.

Fig. 44 Sperm induction. Male *Portia labiata*, hanging upside-down under sperm web, extending right palp over web to contact drop of sperm (arrow).

DISCUSSION

Webs

Web-building is evidently a conservative trait within the genus *Portia*. All species we studied spun both Type 1 and 2 webs, and there were no interspecific differences in web design or spinning behaviour. Both types of webs were structures with definite geometry that the spider spun frequently.

The informal division of spiders into web-builders and cursorial hunters is potentially confusing. Use of the term 'web' is not always appropriate for this dichotomy (e.g., 'sperm web'). Even the nests of cursorial salticids are sometimes referred to as 'webs', and efforts to apply strict definitions to such a widely used term are likely to be counter-productive. In the context of the dichotomy between web spiders and cursorial spiders, the small (relative to spider size) 'nests' of salticids are not webs, whereas the large prey-catching space webs of *Latrodectus* (Szlep 1965) are. Type 2 webs of *Portia* functioned in prey-capture and were comparable in size (relative to the spider) to webs of many species from other families (e.g., *Latrodectus*). *Portia* is clearly a web spider.

Type 1 webs were small platforms, often incorporated into Type 2 webs, and they had no apparent function in prey capture. As resting sites, they were functionally more like the nests of typical salticids than the prey capturing webs of spiders like *Latrodectus*. Salticids typically rest enclosed within more or less tubular nests; *Portia* never spun enclosing nests. Enclosing nests are common in cursorial spiders from many families (e.g., Clubionidae, Gnaphosidae), but they are also spun by some typical web spiders (e.g., Dictynidae, Theridiidae). The web spiders place their nests within or to the side of the web. Webs of species from other families also include non-enclosing resting platforms (e.g., the hub of the orb of some araneid webs) which are generally similar to the Type 1 webs of *Portia*.

Portia selected leaves and other objects to hoist up into its web. It might rest on the leaf in lieu of a Type 1 platform, and females oviposited on the leaves. Similar behaviour occurs in some other web spider families (e.g., Araneidae, Theridiidae). The behaviours used by *Portia* and other web spiders to spin webs and lift leaves were similar (Peters 1932; Jacobi-Kleemann 1953).

As 3-dimensional arrays of threads, Type 2 webs of *Portia* are referred to as 'space webs' (Burgess & Witt 1976). In design detail they seemed to be unique (see Kaston 1964), but detailed information about web geometry is scarce for most spiders other than orb weavers (Witt et al. 1968).

In spiders, males are usually more active than females in courting and searching for mates. Females tend to feed more voraciously and often increase dramatically in size as they become gravid. Males of web-building species often cease to spin prey-capture webs, but males of cursorial species often continue to build normal nests for shelter (Jackson 1978a; Robinson 1982). *Portia* was like a typical web spider in its Type 2 webs (spun by females and by juveniles of both sexes, but not by adult males) and like a typical cursorial spider in its Type 1 webs (spun by all sex and age classes). However, males of many web-building species spin arrays of threads on which they rest (Jackson pers. obs., and see Montgomery 1908), and these arrays seem to be at least crudely analogous to Type 1 webs of *Portia*. At certain times of the day or year, females of many web-building species hide in isolated nests or on small arrays of silk. *Portia's* use of Type 1 and 2 webs was therefore roughly similar to the pattern of web use by other web spiders (Wiehle 1927; Levi 1980).

Interspecific variation in method of oviposition

Portia made two types of egg sacs. Each species probably can make both. Silken egg sacs seemed to be normal for *P. fimbriata* (NT) and possibly for *P. albimana*. Detrital egg sacs seemed to be normal for other *Portia*, with silken egg sacs only used if suitable materials for a detrital egg sac were not available. Silken egg sacs suspended in webs were roughly similar to egg sacs of many typical web spiders (e.g., *Badumna longinquus*), but were uncharacteristic of salticids or any family of cursorial spiders. Therefore, silken egg sacs may be ancestral, conserved from non-salticid web-building ancestors. Alterations for the construction of detrital egg sacs include adoption of hoisting behaviour and shifting of spinning to surfaces of the suspended leaves. Compared to eggs in silken egg sacs, eggs in detrital egg sacs were more thoroughly concealed, as *Portia* normally positions the leaf so that the eggs are out of view (e.g., facing a tree trunk).

Although *P. fimbriata* (NT) seemed to lack leaf hoisting behaviour, that the female of this species was observed in nature with eggs on a leaf suggests that *P. fimbriata* (NT) will make detrital egg sacs if suitable detritus is passively available in the web. This may be a stage other *Portia* passed through in their evolution, before developing hoisting behaviour.

Web invasion

Araneophagy, systematic invasion of alien webs, and use of vibratory behaviour probably are characteristic of all species in the genus *Portia*. Even specific elements of vibratory behaviour seem to be conservative traits within the genus. Yet these are not the only feasible vibratory behaviours for a web-invading spider, the behaviour of web-invading mimetids and gnaphosids being different (Czajka 1963; Jackson & Whitehouse 1986; Jarman & Jackson 1986).

By fluttering, striking, and plucking with legs and palps, *Portia* vibrated the web; often the web could be seen to move rhythmically and the prey spider often oriented toward and approached the *Portia*. Abdomen twitching was more enigmatic. As it moved, the abdomen rarely struck the silk and there was no apparent movement of the web or attraction of the prey-spider as a result of abdomen twitching. This puzzling behaviour occurs during intraspecific interactions of numerous spiders, of both web-building and cursorial genera, including *Portia*; its possible origins and significance have been discussed elsewhere (Jackson 1977b). It is possible that low amplitude vibrations were transmitted through the legs of the *Portia* to the substratum during abdomen twitching.

Behaviours similar to the plucking and, perhaps, fluttering of *Portia* during predatory sequences are performed by males of many web spiders from other families during courtship and other intraspecific interactions (Krafft & Leborgne 1979; Robinson 1982). Some web spiders also manipulate lines in their webs during predatory sequences with insects (Barrows 1915; Peters 1933; Robinson & Olazarri 1971). These movements are generally less rhythmical and of greater amplitude than the plucking and fluttering by *Portia*, and seem to function either in assisting the spider to locate the prey (Barth 1982) or to enhance the entanglement of the prey. For example, loading of lines may be detected during thread manipulation or the insect may be induced to move, thereby providing feedback to the spider and possibly also causing the insect to thoroughly entangle itself in the web. By vibrating, *Portia* also induced prey to move and could then locate the prey visually; even inactive prey could be located visually by being moved passively when the *Portia* vibrated on the web, suggesting that the vibratory behaviour of *Portia* functions both to deceive its prey and to assist in visual location. Vibratory and manipulatory behaviours normal to web spiders during predatory and intraspecific sequences may have been the evolutionary precursors of the vibratory behaviours of *Portia*.

Generally, cursorial spiders cannot walk easily if placed on a web; they miss lines, trip over lines, and become entangled. The locomotory behaviour of *Portia* was, however, appropriate for walking on webs (e.g., rotary probing lets *Portia* catch hold of widely spaced threads and slowly 'ambulate' through space webs). Cribellate and non-cribellate spiders generally fail to adhere to the 'glue' in their respective webs but succumb to each other's 'glue' (Jackson unpublished data), and the mechanisms by which adhesion is avoided are poorly understood. *Portia*, however, is not vulnerable to either type of glue.

The effectiveness with which *Portia* captured prey is attributable not only to locomotory abilities and avoidance of sticking but also to its proficiency at identifying and locating prey on webs. Web-borne vibrations generated by the prey may provide *Portia* with limited information on the presence of prey and its approximate compass direction, but accurate determination of prey size and distance depends ultimately on vision (Jackson unpublished data). Using vision, even inactive prey can be stalked effectively.

The efficiency of vision in identifying and locating prey on webs is independent of the vibrational characteristics of webs. Possession of acute vision was probably a condition that set the stage for the evolution of proficient locomotion on diverse web types and mechanisms for avoiding sticking to cribellate and non-cribellate 'glue', abilities that would be of little use to a web invader relying on vibrational cues (Jarman & Jackson 1985).

Scavenging

Although spiders are generally considered to be predators, scavenging is important for some lycosid species (Knost & Rovner 1975). As *Portia* fed on dead insects in alien webs in the laboratory and as dead, uneaten insects were frequently found in some of the types of alien webs that *Portia* invaded in nature, it seems likely that *Portia* scavenges, in nature, at least occasionally. Scavenging may not be free of risks because competitors may rapidly locate and defend the food source. Ants, for example, will enter webs and take dead arthropods, but they are less proficient than *Portia* at walking on webs, and generally they are unable to cross fresh cribellate silk of social amaurobiids and uloborids (the webs of which are especially likely to contain dead, uneaten arthropods). *Portia* may, however, be vulnerable to the chemical defences of competing microorganisms (see Janzen 1977); in the laboratory, *Portia* either ignored or bit then soon released arthropods that showed signs of decay or had been dead for several days.

Regardless of the frequency of scavenging in nature, its occurrence in the laboratory demonstrated that prey need not be mobile to elicit stalking and feeding by *Portia*. *Portia's* well-developed vision and specialised vibratory behaviours, by means of which dead arthropods can be made to move passively, may make *Portia* an unusually effective scavenger.

Oophagy

Eggs are another non-motile item in the diet of *Portia*. As with scavenging, *Portia* may be unusually efficient at oophagy because of its vibratory behaviours and acute vision. Eggs were more likely to be approached and eaten if they were made to move passively by *Portia's* vibratory behaviour and also if the maternal female accompanied her eggs, as *Portia* first stalked the spider then switched to the eggs.

Spider egg cases are highly variable in design, and some types apparently provide effective protection against predators and parasites (Holm 1940; Humphreys 1983), but *Portia* used specialised behaviours to open every type of spider egg sac with which it was tested. Only a few other spiders are known to be oophagic and use special behaviours to open egg sacs (see Pollard 1984).

Kleptoparasitism and araneophagic Web-invasion

Although feeding on insects ensnared in alien webs is a specialised feeding tactic found in a few insects and spiders (Vollrath 1979; Nyffeler & Benz 1980), it is unusual for a salticid. On alien webs, *Portia* acted as a kleptoparasite by forcefully taking insects from the chelicerae of the spider which spun the web and captured the prey. Instances in which *Portia* took insects from alien webs, but not directly from the host spider, are less satisfactory examples of kleptoparasitism. *Portia* may be more significant to host spiders as predators than as kleptoparasites in nature, but *Portia* can still be broadly called a 'kleptoparasitic spider'.

