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The biology of *Phyaces comosus* (Araneae: Salticidae), predatory behaviour, antipredator adaptations and silk utilization

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Introduction

The salticids are generally considered to be the classic examples of cursorial hunting spiders which, instead of building webs to ensnare their prey, use acute vision to stalk, chase, and leap on active insects (Land, 1969a,b). However, the evolutionary origins of the salticids and their unique, complex eyes are poorly understood.

Recent studies of *Portia* (Jackson & Blest, 1982; Jackson & Hallas, in press), an unusual salticid genus from Africa, Asia, and Australia, suggest that questions about salticid evolution may not be as intractable as they formerly seemed. Although it moves with apparent ease across open ground and captures prey as a cursorial predator, *Portia** also spins prey-capture webs and invades diverse types of alien webs to prey on the host spiders. Lacking acute vision, typical web-building spiders detect and localize prey and predators by interpreting vibratory disturbances of their webs. Using specialized movements of its legs and palps, *Portia* creates vibrations of the silk that deceive the host spider and assist with predation.

Portia also feeds kleptoparasitically on insects ensnared in alien webs and eats the eggs of the host spider. Eggs are an unusual prey for a salticid, since they are non-motile and salticids are generally envisaged as predators of motile arthropods.

Morphological specializations give *Portia* the appearance of detritus in webs, probably affording it protection from visually hunting predators. Normally, locomotion is slow and 'mechanical', rendering *Portia* difficult to recognize even when moving. When inactive in a web, *Portia* adopts a specialized posture, the cryptic rest posture, with palps retracted to beside the chelicerae and legs retracted to beside and under the body, thus obscuring the outlines of appendages. Away from webs, *P. fimbriata* from Queensland has a specialized means of stalking and catching typical cursorial salticids, a prey which, like *Portia*, has acute vision. This behaviour is unique to this species. When stalking salticids, but not other prey, *P. fimbriata* exaggerates the slow, mechanical nature of its locomotion, retracts its palps as in the cryptic rest posture and ceases to advance when the salticid faces. Apparently, as a result of these behaviours and the cryptic morphology of *P. fimbriata*, salticids fail to recognize *P. fimbriata* as an approaching predator.

Although typical cursorial salticids neither spin webs nor use silk in prey capture, they build silken nests in which they moult, oviposit, mate, and generally stay at night and during other periods of inactivity. A salticid in a nest is probably safe from attacks by many of its predators. However, *P. fimbriata* preys on salticids it locates in nests; it vibrates on the silk, enticing the salticids to come out, or waits patiently until the salticid leaves the nest spontaneously.

Although it is a specialized and complex animal, *Portia* has some morphological characters which are apparently pleisiomorphic (Wanless, 1978, 1984). The occurrence of pleisiomorphic traits in *Portia* raised the intriguing possibility that some of the behaviours of *Portia* are also pleisiomorphic. Recognition of this possibility led to a hypothesis, presented in detail elsewhere (Jackson & Blest, 1982), that the Salticidae evolved from web-building spiders with poorly

*Except when ambiguity is likely to result *Portia* species will be referred to simply by genus i.e. *Portia* instead of *Portia* spp.

developed vision and that acute vision evolved originally in a spider similar to *Portia* which became an araneophagic predator proficient at invading diverse types of webs.

It was proposed that some, but not all, of the unusual traits of *Portia* have been inherited from a common ancestor of *Portia* and all other salticids, and that these traits have been lost by most salticids but conserved in members of the genus *Portia*. The specialized manner in which *P. fimbriata* stalks ordinary salticids may have evolved secondarily and uniquely in this species.

Varied types of information are potentially useful for evaluating the Jackson & Blest hypothesis, comparative studies of predatory behaviour and silk utilization in other salticid genera being especially important. *Phyaces comosus* Simon is of special interest because this small salticid, like *Portia*, is a highly cryptic detritus mimic; but *Portia* and *Phyaces* belong to different subfamilies (Wanless, 1986). An opportunity arose to study *P. comosus*, and the results of this study will be reported here.

Materials and Methods

Observations were carried out in the laboratory in Christchurch on a female *P. comosus* collected at Peradeniya, Sri Lanka by F. R. Wanless. Maintenance and testing procedures, terminology, and conventions used in describing behaviour were as in earlier studies (Jackson & Hallas, in press). Various potential nest sites were provided in the form of green leaves, dry dead leaves, stems, pieces of bark, and similar objects spread about in the cage of the *P. comosus*. The spiders and insects with which *P. comosus* was tested and the types of tests for which each species was used are indicated in Table 1 (for additional information, see: Jackson & Hallas, in press).