Certain species in the theridiid genus *Argyrodes* are the best known kleptoparasitic spiders. Mimetids are widely regarded as being araneophagic web invaders. *Portia* was both, but was not unique in this respect; *Argyrodes* sometimes eats the host spider, and mimetids sometimes feed on insects and eggs in alien webs (Trail 1980; Wise 1982; Whitehouse 1986; Jackson & Whitehouse 1986). These three types of food (insects, spiders, spider eggs) seem to form a natural combination that is potentially exploitable by spiders that inhabit alien webs.

Portia also ate other kleptoparasites. *Argyrodes* seems to be primarily a kleptoparasite whereas *Portia* and the mimetids seem to be primarily araneophagic web invaders. Perhaps spiders that are primarily kleptoparasites can afford to be more sedentary than the araneophagic web invaders that eat their host.

The ease with which *Portia* moved about while away from webs may have contributed significantly to its effectiveness as an araneophagic web invader. Despite its peculiar mechanical gait, *Portia* walked easily on non-silken surfaces. Gaps in its path could be efficiently and quickly crossed by visually-directed leaping. Typically, salticids have claw tufts or scopulae at the tips of their tarsi which enable them to grip and climb smooth surfaces (Homann 1957; Foelix & Chu-Wang 1975; Hill 1977). The terms 'scopulae' and 'scopulate hairs' are restricted by some authors (e.g., Wanless 1978) to similar hairs elsewhere on the leg, and an earlier statement (Jackson & Blest 1982a) incorrectly suggested that *Portia* lacks claw tufts. *Portia*, like all salticids, has claw tufts and walks easily up vertical rock ledges and tree trunks (Foelix et al. 1984).

Predation on insects in webs

On webs *Portia* simply walked to the insect and lunged or picked it up, a tactic that tended to be more effective on alien webs than on its own web. Alien webs, which are often sticky or densely woven, may be somewhat more likely to entangle an insect long enough to be captured in a slow, casual pursuit than are the webs of *Portia*; even so, *Portia* was not a particularly effective predator of insects on either alien or its own webs. Spiders, which were pursued more readily and captured more efficiently, were evidently its primary prey. Insects on webs seemed to be secondary prey that *Portia* pursued occasionally and captured opportunistically when rapid, agile movement was not necessary. Capture of insects on webs cannot be attributed to mistaken identity, however, as *Portia* treated spiders and insects on webs as discrete classes of prey, routinely vibrating webs when pursuing spiders but not when pursuing insects. Discrimination depends primarily on vision (Jackson, unpublished data).

Predation on insects away from webs

Typical cursorial salticids usually respond rapidly and agilely to their insect prey by suddenly pivoting around to face it, rapidly advancing, then approaching slowly with body lowered before leaping on a more or less stationary prey. Salticids often chase moving prey, and flying insects may be intercepted in mid-air. The behaviours of typical cursorial salticids are usually very effective in subduing insects; the behaviour of *Portia* is not. Basic elements of salticid predatory behaviour, such as those described in detail by Forster (1977), might be omitted by *Portia* or be present but aberrant. The chasing of mobile prey and the almost feline creeping forward in a crouched posture when close to stationary prey are characteristic of many cursorial salticids but were not of *Portia* when approaching insects. Instead, *Portia* simply walked to the prey, more or less normally (moving slowly and waving palps and legs mechanically).

Portia usually attacked by picking up or lunging, after moving to less than a body length from the insect. Highly mobile insects, such as flies, did not normally stay still long enough to be lunged at or picked up by the *Portia*. Because *Portia* does not crouch and slow to a creeping advance when close, some insects may detect its approach and flee.

When *Portia* did manage to get close, picking up was singularly ineffective against highly mobile insects, although it was successful against such slow-moving insects as caterpillars. *Portia's* most effective mode of attack against insects was to leap; but, unlike typical cursorial salticids, *Portia* did not normally leap on insect. Insects away from webs, like insects on webs, seemed to be a secondary prey that *Portia* pursued occasionally and captured opportunistically when rapid, agile movement was not necessary.

The web as a device for catching neighbouring spiders

Although *Portia* was not a very effective predator of insects on webs it did spin a non-sticky web, comparable to those of many other families of typical web spiders in that it was used to ensnare insects temporarily (Hallas & Jackson 1986).

In nature, especially in the tropical habitats of *Portia*, webs of inter- and intraspecific individuals are frequently contiguous (Krafft 1970; Burgess & Uetz 1982), and spiders in these complexes often enter neighbouring webs to pursue insects. Webs of *Portia* were common in interspecific complexes. In the laboratory and the field, spiders that enter webs of *Portia* to pursue insects are likely to be pursued and captured by the *Portia*. Within web complexes, migration of spiders between the webs tends to be frequent, and a web left vacant when its occupant is killed by a *Portia* is likely to be soon filled by another spider (Jackson, unpublished data). Therefore, the insects that are captured within the *Portia* web of an interspecific complex seem to function primarily as bait for other spiders.

Pursuit of dangerous prey

Because *Portia* is often smaller than the spider it pursues, and even spiders smaller than the *Portia* (e.g., many theridiids) frequently subdue arthropods as large as *Portia*, the predatory habits of *Portia* can be dangerous for itself. Aggresive mimicry, proficiency at locomotion on varied types of webs, potent venom, and acute vision apparently placed *Portia* in an advantageous position in most encounters with other spiders. Vision seemed to be of primary importance throughout the encounter, enabling *Portia* to locate accurately, identify, and track its prey while the prey was receiving deceptive signals from the predator. If a large spider was lured by vibrations from *Portia* and approached with threatening speed, *Portia* usually moved aside. Even if it was attacked by another spider, *Portia* often escaped because its tough cuticle and easily autotomised legs gave it an advantage.

The venom of *Portia* quickly immobilised the prey-spider and rendered it harmless. Even during the short interval while the venom was taking effect, *Portia* could remain at a safe distance by stabbing the spider and letting it run away. Large prey that succumbed less quickly to venom was often stabbed repeatedly until it was safe to seize. *Portia* could, with its acute vision, maintain sensory contact with prey that had decamped.

Despite the apparent edge *Portia* has over its predatory prey, *Portia* was sometimes injured or killed. Even non-predatory prey are potentially dangerous to spiders, because they can kick, bite, and possibly use chemical defences. For any predator of dangerous prey, the dangers must be, on average, outweighed by the benefits of obtaining a meal, but it is interesting that *Portia* seemed less inclined to take risks with insects than with spiders, as most salticids seem to do the opposite.

Large insects were attacked infrequently except when in alien webs that gave *Portia* more of an advantage than it had on its own web or away from webs. *Portia* sometimes waited many hours for the insect's struggles to subside before attacking in earnest. If the *Portia* waited, the insect was likely to become less dangerous, but the insect might also escape from the web or be taken by a competitor. Leaping on the insect seemed to be the most effective mode of attack used against insects, but it was also likely to be the most dangerous because it brought *Portia* into sudden close contact with the insect.

Portia often used less efficient, but probably safer, lunging and picking up attacks against insects. Picking up, which seemed particularly inefficient but safe, was not used against spiders. To pick up an insect, *Portia* first reached out and touched the insect with its forelegs; an insect that was going to fight back was likely to do so at this point, before the *Portia* came into close contact. *Portia* might have also, with its forelegs, tested the insect's chemical defenses before making contact with its mouth parts.

Venom

Although medically important spider venoms have been studied extensively, little is known about the venoms of most spiders, and especially little is known about how venoms act on the natural prey and the possible specialisations of venoms for specific types of prey (Bettini & Brignoli 1978). The venom of *Portia* seemed to be specifically potent to spiders, its primary prey. Spiders, including *Portia*, were paralysed rapidly when attacked by *Portia*; insects generally were not. Although pompilid wasps that attack spiders and araneophagic mimetid and gnaphosid spiders also tend to have venoms that are very potent to spiders (Rathmayer 1978; Jarman & Jackson 1986; Jackson & Whitehouse 1986), typical salticids, being primarily insectivores, generally do not (Jackson, unpublished data). Apparently, the unknown characteristics that render venoms especially potent to spiders are unlikely to evolve or to be maintained in primarily insectivorous spiders.

Crypsis

Morphologically, *Portia* is both eucryptic (difficult to distinguish from its background) and a detritus-mimic, having special protective resemblance (Robinson 1969) to objects generally treated with indifference by predators. The cryptic rest posture obscures the outlines of appendages, and the slow, mechanical locomotion either fails to attract attention or is noticed but resembles light flickering through the forest canopy and striking a piece of detritus. These characteristics are probably universal in the genus.

All *Portia* studied performed palp flickering, but this behaviour seems to be paradoxical for a highly cryptic spider, as it tends to attract attention. Cursorial salticids commonly wave their palps up and down as they walk about, during pauses as they look around, and while they watch potential prey, mates, rivals, or predators. The palp waving of salticids, including the palp flickering of *Portia*, possibly has an olfactory function (Crane 1949), which may be for *Portia*, sufficiently important to overcome the disadvantage of compromised crypsis. Also, the form of these movements is perhaps not so damaging to crypsis as it first seems. Although they are rapid and non-mechanical, flickering movements are still unspiderlike in appearance and may be mistaken for light reflecting off a piece of detritus. Given that the palps will be waved, typical salticid movements would probably compromise crypsis more than flickering does.

Aggressive mimicry

Portia tightly controlled the vibrations provided to the other spider. The slow deliberate manner in which *Portia* stepped through the web created little vibration; instead, special vibratory behaviours produced vibrations with characteristics normally associated with a less dangerous arthropod on the web. *Portia* is an aggressive mimic (Wickler 1968) that simulates the stimuli normally produced by the prey of its own predatory prey. Although aggressive mimicry has not been widely documented in animals, it is reported in angler fish (Pietsch & Grobecker 1978), termite-eating assassin bugs (McMahon 1982), and certain siphonophores (Purcell 1980). The behaviour of certain mimetid spiders (Jackson & Whitehouse 1986) and sphecid wasps (Coville 1976) more closely resemble that of *Portia*, including invading alien webs, vibrating, and feeding on the host spiders which are deceived by the vibrating predator. As suggested by Czajka (1963) for mimetids, *Portia* may sometimes mimic the intraspecific vibratory displays of its prey. Similar aggressive mimicry is practised by *Photuris* fireflies (Lampyridae) and bolas spiders (Araneidae) which simulate bioluminescent (firefly) or chemical (bolas spider) sexual signals to deceive and lure their prey (Lloyd 1975; Eberhard 1977).

Aggressive mimicry has formal similarities to intraspecific communication (see Smith 1977; Jackson 1982a: Dawkins & Krebs 1984). The sender (predator) produces signals (in *Portia*, vibrations) by which it indirectly manipulates the receiver (prey). The prey responds inappropriately to the predator's signal (e.g., approaches), having received a deceptive message (e.g., 'prey on web'). The predatory impact of *Portia* on any one species that it deceives may not be great. This may account for the apparent failure of the prey to evolve heightened discrimination, greater caution, or other counter-measures against the aggressive mimic.

Photuris fireflies simulate the sexual signals of more than one prey species (Lloyd 1975), and certain paedophagous cichlid fish alter their markings to match and probably deceive parental fish of the different species they exploit (McKaye & Kocher 1983). *Portia*, however, seemed to produce a greater diversity of signals than other aggressive mimics. In order to elicit responses from different prey species, *Portia* used a repertoire of discrete vibratory behaviours, combined behaviours in varied ways, and varied the characteristics (rate, duration, amplitude) of individual behaviours. During an encounter, *Portia* seemed to tailor its signals to a particular prey by using highly varied signalling at first, then repeating signals that elicited responses. If response from the prey subsided, *Portia* reverted to more varied signalling. In addition to allowing *Portia* to exploit diverse types of web spiders as prey, complex signalling may have been important in reducing habituation and facilitating a continuing response in any given prey-type (see Jackson 1982a).

Interspecific variation in effective crypsis

Although all *Portia* are morphologically cryptic spiders, the effectiveness of cryptic morphology and associated special postures and locomotion in concealing *Portia* from visually hunting predators probably varies with levels of ambient light. *Portia*, at least to the human eye, is easier to recognise in brighter light, and this relationhip between ambient light and the effectiveness of both eucrypsis and special protective resemblance is probably widely applicable (Dice 1947).

In its natural habitat, where light tends to be more subdued, *P. fimbriata* (Q) may be more effective at crypsis than other spiders (i.e., less likely to be detected and recognised by visually hunting predators). However, all *Portia* we have studied occupied habitats with relatively subdued light, whereas many salticids live in sun-drenched habitats where the form of crypsis adopted by *Portia* would probably be of little use.

Differences in web sites may accentuate the differences in ambient light levels under which different *Portia* live. The tree trunks, boulders, and ledges on which *P. fimbriata* (Q) often lives provide considerable shade, but the stems and leaves often occupied by *P. africana, P. labiata,* and *P. schultzi* provide less shade. Although they usually occupy more open habitats, with more ambient light, *P. albimana* and the other *P. fimbriata* resembled *P. fimbriata* (Q) in using tree trunks, boulders, and ledges as web sites, so they may also be exposed to lower levels of ambient light than are *P. labiata* and *P. schultzi.*

Differences between the species of *Portia* in defensive behaviour may be related to differences in effective crypsis (effective crypsis = the effectiveness of the cryptic morphology of *Portia* in concealing the spider in its natural habitat). Wild leaping seems to be especially effective as a means of escape from a visually-hunting predator. The species that make wild leaps (*P. albimana, P. labiata,* and *P. schultzi*) are probably less effectively cryptic and more likely to be detected by predators than *P. fimbriata* (Q), which never makes wild leaps. Whether the other *Portia* make wild leaps is uncertain. All *Portia* would simply run and leap away if sufficiently challenged, but *P. fimbriata* (Q) clearly required greater provocation than the other *Portia.* Indeed, *P. fimbriata* (Q) seems to rely more on primary defence (concealment), and secondary defence (Edmunds 1974) may be of only minor importance because *P. fimbriata* (Q) is rarely detected (Table 3).

Although slow, mechanical locomotion seems to be a conservative trait in the genus, it was more pronounced and consistent when performed by *P. fimbriata* (Q) (Table 3). Because choppy leg and palp movements are probably more difficult to superimpose on rapid stepping, differences in speed of walking may be primary. Very slow locomotion may be less likely to attract the attention of visually hunting predators than faster locomotion, but more rapid walking may be advantageous in carrying the spider rapidly to its destination, and perhaps shortening the time during which it is moving in the open and subject to detection by visually hunting predators. Relatively fast walking may be more advantageous for a less effectively cryptic *Portia* than for *P. fimbriata* (Q), and the enhanced concealment to be gained by slower, more mechanical locomotion may be more advantageous for a more effectively cryptic *P. fimbriata* (Q). Because all *Portia,* in comparison to most other salticids, were decidedly cryptic, the correlations of defensive behaviour and locomotion with levels of ambient light in the natural habitats of *Portia* suggest that the behaviour of *Portia* is finely tuned to maintain effective crypsis under different conditions.

Intersexual variation in effective crypsis

Females are more liberally covered than are males by fringes and tufts of hair that obscure outlines of the body and appendages and give the spider the appearance of detritus. The male's larger palps are more conspicuous than the slender, hirsute palps of the female, even in the cryptic rest posture; and the black, white, and yellow markings of the male tend to be more contrasting and conspicuous than the softer greys and browns that predominate on the female. Males of each species were more easily provoked than the females into running and leaping when disturbed, and males generally walked faster than females. Locomotion and defensive behaviour of the two sexes within each species seem, therefore, to be finely tuned to differences in crypsis, parallel to the differences observed between species.

Pursuit times

By using specialised, slow modes of pursuit, *Portia* was able efficiently and safely to capture cursorial salticids and diverse types of web spiders including spiders considerably larger than themselves. A spider in a web can be a difficult prey for many predators. Intervening threads can act as a physical barrier that deflects leaping predators; because they vibrate as the predator walks over, trips over, or blunders into them, intervening threads can also warn the spider of the predator's approach. So warned, the spider may run into a retreat (e.g., go under the bark on a tree), drop out of the web, or start specialised defensive behaviour, such as the twirling behaviour of some pholcids (Foelix 1982). Although *Portia* often took a long time to pursue a web spider, its protracted pursuits enabled it to overcome the web spider's defences. Again, cryptically-stalking *P. fimbriata* (Q) often took a long time to capture a cursorial salticid, but because salticids have acute vision, more rapid and less patient approaches might alert the salticid and give it time to escape or start active defence.

When *Portia* captured insects, pursuit times were usually short because *Portia* tended to walk steadily and directly to the insect; if the insect moved away, as frequently happened, *Portia* usually did not continue pursuing.

Yet, *Portia* was generally an inefficient predator of insects. The normal locomotion of *Portia*, which was largely maintained when approaching an insect, tended to preserve this spider's specialised crypsis. Slow pursuits of web spiders, and the cryptic stalking used by *P. fimbriata* (Q) to capture cursorial salticids, were consistent with the cryptic morphology of *Portia*. However, the efficient, but more rapid and agile, insect-catching behaviours of typical cursorial salticids, if adopted by *Portia*, would probably compromise the spider's elaborate camouflage.

Not using cryptic stalking, *Portia* other than *P. fimbriata* (Q) were inefficient predators of cursorial salticids. When they occasionally captured salticids, pursuit times were usually short, comparable to pursuits of insects. Successful pursuits occurred primarily on occasions when the salticid failed to detect the approaching *Portia*. Once it detected the *Portia*, the salticid was usually effective at avoiding the stalking *Portia*; often, after being faced by the salticid, *Portia* displayed and made itself even more conspicuous.

Interspecific variation in predatory behaviour and capture efficiency

Very slow, patient pursuits were characteristic of all species of *Portia*, although they also made rapid pursuits, especially by leaping into webs or chasing after fleeing prey. *P. fimbriata* (Q), however, used vibratory behaviour and moved slowly on alien webs more consistently than did other *Portia*. Other *Portia* were more likely than *P. fimbriata* (Q) to leap into the web (and onto the web spider) when a suitable vantage point was available outside the web. *P. labiata* even cleared its prospective path through the threads before leaping.

Related to these differences in predatory behaviour, *P. fimbriata* (Q) tended to take longer to pursue web spiders than did other *Portia*, and *P. fimbriata* (Q) was more efficient at capturing web spiders and was less likely to be killed or injured.

Interspecific differences in predatory behaviour and effective crypsis may be related. It may be more advantageous for *Portia* other than *P. fimbriata* (Q) to take 'short-cuts' such as leaping into webs. Although risky (*Portia* becomes more vulnerable to the defensive and predatory responses of the web spider), these behaviours may shorten the time the *Portia* remains exposed and vulnerable to its own predators while moving across its prey's web.

Since efficient stalking of cursorial salticids was practised only by *P. fimbriata* (Q) and often required lengthy pursuits, perhaps it is advantageous for less effectively cryptic *Portia* to take 'short-cuts' and move more rapidly than *P. fimbriata* (Q). However, other considerations may be more important. As salticids have acute vision, the degree to which *Portia* is cryptic is unusually relevant. Even in a well illuminated laboratory, salticids rarely seemed to recognise cryptically stalking

P. fimbriata (Q). In its dimly lit natural habitat, *P. fimbriata* (Q) may not be recognised easily by salticids, even if it is not stalking cryptically; this may not be so for a less effectively cryptic *Portia* in its natural habitat. Greater effective crypsis may have been an important condition that set the stage for the evolution of cryptic stalking in *P. fimbriata* (Q). However, the superabundance of cursorial salticids in the Queensland habitat was probably another important (perhaps more important) factor. A specialised predatory tactic specifically effective against cursorial salticids as prey is likely to be highly advantageous in Queensland but not as advantageous in other areas.

Besides their not using cryptic stalking, *Portia* other than *P. fimbriata* (Q) often performed the same threat displays in encounters with cursorial salticids that they used in intraspecific intrasexual interactions, and the cursorial salticids often themselves displayed to the *Portia*. In fact, interspecific exchange of threat displays by salticids is frequent in nature (Jackson, unpublished data). Although threat displays of salticids vary in detailed characteristics, there are often broad similarities between species (Jackson 1982a). Displaying salticids tend to be wary of each other and to keep their distance. The use of threat displays would, however, be antithetical to a *Portia* attempting to capture another salticid.

Apart from *P. fimbriata* (Q), *Portia* responded to other salticids in the general way that other salticids respond to each other; i.e., acting as predators when the opportunity arises, but otherwise performing threat displays when the potential prey is likely to be dangerous. Yet, *Portia* other than *P. fimbriata* (Q) performed only isolated elements of cryptic stalking, and all *Portia* are highly cryptic in comparison to most salticids. This suggests that other *Portia* have preadaptations which may have been important in the evolution of cryptic stalking behaviour of *P. fimbriata* (Q).

P. fimbriata (Q), unlike other *Portia*, made consistent use of vibratory behaviours to pursue cursorial salticids and other cursorial spiders that it found in nests. Sometimes signals of *P. fimbriata* (Q) may simulate the intraspecific displays used by the cursorial spider during interactions at nests or movements of small predators, parasitoids, or egg parasites walking or probing on the nest. Spiders often come out and attempt to chase away or run away from less dangerous intruders (Jackson 1976). By exploiting this behaviour of its victim *P. fimbriata* (Q) increased its chances of obtaining a meal by enticing the spider out of the nest. The use of vibratory behaviours on alien webs may have been a preadaptation for using vibratory behaviours on alien nests. The behaviours are the same, only the site of performance is altered to derive the way in which *P. fimbriata* (Q) pursues nesting spiders.

The unusual habitat of *P. fimbriata* (Q) may have favoured the pursuit of nesting cursorial salticids. Accessible nests were superabundant only in Queensland, where *Lagnus kochi* and other salticids place their nests in slight depressions on boulders, ledges, and tree trunks. *P. fimbriata* (Q) can simply walk onto these nests; avoiding them might, in fact, be more difficult than locating them.

Animals generally pursue prey they are efficient at capturing. *P. fimbriata* (Q) had a stronger tendency than other *Portia* to pursue web spiders and insects, and it was more efficient than other *Portia* at capturing these prey. Other *Portia* had a stronger tendency than *P. fimbriata* (Q) to pursue insects, and they were more efficient then *P. fimbriata* (Q) at capturing insects. Therefore, within *Portia*, thresholds for eliciting pursuit of prey would seem to be adjusted to the relative efficiency with which the prey can be captured.

Intersexual variation in predatory behaviour

Males were usually less likely to pursue and less efficient at capturing all types of prey. Their tendency to move more rapidly than females may partially account for their lower efficiency at catching spiders; their lower likelihood of pursuing these prey may also be an adjustment to a lower capture efficiency. If no other factors were involved, however, faster moving males should be superior as predators of insects. A more fundamental intersexual difference (mentioned earlier in relation to web-building) is probably important: males tend to place greater emphasis on obtaining mates; females on food.

Intersexual differences were less obvious when prey were insects rather than spiders. Males were inferior as predators of large insects and of spiders of varied sizes, but male predatory behaviour against spiders was not degenerative. Males continued to use the same vibratory behaviours as females and, although they were inferior predators of web spiders, they were still efficient. Males of *P. fimbriata* (Q) used cryptic stalking to pursue cursorial salticids, but more often than females, resorted to displaying at their potential prey and thus reduced their chances of capturing it.

Courtship versatility

Where there is enough light all salticids, including *Portia*, employ visual displays during interspecific interactions. Interacting *Portia*, like other salticids, performed postcontact behaviours that evidently conveyed tactile and chemotactic stimuli. During male-female interactions in webs, *Portia* used vibratory displays that were at least crudely similar to the vibratory displays used by certain salticids while interacting at their silken nests. *Portia*, therefore, provides another example of courtship versatility, with Type 1 courtship away from silken structures and Type 2 at webs (*Portia*) and nests (other salticids); however, the disparity between the two types of courtship was less for *Portia* than for other salticids. The cursorial salticids used vibratory courtship under circumstances in which visual displays would be inefficient or impossible. On webs, *Portia* used vibratory displays in addition, not as an alternative, to visual displays.

Because they have poor vision, typical web spiders use vibratory displays during interactions on webs. The hypothetical web-building ancestors of the salticids presumedly used similar displays. Visual displays can be used efficiently on or off webs and because they are not affected by the vibrational properties of webs, can be used efficiently on diverse web types. Once acute vision had evolved, rapid adoption of visual display behaviour might have been expected. *Portia* used visual displays on webs, consistent with its possessing acute vision; but *Portia* also used vibratory displays while on webs, perhaps having retained these displays from web-building ancestors that lacked acute vision.

Vibratory and postcontact displays

Portia used one small set of less variable vibratory displays when interacting with conspecifics and a larger set of distinctive, different, and more variable displays when interacting with heterospecific prey. The intraspecific vibratory displays of *Portia* cause distinctive movements of the web to which the other *Portia* responds under experimental conditions that preclude the use of vision (Jackson, unpublished data). Web spiders from other families have behaviours which are, in general, similar to the vibratory displays of *Portia*. Some of the intraspecific vibratory displays of *Portia* (e.g., drumming and tugging by females) were performed both on and away from webs and were probably vibratory and visual displays.

If non-salticid ancestors of salticids used vibratory behaviours similar to these displays of *Portia*, once acute vision had evolved, the same display could be perceived by both vibration and vision. These displays may have become modified in ways which made them more visually effective, and the originally vibratory displays could then have been used away from webs. For example, the jerky waving display of *P. albimana* may have evolved as a means of enhancing the visual effect of jerky walking, and something like jerky waving may have been the precursor of the leg waving displays in *Portia* and many other salticids. Perhaps many salticid visual displays evolved via similar routes.

Postcontact tactile and chemotactic displays similar to the postcontact displays of *Portia* are present in many other salticids, in cursorial species from other families, and in other web spiders. For some species, this type of display may be the primary or only mode of intraspecific communication (Bristowe 1941). For males of *P. albimana, P. labiata,* and *P. schultzi*, leg shaking seemed to be both a postcontact and a vibratory display, the male's moving legs contacting both the female and the web. Leg shaking by male *P. fimbriata* (Q) was not, however, part of postcontact courtship, as the male premount tapped at this stage. Instead, males of *P. fimbriata* (Q) performed leg shaking as a visual display before contacting females. The leg shaking display of *P. fimbriata* (Q) may have been ancestrally tactile-vibratory, and the evolution of acute vision may have allowed its transformation into a visual display.

Threat displays

Embracing, grappling, and palpal pushing are postcontact threat displays and formal fighting procedures that may allow *Portia* to assess the ability of its rival to inflict injury. For instance, spiders may assess their relative strengths when palpal pushing or stepping and lunging forward while embracing. Although they differed from typical predatory attacks, postcontact intrasexual behaviours were far from being harmless rituals. A spider might be upended and killed by a rival, or it might lose legs during grappling. A rival with fewer legs would probably be hampered in future predatory and intraspecific encounters, and its locomotion might be impaired. Easy autotomy of legs, which was apparently advantageous to *Portia* when a predator of potentially dangerous prey, seemed to be a liability when grappling with a conspecific. Loss of a leg is better than loss of life if attacked by a theridiid, for example, but less easily autotomised legs would surely be an asset during grappling. Grappling seems to be a ritual by which *Portia* attempted to exploit a defence mechanism of its rival to inflict a type of injury (leg loss) to which these spiders are peculiarly susceptible.

Hunched legs and swaying seem to be displays by which *Portia* gives its rival information (visually) about its ability to inflict injury. Hunched legs and swaying are common salticid displays; like the threat displays of many animals, these behaviours increase apparent size and make the animal's weapons more evident. Swaying may be partly explained as an amplification of the visual effects of hunched legs; movement side-to-side probably attracts the rival's attention and further increases apparent size.

Propulsive displays, consisting of sudden, rapid movement toward the rival, may be especially effective threat displays. Similar threat displays are performed by many cursorial salticids and by other animals. It would generally be an advantage for a *Portia* to be startled by and wary of such displays, because potential predators are likely to move this way when attacking. Striking, charging, and truncated leaping seem like violent dashes or leaps toward the rival that have been reduced to 'intention movements'. If, however, this interpretation is correct, *Portia* is mimicking roughly the movements of its own predators, but not movements normally adopted against its own prey. Although *Portia* occasionally leapt on its prey, it usually did not dash about or leap violently.

Striking with legs was an exceptional propulsive display because it was also used during predatory encounters on alien webs. Although in that context, it was anamalous because it was conspicuous and should attract the attention of visually hunting predators, striking was largely restricted to a brief performance early in the encounter.

Portia struck with palps as well as legs when acting as a web-invading predator, but only the legs struck during intraspecific interactions. When acting as a predator, the striking appendages contacted the web and vibrated it, usually with the web spider many centimetres away and not necessarily visible to the *Portia.* In contrast, during intraspecific interactions the striking *Portia* was usually facing a rival only a short distance away and not necessarily on a web. Although striking with palps caused vibration of webs, it was not a very conspicuous behaviour; it may be less suitable as a visual display than striking with legs.

Although threat displays and aggression are common in the Salticidae, the adaptive significance of intraspecific intolerance in these spiders is only poorly understood. Male-male aggression, which may be related to competition for mates (intrasexual selection), is probably more pronounced than female-female aggression in most salticids (Crane 1949), but female-female interactions of *Portia* were unusually ferocious. The resources at stake in female-female interactions of most salticids are often obscure, but for *Portia* they were readily apparent: webs and eggs. Webs spun by one female can be used by another, and the eggs in a web, the resident female's progeny, are potential food for an intruder. Even the leaf on which a female has placed her eggs is valuable as a potential oviposition site for the rival female.

Palp postures adopted during intraspecific interactions

When interacting with conspecifics and performing threat displays, *P. labiata* and *P. schultzi* often exposed their chelicerae by holding their palps lateral and extending their fangs. Palps were held lateral during cryptic stalking of salticids by *P. fimbriata* (Q) and in the cryptic rest posture of all *Portia*, and this made their outlines less noticeable than usual. *P. fimbriata* (Q), the only *Portia* that used cryptic stalking as a predatory tactic, almost never adopted the lateral palp posture when interacting with conspecifics, which indicated to the human observer, and presumably to its rival, that it recognised that the rival was another *Portia* rather than some other salticid. Apparently, a cryptically stalking *Portia* could conceal itself very effectively from most salticids, but not from another *Portia.* Cues by which a *Portia* recognises a conspecific include some of the same morphological features that conceal the *Portia* from other salticids (Jackson, unpublished data). Because a cryptically stalking *Portia* is likely to be ineffective at injuring or killing another *Portia*, adoption of components of cryptic stalking behaviour is unlikely to be especially effective as a threat display.

When performing threat displays, *P. fimbriata* (Q) more often adopted the arched palp posture. In this posture, as in the lateral posture, the chelicerae were exposed. Arched palps may also increase the apparent size of the chelicerae by providing an apparent, but false, downward extension of them. *P. labiata* and *P. schultzi* adopted lateral-forward, raised, raised-forward, and downward palp postures when performing threat displays, and each of these postures exposed the chelicerae, too. Males held their palps in the frontal posture when courting females. Although this posture tended to hide the chelicerae from view, perhaps informing the female of his non-threatening nature, it may be more important that the frontal posture made the distinctive palps of the male more conspicuous.

Intersexual and intrasexual interactions compared

Although precontact visual displays and postcontact tactile and chemotactic displays occurred during intrasexual interactions, vibratory displays were restricted to male-female interactions. Rapid give-and-take and the intimidation of rivals, characteristic of intrasexual interactions, might be more efficient with visual rather than vibratory displays. During courtship, however, the object is more to appease and to facilitate peaceful union; vibratory displays are more likely to be useful during the slower, more deliberate interactions that ensue. In particular, vibratory displays during male-female interactions allowed the two *Portia* to communicate even while not facing each other on webs, but this consideration is less relevant during intrasexual interactions when the spiders moved more rapidly and tended to continually attract each other's attention visually and to face each other. Females of *P. fimbriata* (Q) were also more likely than other *Portia* females to make large rapid movements; females of this species did not perform obvious vibratory displays.

The sexes in *Portia* must quickly and efficiently recognise each other because inter- and intrasexual interactions usually differed from their inception. Male *P. fimbriata* (Q), for instance, displayed with elevated legs when interacting with males and with hunched legs when interacting with females. Male *P. labiata* and *P. schultzi* displayed to other males with both elevated and hunched legs, but this seemed not to be the result of mistaken identity because the male jerky walked only with females and approached rapidly only with males.

Postmount courtship

The stereotyped pattern by which males of *P. labiata* and *P. schultzi* alternated sides of the female before the first palp was engaged and the timing of abdomen twitching (just before and after engaging and disengaging palps) by males were unusual for a salticid and suggested that they are important in communication. Spinning on the female, a male postmount behaviour of *P. fimbriata* (NT, Q) is performed also by various web-building araneids, cursorial thomisids, and cursorial salticids (Gerhardt & Kaestner 1938; Bristowe 1941; Robinson & Robinson 1980; Jackson & Harding 1982). Spinning by all of these species is probably primarily communicatory, but the mechanical function of helping to support the suspended female during copulation may also be important for *P. fimbriata* (NT, Q).

Copulation

Generally, salticids adopt copulatory Position 2 of the classification by Gerhardt & Kaestner (1938), in which the male, while mounted on the female and facing in the opposite direction, applies his palps one at a time by leaning from one side of the female to the other. Variations that are easily derived from Position 2 occur occasionally (Jackson 1982c). Position 2 is adopted by many other cursorial species, but not by all, and it is uncommon in web spiders. *Portia*, like most salticids, copulated in Position 2.

The strong tendency of *Portia* to mate suspended from silk, especially on the female's dragline, is unusual for a salticid. Some typical web-building spiders also mate suspended on draglines connected to their webs (Peaslee & Peck 1983), and most web spiders mate on the silk of the female's web or on threads added to the web by the male (Robinson 1982). In the Oxyopidae, a family traditionally included among the cursorial spiders, some species routinely mate suspended from draglines (Gerhardt 1933; Whitcomb & Eason 1965), and this observation has been used to argue that oxyopids evolved from web-building ancestors (Rovner 1980). Recent discovery of web-building oxyopids in Costa Rica supports this hypothesis (Griswold 1983).

The durations of copulation in *Portia* were at the lower end of the range recorded for salticids. Some cursorial salticids usually copulate for hours or even days at a time (Jackson 1980a), and shorter copulations may be more characteristic of web spiders than of cursorial salticids (see Gerhardt & Kaestner 1938).

Sperm induction

In practising indirect sperm induction, *Portia* was more like a typical cursorial spider than a typical web spider. Why this should be so is unclear; but, because detailed descriptions of sperm induction are available for only a few families of spiders and for only a few species in each family, we are not confident that the relationship between web-building and the method of sperm induction is valid. Comprehensive comparative studies are necessary but sperm induction tends to be difficult to observe. It is generally difficult to predict exactly when it will happen, and spiders preparing to perform sperm induction are often easily disturbed. Salticids often compound observational problems by performing sperm induction while concealed in their nests (Jackson, unpublished observations). In fact, very little is known about sperm induction by salticids other than *Portia.*

Cannibalism and predatory versatility

Intraspecific interactions and predatory interactions overlap in *P. labiata* and *P. schultzi.* Although female *P. fimbriata* (Q) and males of all three species were never observed to feed on conspecifics during intraspecific interactions, female *P. labiata* and *P. schultzi* used prey-specific predatory behaviours against conspecifics. Female *P. labiata* and *P. schultzi* frequently pushed and lunged while embracing, but females of *P. fimbriata* (Q) were more inclined to grapple. Males of all species normally embraced only briefly. Grappling, although it was often damaging and was likely to cause the rival to lose legs, did not directly facilitate cannibalism. Pushing and lunging, however, were likely to upend the rival and make it more vulnerable to a predatory attack.

Against courting and mating males, female *P. labiata* and *P. schultzi* used predatory attack behaviours (lunging forward and twist lunging) that were not performed by females of *P. fimbriata* (Q) or by the males of any species. Twist lunging was performed only when a male was mounted on a female suspended from silk. Females of *P. labiata* and *P. schultzi* were especially likely to drop on draglines when mating, and they often moved to a position from which this was more easily accomplished before copulation began. Once suspended, female *P. labiata* and *P. schultzi* always twist lunged.

Females of *P. labiata* and *P. schultzi* captured conspecific spiders less efficiently than they captured heterospecific web spiders. Killing and eating a conspecific may also be related to factors other than obtaining a meal — female unreceptivity to mating and female-female competition — but the cannibalistic *Portia* did obtain a large meal, and it would be wrong to exclude cannibalism, and the behaviours that facilitate it, from a consideration of predatory versatility. Reasons for the interspecific differences in behaviours related to cannibalism are, however, unclear.

Interspecific differences in courtship

Male *P. labiata* and *P. schultzi* seemed to approach their more cannibalistic females more cautiously than male *P. fimbriata* (Q) approached their less dangerous females. Interspecific differences in the cannibalistic behaviours of females are probably mainly responsible for interspecific differences in male courtship behaviour. Males of *P. labiata* and *P. schultzi*, but not *P. fimbriata* (Q), employed a specific behaviour, frantic decamping, which could rapidly separate them from the females. When females made even slight movements, male *P. labiata* and *P. schultzi* were very likely to decamp frantically, but male *P. fimbriata* (Q) tended to stand their ground. Gravity might assist the female in her attack if she is above the male, and this may help to explain why male *P. labiata* and *P. schultzi* often made detours and approached the female from above, although females often outmanoeuvred them and gained the higher ground first. Forward and twist lunges probably are executed less efficiently by females whose legs are retracted, and this may explain why *P. labiata* and *P. schultzi*, in contrast to *P. fimbriata* (Q), rarely mounted before the female retracted her appendages.

The active, 'business-like' way that males of typical cursorial salicids usually approach females contrasts sharply with the slower, more tentative approach of male *P. labiata* and *P. schultzi*. Males of cursorial species often begin mating after a courtship of only a few minutes (Jackson 1978b), instead of the typical 10–30 min courtship of *P. labiata* and *P. schultzi*. Although they were still much slower and more hesitant than courting males of typical cursorial species, male *P. fimbriata* (Q) were much quicker than *P. labiata* and *P. schultzi*. Courtship duration did not, however, vary significantly among the species of *Portia*; this seemed to result from differences in female behaviour that compensated for the differences in how rapidly males approached. Female *P. fimbriata* (Q) moved about actively, performing hunched legs and propulsive displays, and frequently decamping with the male following; although the male *P. fimbriata* (Q) approached the female relatively rapidly, he had to approach repeatedly because of the females activity. The more cannibalistic females of *P. labiata* and *P. schultzi* spent more time stationary and acted as sit-and-wait predators of a prey (males) that had an active interest in approaching. The defensive behaviour or 'caution' of males seems to make the active style of female *P. fimbriata* (Q) impractical for female *P. labiata* and *P. schultzi*. Instead, hunched legs and propulsive displays of female *P. labiata* and *P. schultzi* are very effective means of indicating their unreceptivity and quickly ending the interaction.

The courtship of *P. fimbriata* (NT, SL) and *P. albimana* was more like that of *P. labiata* and *P. schultzi* than that of *P. fimbriata* (Q). Although cannibalism was not observed, female *P. fimbriata* (NT, SL) did make twist lunges, and males of *P. albimana* and *P. fimbriata* (NT) approached females as cautiously as those of *P. labiata* and *P. schultzi*.

Salticid males generally display more actively than females during intersexual interactions. Males usually begin interactions and display almost continuously until the interaction ends or mating begins. Although females might display intermittently, they often do little more than watch the courting male. In contrast, females of all *Portia* we have studied were relatively active in display during intersexual interactions, and females of *P. labiata* and *P. schultzi* were especially active, drumming and tugging. The active participation of the female *Portia* was perhaps, frequently related to her interest in the male as both a potential mate and a potential meal, so she actively encouraged his approach.

Female receptivity

The males of various species of salticids and other spiders leave sperm plugs over the female's copulatory openings after mating (Austad 1983). Sperm plugs of arthropods seem to function primarily in sperm competition (Parker 1970), and the sperm plugs left by males of the salticid *Phidippus johnsoni* have been shown to hinder insemination by subsequent males that attempt copulation with the female (Jackson 1980a). The plugs of *Portia* presumably function in a similar manner, and their presence on wild-caught females suggests that females in nature, as in the laboratory, mate repeatedly. The adaptive significance of remating for the female may be related to intersexual selection (Jackson 1981); but for cannabalistic female *P. labiata* and *P. schultzi*, obtaining a meal is another factor which is not so obvious for *P. fimbriata* (Q) or most salticids. The tendency of female *P. labiata* and *P. schultzi* to remate more often than female *P. fimbriata* (Q) may be related to the more cannibalistic nature of the females of *P. labiata* and *P. schultzi*, because their greater receptivity gives them more chances to be cannibals.

Interactions between males and subadult females

Male *Portia* cohabited with subadult females and mated with them when they matured. This mating tactic is widespread among salticids and other spiders, including many web spiders (Robinson 1982; Jackson 1986c). Pheromones seem to be important in allowing males of *Portia* to distinguish adult from subadult females (Jackson, unpublished data), but subadult females of *P. labiata* and *P. schultzi* might sometimes drum and tug as the male approaches while courting in a manner indistinguishable from how he courts adult females. The male might even mount and perform pseudocopulations. Subadult females resembled adult females by making forward and twist lunges at males, and sometimes killing and eating them. By drumming and tugging, subadult females seem to practise intraspecific aggressive mimicry to deceive males into responding to them as though they were adults and so luring the males to within range to attack them with prey-specific behaviours. Once cohabitation had begun, however, the pair of *Portia* seemed to reside together harmoniously on the web, but when mating after she matured, the female again resorted to her lethal habits.

The function of courtship

Reproductive isolation, reduction of cannibalism, and intersexual selection are three major factors that have been discussed widely in reference to the evolution of spider courtship. Notwithstanding this, the adaptive significance of courtship in spiders continues to be largely unresolved.

Few hypotheses have held a more important position in biology than that of courtship evolving as an isolating mechanism. There is evidence that reproductive isolation has been important in the evolution of courtship in some spiders (Stratton & Uetz 1981), but support for this hypothesis is scarce in salticids (Jackson 1982a), including *Portia*, and in most groups of animals (Hailman 1977). Despite interspecific differences in courtship, interspecific mating occurred in *Portia*. Although these observations do not preclude the possibility that reproductive isolation has been an important factor in the evolution of courtship in *Portia*, they certainly do not support it.

According to the cannibalism reduction hypothesis (Jackson 1979b), the function of male courtship is to provide the female with information that renders her less likely to treat the male as prey (cannibalism). This hypothesis seems very compelling. In one form or another, it is more frequent than any other in the general literature when spiders are discussed (e.g., Uetz & Stratton 1983). Upon close scrutiny, however, the evidence is not compelling for its importance in salticids and most spiders (Jackson 1980b, 1982a). Because female *P. labiata* and *P. schultzi* were distinctly cannibalistic toward males, the cannibalism reduction hypothesis might seem to be supported, but this is only superficial. Male courtship did not seem to inhibit cannibalism. At most, courtship might be said to elicit prey-specific predatory behaviours, but even this conclusion is difficult to defend because females often began to drum and tug before the male began to display. Females must have rarely mistaken males for some other type of prey, regardless of whether the male courted or not.

Serious study of salticid courtship largely began with Peckham & Peckham (1889) who described the displays of many North American species and used their observations to argue that intersexual selection has been of major importance in the evolution of male behaviour and sexually dimorphic morphology. Although there is insufficient evidence available for evaluating the importance of sexual selection in the courtship of *Portia*, recent studies of other salticids (Jackson 1981) have implicated intersexual selection as an important factor in salticid evolution.

The taxonomic status of *P. fimbriata* populations

The infertility of female *P. fimbriata* (SL), after mating with male *P. fimbriata* (Q), suggests that postcopulatory isolating mechanisms are operating, and these two populations are probably distinct species. *P. fimbriata* (Q) also differed considerably from *P. fimbriata* (NT, SL) in behaviour (including courtship), but *P. fimbriata* (NT) and *P. fimbriata* (SL) were basically similar. Very little is known about *P. fimbriata* (M). '*P. fimbriata*', as currently defined, probably includes two or more closely related species.

Intraspecific and predatory behaviour compared

All species of *Portia* that have been studied used the same repertoire of vibratory displays during encounters with heterospecific prey on webs, but they differed in their display repertoires during intraspecific interactions. *Portia's* intraspecific threat and courtship displays may be more labile in evolution than are the vibratory displays used in predatory encounters with other spiders.

The relatively rapid and smooth movement during intraspecific interaction was almost the antithesis of the generally slow, less conspicuous movement of *Portia* during predatory encounters with other spiders and during normal locomotion. For *Portia* the risk of smooth, rapid movement sacrificing crypsis is presumably overridden by the requirements of the intraspecific encounters. These include the need of the *Portia* to communicate visually with a conspecific and to move rapidly and agilely to avoid eviction or injury by, or to bring about eviction or injury of, the conspecific.

A slow, mechanically moving *Portia* is reminiscent of an African chameleon, but the lizard cannot walk smoothly and rapidly (Guppy & Davison 1982). Intraspecific interactions vividly demonstrate that *Portia*, including the extremely slow and mechanical *P. fimbriata* (Q), is capable of rapid movements similar to those of typical cursorial salticids. Facility at agile, rapid, and visually-directed movement perhaps evolved specifically in the context of intraspecific encounters, and was transferred to predatory behaviour in most salticids.

Evolutionary grades in the genus *Portia*

In locomotory, defensive, predatory, cannibalistic, and intraspecific behaviour, the species of *Portia* segregated into two groups, one of which consisted of *P. fimbriata* (Q), and the other contained all other species. Although either group of *Portia* is very unlikely to have evolved from the other, one group might be viewed as occupying an evolutionary grade (Wilson 1975) through which the ancestors of the other group passed. If not taken too literally, this view might lead to valuable insights into the evolution of *Portia.*

Accepting the basic tenets of the Jackson & Blest hypothesis for the moment, *P. fimbriata* (Q), in some of its characteristics, might occupy an evolutionary grade through which the other studied *Portia* passed during their evolution. The Queensland habitat, with its dense populations of diverse types of web spiders, is the type of habitat in which spiders specialising at invading diverse types of webs might be expected to have evolved. Basic adaptations related to crypsis, including the unusual morphology and locomotory gait of all *Portia*, might have originated in a habitat like the Queensland rain forest where they would be especially effective. Despite all *Portia* being morphologically cryptic, effective crypsis seems to be greatest for *P. fimbriata* (Q), as a result of living in a habitat with very low levels of ambient light. If the ancestral spiders were basically similar to *P. fimbriata* (Q), later lineages moving into other types of habitats might have become effectively less cryptic, and their behaviour may have altered as a result. Basic adaptations related to crypsis and araneophagic web-invasion are unlikely to have evolved first in habitats where they would be less advantageous.

Some of the behaviours of *P. fimbriata* (Q) may not, however, represent an evolutionary grade through which the other *Portia* passed. In particular, cryptic stalking, by which *P. fimbriata* (Q) preys on cursorial salticids, probably evolved in this species alone, and the ancestors of the other *Portia* probably never possessed it. With cryptic stalking, the other *Portia* might be viewed as occupying an evolutionary grade through which the ancestors of *P. fimbriata* (Q) passed. A similar argument might be given for the less pronounced vibratory courtship of *P. fimbriata* (Q) as compared to that of other *Portia.*

To continue using the concept of evolutionary grades, those *Portia* studied should be grouped differently when ovipositional behaviour is considered. If, as discussed earlier, silken egg sacs are ancestral, *P. fimbriata* (NT), and perhaps *P. albimana*, are on an evolutionary grade through which the other *Portia* passed in their evolution. The characteristics of individual *Portia* are probably a mosaic of primitive and derived states. Comparative study may have provided insights into the evolution of the genus, but it will be important to extend this study to other species and populations.

Evolution of the Salticidae

Although the study of *Portia* alone cannot resolve the problems of salticid evolution, knowledge of *Portia* is likely to be pivotal for efforts to understand how the salticids evolved. The specific hypothesis about salticid evolution suggested by the earlier study of *P. fimbriata* (Q) can be reconsidered now in relation to current knowledge of *Portia.*

According to the Jackson & Blest hypothesis, early salticids that were ancestral to all modern salticids were web-builders, web-invaders, vibratory aggressive mimics, predators of spider eggs, and kleptoparasitic predators of insects on alien webs. Each of these behaviours has been found to be well developed in all *Portia* studied, but other findings were conceivable before this comparative study was undertaken. For instance, this set of behaviours might have been found to be only sporadic in the genus. If it had been unique to *P. fimbriata* (Q), for instance, a more strictly adaptationist explanation would have seriously rivalled the hypothesis. It could have been argued that these behaviours were largely the product of the unique selection pressures in the habitat of *P. fimbriata* (Q), especially the super-abundance of web spiders. The Jackson & Blest hypothesis would not have been falsified so easily, but certainly its credibility would have been diminished. Instead, a continued exploration of the implications of the hypothesis, viewing *Portia* as occupying an evolutionary grade through which other salticids have passed in their evolution, is justified.

Portia spun large, distinctive webs for varied uses (e.g., for moulting, mating, and oviposition). Insects may be captured on the web occasionally, and neighbouring spiders may stray into the web and become prey of the *Portia*. Perhaps advantages such as these could account for the evolution of web-building, if *Portia* had had strictly cursorial ancestors; however, the alternative hypothesis that *Portia* conserved web-building from non-salticid web-building ancestors that used webs to capture insects and co-opted the webs for other functions is more plausible. It is also interesting that *Portia* never spun enclosing nests of the sort spun by many cursorial salticids and of the sort *Portia* might have been expected to spin had its ancestors been strictly cursorial.

According to the hypothesis, acute vision evolved in conjunction with araneophagic web-invasion, then became a powerful pre-adaptation for efficient cursorial predation on insects, with most salticids quickly making the transition to a cursorial life-style. Highly developed crypsis was suggested as an important factor favouring the retention of web-invading behaviour by *Portia*. Although all *Portia* are highly cryptic, effective crypsis seems to vary in important ways as a result of the different habitats occupied by *Portia*, and apparently this has had far-reaching effects on predatory and other behaviour. Remarkably, as predicted, the *Portia* that have less effective crypsis were more efficient cursorial predators of insects. This may be largely an effect of changes in locomotory behaviour rather than an adaptive alteration. Changes in locomotory behaviour may also have diminished the effectiveness of these spiders as araneophagic web-invaders.

However, their increased effectiveness as cursorial predators of insects seems not to be entirely incidental. It is especially noteworthy that the less effectively cryptic *Portia* were more likely to pursue cursorial insects than were more effectively cryptic *P. fimbriata* (Q), which suggests that the former have a greater interest in this type of prey. The less effectively cryptic *Portia* may have taken the first steps toward evolving into cursorial insect predators (see Jackson & Hallas 1986).

It is interesting that *Portia* was not found to be as much a predator of salticids as it is a web-builder and a web-invader: cryptic stalking is characteristic of *P. fimbriata* (Q), only. Specialised behaviours used to capture cursorial salticids may have evolved uniquely in a habitat with superabundant cursorial salticids available as prey, and these behaviours were obviously not considered to be characteristic of salticid ancestors in the Jackson & Blest hypothesis.

Vibratory courtship and other aspects of the reproductive and intraspecific behaviour of *Portia*, as discussed above, may have been conserved from non-salticid web spider ancestors, but there are other behavioural and morphological characteristics of *Portia* that are not so readily accounted for by the Jackson & Blest hypothesis. Indirect sperm induction and copulation in Position 2 have been mentioned before, but the origins of trends among spiders in sperm induction and copulation methods are poorly understood. Also, in the Lycosidae (another family consisting primarily of cursorial species), the Hippasinae are web-builders, and web-building has been considered primitive in the Lycosidae. Yet web-building lycosids, like web-building salticids, practise indirect sperm induction and mate in Position 2 like cursorial lycosids (Job 1974).

Web spiders usually have three tarsal claws and lack claw tufts. Cursorial spiders often, but not always, have claw tufts but only two claws. The third claw seems to be readily lost by spiders; both three and two-clawed species occur in some families, and, in a few species, individuals lose the third claw during post-embryo development (Homann 1971). The third claw assists at least some web spiders in grasping threads (Foelix 1970). Claw tufts allow cursorial spiders to climb up rocks, leaves, and other smooth surfaces; but *Portia* is both a web spider and a cursorial spider and, like other salticids, is two-clawed and has claw tufts. Although as a two-clawed web spider *Portia* is aberrant, absence of a third claw does not seem to seriously hinder its locomotion on webs.

An attempt at this stage to decide whether the Jackson & Blest hypothesis is true or false is not justified, but findings from this study have, overall, increased our confidence in it.

Complexity and the transitional status of *Portia*

By almost any criterion (see Hinegardner & Engelberg 1983), *Portia* is an unusual and complex spider. In its behaviour, rivals are indeed difficult to find. *Portia* has been shown to be a web-builder, a cursorial spider, an araneophagic web invader, an aggressive mimic, a kleptoparasite, and a predator specialised in opening egg sacs and eating and eating spider eggs. It spun two types of webs, and individual females made two types of egg sacs. Each individual used a repertoire of vibratory behaviours in predatory encounters on webs. *P. fimbriata* (Q) used special predatory behaviours to capture other salticids. Females of the other species used special predatory behaviours to capture conspecifics. Subadult females seemed to practise intraspecific aggressive mimicry. Each species performed diverse intraspecific displays and practised courtship versatility. Copulation might occur with the female standing on a non-silk substratum, hanging in a web, or suspended on a dragline. Crypsis was enhanced by special postures and modes of locomotion. Specialised defensive behaviours (wild leaps) were performed by some species, and more behaviours could be added to the list.

The list can be extended to morphology and physiology. *Portia* has a venom with unusual potency to spiders, its legs autotomise with unusal ease, and the spiders have unusual hairs and other structures on the abdomen and legs (Murphy & Murphy 1983; Foelix et al. 1984; Wanless 1984). The eyes are complex and possess unique features. All *Portia* mimic detritus in their morphology. And the list could go on.

Yet *Portia* is, by some criteria, considered to be primitive. According to the Jackson & Blest hypothesis, *Portia* is considered to be more or less representative of an early transitional grade in salticid evolution. Is it merely ironic that this exceptionally complex salticid is also considered to be primitive? Perhaps not. Perhaps it is especially among transitional species that unusually complex animals should be expected.

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Appendix 1

Spiders and insects used as prey in tests with *Portia*, listed alphabetically by species. When possible, identifications are at least tentatively to genus and species; otherwise, prey are designated as sp. 1, etc. At least one species of *Portia* was observed to eat each species of prey listed. Information will be given in the following order: species of prey, order (for insects only), family, description of prey, locality of origin of prey, species of *Portia* used in tests with prey, types of tests in which prey was used. A, B, C: used in Type A, B, and C tests, respectively. Most spiders were used in informal tests either exclusively or in addition to being used in formal tests. ANU: laboratory culture, Australian National University. CS: spins cribellate sticky web. CU: cursorial spider. DW: spins dome-shaped web. DSW: makes densely spun sheet web. E: eggs of the spider were used in test. ES: spins non-cribellate sticky web. F: no web present during test. GR: Game Reserve. K: insect put in cage with *Portia* on alien web. KP: specialised kleptoparasitic inhabitant of webs of other species. N: cursorial spider in nest during test. NP: National Park. NR: National Reserve. NS: spins non-sticky web. OW: spins orb web. P: web of *Portia* present during test. Paf: *P. africana*. Pal: *P. albimana*. Pf: *P. fimbriata*. Pl: *P. labiata*. Ps: *P. schultzi*. S: spider dead and in alien web during test (alien web: not spun by *Portia*). SS: social spider (communal webs). SSW: makes sparsely spun sheet web. SW: spins space web. TW: spins silken tube with lines radiating from mouth. UC: laboratory culture, University of Canterbury. W: prey-spider in its own web during test. Z: prey spider in its own web in nature during test; otherwise, all tests were with captive spiders. M: *Portia* from Malaysia; NT: *Portia* from Northern Territory; etc.: see text. Unless stated otherwise, all holometabolous insects are adults.

Achaearanea camura (Simon). Theridiidae. SW, ES. Australia: Cairns. Pf(NT), Pf(Q). A, B, C, E, P, W.

Achaearanea mundula (L. Koch). Theridiidae. SW, ES. Sri Lanka: Peradeniya. Pf(SL), Pl(SL). P, W.

Achaearanea ventricosa (Rainbow). Theridiidae. SW, ES. Australia: Cairns. Pf(NT), Pf(Q). P, W.

Achaearanea sp. 1. Theridiidae. SW, ES. New Zealand: Christchurch. Pal, Pf(Q), Pf(SL), Pl, Ps. A, B, C, E, P, W.

Achaearanea sp. 2. Theridiidae. SW, ES. Sri Lanka: Peradeniya. Pf(SL), Pl(SL). P, W.

Agelena leucopyga Pavesi. Agelenidae. DSW, NS, SS. Kenya: Nanyuki. Pf(Q), Pl, Ps. B, W.

Anzacia gemmea (Dalmas). Gnaphosidae. CU. New Zealand: Christchurch. Pf(Q), Pl(SL), Ps. B, F, P.

Arachnura feredayi (L. Koch). Araneidae. OW, ES. New Zealand: Christchurch. Pf(Q), Pl(SL). B, W.

Araneus pustulosus (Walckenaer). Araneidae. OW, ES. New Zealand: Christchurch, Hari Hari. Pal, Pf(NT), Pf(Q), Pf(SL), Pl(SL), Ps. B, E, P, W.

Argyrodes flavescens O. P.-Cambridge. Theridiidae. KP. Sri Lanka: Peradeniya. Pl(SL). W.

Argyrodes nasutus O. P.-Cambridge. Theridiidae. KP. Sri Lanka: Kaneliya. Pal, Pf(SL), Pl(SL). W.

Ariadna sp. 1. Segestriidae. TW, NS. New Zealand: Arthur's Pass. Pf(Q), Pl(SL), Ps. P, W.

Badumna candida (L. Koch). Amaurobiidae. DSW, CS, SS. Australia: Mareeba. Pal, Pf(NT), Pf(Q), Pf(SL), Pl(SL), Ps. B, E. W.

Badumna insignis (L. Koch). Amaurobiidae. SSW, CS. Australia: Cairns. Pf(NT), Pf(Q). W.

Badumna longinquus (L. Koch). Amaurobiidae. SSW, CS. New Zealand: Christchurch. Pal, Pf(NT), Pf(Q), Pf(SL), Pl(SL), Ps. A, B, C, E, P, W.

Bavia aericeps Simon. Salticidae. CU. Australia: Cairns Pf(Q). B, F.

Calliphora vicina (Robineux-Desvoidy). Diptera. Calliphoridae. UC. Pal, Pf(NT), Pf(Q), Pf(SL), Pl(SL), Ps. B, F, K, P.

Cheiracanthium stratioticum L. Koch. Clubionidae. CU. New Zealand: Christchurch. Pf(Q), Pl(SL). B, F, N.

Cambridgea antipodiana (White). Stiphidiidae. DSW, NS. New Zealand: Christchurch. Pf(Q), Pf(SL), Pl(SL), Ps. B, C, E, P, W.

Clubiona cambridgei (L. Koch). Clubionidae. CU. New Zealand: Christchurch. Pf(Q), Pf(SL), Pl(SL), Ps. B, E, F, N, P.

Clubiona sp. 1. Clubionidae. CU. Australia: Canberra. Pf(NT), Pf(Q). B, F, P.

Cosmophasis micarioides (L. Koch). Salticidae. CU. Australia: Cairns. Pf(NT), Pf(Q), Ps. F, N.

Cosmophasis sp. 1. Salticidae. CU. Kenya: Malindi. Paf, Ps. E, F, N.

Ctenopseustis sp. Lepidoptera. Tortricidae. New Zealand: Christchurch. Pf(Q), Pf(SL), Pl(SL), Ps. B, F, K, P.

Cycloctenus westlandicus Forster. Cycloctenidae. CU. New Zealand: Westport. Pf(Q), Pl(SL). F, P.

Cyrtophora citricola (Forskal). Araneidae. DW, NS. Kenya: Malindi. Ps. Z.

Cyrtophora sp. 1. Araneidae. SW, NS. Malaysia: Pasoh. Pl(M). Z.

Diaea sp. 1. Thomisidae. CU. New Zealand: Arthur's Pass. Pf(Q), Pl(SL), Ps. F, P.

Dolomedes minor L. Koch. Pisauridae. CU. New Zealand: Christchurch. Pf(Q), Pf(SL), Pl(SL), Ps. F, P.

Drosophila hydei (Sturtevant). Diptera. Drosophilidae. UC. Pf(Q), Pf(SL), Pl(SL), Ps. B, F, K, P.

Drosophila immigrans (Sturtevant). Diptera. Drosophilidae. UC. Pal, Pf(NT), Pf(Q), Pf(SL), Pl(SL), Ps. B, F, K, P.

Drosophila melanogaster (Meigen). Diptera. Drosophilidae. ANU, UC. Pal, Pf(NT), Pf(Q), Pf(SL), Pl(SL), Ps. B, F, K, P.

Dysdera crocata (L. Koch). Dysderidae. CU. New Zealand: Christchurch. Pf(Q), Pl(SL), Ps. E, F, N, P.

Euophrys parvula Bryant. Salticidae. CU. New Zealand: Kumara Junction. Pf(Q), Pl(SL). B, F.

Euryattus bleekeri (Doleschall). Salticidae. CU. Australia: Cairns. Pf(Q). B, F.

Euryattus sp. 1. Salticidae. CU. Australia: Cairns. Pf(Q), Pl(SL), Ps. B, F.

Fecenia macilenta (Simon). Psechridae. OW, ES. Sri Lanka: Kaneliya. Pl(SL). Z.

Galleria melonella (Linnaeus). Lepidoptera. Pyralidae. ANU. Pf(NT), Pf(Q). B, F, K, P.

Gasteracantha minax (Thorell). Araneidae. OW, ES. Australia: Canberra. Pf(NT), Pf(Q). B, W.

Gasteracantha sp. 1. Araneidae. OW, ES. Malaysia: Pasoh. Pl. W.

Gasteracantha sp. 2. Araneidae. OW, ES. Kenya: Mombassa. Ps. W.

Herennia ornatissima (Doleschall). Araneidae. OW, ES. Sri Lanka: Peradeniya. Pl(SL). Z.

Holoplatys sp. 1. Salticidae. CU. New Zealand: Christchurch. Pf(Q), Pl(SL), Ps. B, E, F, N, P.

Inola subtilis Davies. Pisauridae. DSW, NS. Australia: Cairns. Pf(NT), Pf(Q), Pl(SL). B, E, W.

Ischnothele karschi (Bösenberg and Lenz). Dipluridae. DSW, NS. Kenya: Malindi. Ps. W.

Lagnus kochi (Simon). Salticidae. CU. Australia: Cairns. Pal, Pf(NT), Pf(Q), Pf(SL), Pl(SL), Ps. A, B, E, F, N, P.

Lampona sp. 1. Gnaphosidae. CU. Australia: Canberra. Pf(NT), Pf(Q). F.

Latrodectus katipo Powell. Theridiidae. SW, ES. New Zealand: Christchurch. Pf(Q), Pl(SL), Ps. B, E, W.

Lycosa sp. 1. Lycosidae. CU. Australia: Canberra. Pf(NT), Pf(Q). F, P.

Lycosa sp. 2. Lycosidae. CU. New Zealand: Christchurch. Pf(Q), Pf(SL), Pl(SL), Ps. E, F, P.

Marpissa marina Goyen, Salticidae. CU. New Zealand: Christchurch. Pf(NT), Pf(Q), Pf(SL), Pl(SL), Ps. B, F, N.

Melancha sp. 1. Lepidoptera. Noctuidae. New Zealand: Christchurch. Pal, Pf(NT), Pf(Q), Pf(SL), Pl(SL), Ps. B, F, K, P.

Menemerus sp. 1. Salticidae. CU. Kenya: Kisumu. Paf. F, N.

Micromus tasmaniae (Walker). Neuroptera. Hemerobiidae. New Zealand: Christchurch. Pal, Pf(Q), Pf(SL), Pl(SL), Ps. B, F, K, P.

Miturga sp. 1. Miturgidae. CU. New Zealand: Christchurch. Pf(Q), Pf(SL), Pl(SL), Ps. B, F, P.

Mopsus mormon Karsch. Salticidae. CU. Australia: Cairns. Pf(NT), Pf(Q). B, F.

Mopsus sp. 1. Salticidae. CU. Malaysia: Pasoh. Pl(M). E, F.

Musca domestica (Linnaeus). Diptera. Muscidae. ANU, New Zealand: Christchurch. Pal, Pf(NT), Pf(Q), Pf(SL), Pl(SL), Ps. A, B, F, K, P.

Neoramia setosa (Bryant). Agelenidae. SSW, CS. New Zealand: Christchurch. Pf(Q), Pf(SL), Pl(SL), Ps. B, E, P, W.

Nephila edulis (Labillardière). Araneidae. OW, ES. Australia: Canberra. Pf(NT), Pf(Q). B, W.

Nephila maculata (Fabricius). Araneidae. OW, ES. Australia: Cairns. Pf(NT), Pf(Q). W.

Nephila sp. 1. Araneidae. OW, ES. Kenya: Mombassa. Paf, Ps. W.

Nephilengys malabarensis (Walckenaer). Araneidae. OW, ES. Sri Lanka: Kaneliya. Pl(SL). Z.

Olios diana (L. Koch). Sparassidae. CU. Australia: Mareeba. Pf(NT), Pf(Q), Pl(SL), Ps. B, F.

Oxyopes sp. 1. Oxyopidae. CU. New Zealand: Christchurch. Pf(NT), Pf(Q). B, F.

Phidippus johnsoni Peckham & Peckham. Salticidae. CU. U.S.A.: San Francisco. Pf(Q), Pl(SL). B, F. N.

Philoponella congregabilis (Rainbow). Uloboridae. OW, CS, SS. Australia: Canberra. Pf(NT), Pf(Q). B, E, W.

Philoponella variabilis (Keyserling). Uloboridae. OW, CS, SS. Australia: Cairns. Pal, Pf(NT), Pf(Q), Pf(SL), Pl(SL), Ps. B, E, W.

Philoponella sp. 1. Uloboridae. OW, CS. Kenya: Malindi. Paf, Ps. E, W.

Pholcus ancoralis L. Koch. Pholcidae. SW, NS. Australia: Cairns. Pf(Q). B, W.

Pholcus phalangioides (Fuesslin). Pholcidae. SW, NS. Australia: Canberra, New Zealand: Auckland, Murchison. Pf(NT), Pf(Q), Pf(SL), Pl(SL), Ps. B, C, E, P, W.

Porrhothele antipodiana (Walckenaer). Dipluridae. DSW, NS. New Zealand: Kaikoura. Pf(Q), Pl(SL), Ps. B, W.

Psechrus torvus (O. P. Cambridge). Psechridae. SSW, ES. Sri Lanka: Kaneliya. Pl(SL). W.

Psilochorus sphaeroides (L. Koch). Pholcidae. SW, NS. Australia: Cairns. Pf(Q). B, E, W.

Pystira orbiculata (Keyserling). Salticidae. CU. Australia: Cairns. Pf(Q). B, F.

Rhene sp. 1. Salticidae. CU. Malaysia: Kuala Lumpur. Pf(M), Pl(M). F, P.

Rhene sp. 2. Salticidae. CU. Sri Lanka: Peradeniya. Pf(SL), Pl(SL). F.

Rhene sp. 3. Salticidae. CU. Sri Lanka; Kaneliya. Pf(SL), Pl(SL), F.

Saitis sp. 1. Salticidae. CU. Australia: Cairns. Pf(Q). B, F.

Steatoda sp. 1. Theridiidae. SW, ES. New Zealand: Christchurch. Pf(Q), Pl(SL), Ps. B, E, P, W.

Stegodyphus mimosarum (Pavesi). Eresidae. DSW, CS, SS. Kenya: Samburu GR. Pf(Q), Pf(SL), Pl(SL), Ps. B, P, S, W.

Stegodyphus sarasinorum Karsch. Eresidae. DSW, CS, SS. Sri Lanka: Werawila. Pal, Pf(SL), Pl(SL). W.

Supunna picta (L. Koch). Clubionidae. CU. New Zealand: Christchurch. Pf(Q), Pl(SL), Ps. F.

Sidymella sp. 1. Thomisidae. CU. New Zealand: Christchurch. Pf(Q), Pl(SL). F.

Tetragnatha sp. 1. Tetragnathidae. OW, ES. New Zealand: Cass. Pf(Q), Pl(SL), Ps. B, W.

Tegenaria domestica (Clerck). Agelenidae. DSW, NS. New Zealand: Christchurch. Pf(NT), Pf(Q), Pl(SL), Ps. B, C, P, W.

Thiania demissa (Thorell). Salticidae. CU. Malaysia: Pasoh. Pf(M), Pl(M). F.

Thyene ogdeni Peckham & Peckham. Salticidae. CU. Kenya: Meru NP. Paf. F.

Thyene sp. 1. Salticidae. CU. Kenya: Tsavo NP. Paf, Ps. F.

Trichocera annulata (Meigen). Diptera. Trichoceridae. New Zealand: Christchurch. Pf(Q), Pf(SL), Pl(SL), Ps. B, F, K, P.

Trite auricoma (Urquhart). Salticidae. CU. New Zealand: Christchurch. Pal, Pf(NT), Pf(Q), Pf(SL), Pl(SL), Ps. A, B, E, F, N, P.

Trite planiceps Simon. Salticidae. CU. New Zealand: Christchurch. Pf(NT), Pf(Q), Pf(SL), Pl(SL), Ps. A, B, E, F, N, P.

Viciria hasselti (Thorell). Salticidae. CU. Malaysia: Kuala Lumpur. Pf(M), Pl(M). F.

Sp. 1. (Astianae). Salticidae. CU. Australia: Cairns. Pf(Q), Pl. F, N.

Sp. 2. Diptera. Tipulidae. New Zealand: Christchurch. Pal, Pf(Q), Pf(SL), Pl(SL), Ps. B, F, K, P.

Sp. 3. Larva. Lepidoptera. Noctuidae. New Zealand: Christchurch. Pf(Q), Pl(SL), Ps. B, F, K, P.

Sp. 4. Lepidoptera. Noctuidae. Malaysia: Pasoh. Pl(M). F, P.

Sp. 5. Lepidoptera. Noctuidae. Kenya: Malindi. Ps. F, P.

Sp. 6. Neuroptera. Unknown. Australia: Townsville. Pf(NT). F, K.

Sp. 7. Neuroptera. Unknown. Kenya: Malindi. Paf, Ps. F, K, P.

Sp. 8. Isoptera. Unknown. Malaysia: Pasoh. Pl(M). F, P.

Sp. 9. Isoptera. Unknown. Kenya: Malindi. Paf, Ps. F, K, P.