Cryptic appearance

Because of its unusual morphology and a specialized posture, *P. comosus* was exceedingly well concealed from human observers while standing on dead brown leaves; and on green leaves it was

Table 1. Spiders and insects (*Drosophila* only) used as potential prey or as sources of eggs, webs, and nests in tests with *Phyaces comosus*, listed alphabetically by species. A: adult spider or insect; body lengths: salticids (10-14 mm), insect (*c.* 2 mm). CF: *P. comosus* put into cage with spider or insect; cage free of nests and webs. CP: spider or insect put in cage with *P. comosus* in its nest. CS: spins cribellate sticky web. Cu: non-salticid cursorial spider. ES: cribellate sticky web. J: juvenile spider; body length: *c.* 2 mm. NE: eggs in vacant nest. NO: nest occupied by host spider, but no eggs present. NS: non-sticky web. NSE: nest with eggs, occupied by host spider. NV: vacant nest with no eggs. Or: Oregon strain (functional wings). S: typical cursorial salticid. SS: social species; builds communal web. Vg: vestigial winged strain (flightless). WB: web-building spider. WE: eggs in vacant web. WO: web occupied by host spider. WI: insect on vacant web of *S. mimosarum*. WV: vacant web with no eggs.

Species	Family	Description	Types of Tests
<i>Achaearanea</i> sp. 1	Theridiidae	A,WB,ES	WE,WV
<i>Araneus pustulosa</i> (Walckenaer)	Araneidae	A,WB,ES	WV
<i>Badumna longinquus</i> (L. Koch)	Amaurobiidae	J,WB,CS	WO
<i>Bavia aericeps</i> (Simon)	Salticidae	A,S	NE,NSE,NV
<i>Cambridgea antipodiana</i> (White)	Stiphidiidae	A,WB,NS	WV
<i>Clubiona cambridgei</i> (L. Koch)	Clubionidae	A,Cu	NSE
<i>Dolomedes minor</i> (L. Koch)	Pisauridae	J,Cu	CF,CP
<i>Drosophila melanogaster</i> Or (Meigen)	Drosophiliidae	A	CF,CP,WI
<i>Drosophila melanogaster</i> Vg (Meigen)	Drosophiliidae	A	CF,CP,WI
<i>Mopsus mormon</i> (Karsch)	Salticidae	A,S	NSE
<i>Stegodyphus mimosarum</i> (Pavesi)	Eresidae	A,WB,CS,SS	WV
<i>Trite auricoma</i> (Urguhart)	Salticidae	J,S	CF,CP,NO

conspicuous but unanimal-like in appearance, resembling instead a speck of dust or a minute bit of detritus.

P. comosus always stood with its legs and palps held very close to the body. Often tarsi II and III were held slightly under the body. Tarsi I tended to be just in front of the chelicerae. The palps were held very close to the front of the chelicerae, sometimes pressing against them. The femur of each palp angled up, with the remainder of the palp angling straight down. When mildly disturbed, *P. comosus* often pulled its appendages in even closer to the body and remained inactive.

Locomotion

While walking, *P. comosus* remained highly cryptic. Its legs moved in short, slow, barely noticeable steps and remained close to the body. Sometimes legs and palps were held closer to the body while stepping than while standing. While stepping, the spider's body rocked forward and backward in a characteristic 'bouncing' fashion (Fig. 1). Usually, the spider rocked forward-backward-forward, making a net advance of $c. \frac{1}{2}$ a body length, and a pause of 1–10 s occurred before the next bout started.

Although it occasionally leapt as far as 4 body lengths across barriers such as spaces of a few millimetres between stems, *P. comosus* usually made detours by, for example, returning to the base of the stem then walking across to the base of the other stem.

No waving of legs occurred either while stepping or during pauses between bouts of stepping; but an inconspicuous form of palp waving sometimes occurred. As the waving palps moved up and down, in matching phase, a fraction of a millimetre, they remained close to the front of the chelicerae. When chased vigorously with a brush, *P. comosus* stopped rocking and stepped more rapidly than during normal locomotion. Nevertheless, its movements continued to be much slower than the normal locomotion of typical salticids.

If forced on to a web, *P. comosus* always left immediately. Locomotion across non-sticky webs appeared laboured, and *P. comosus* adhered to cribellate and ecribellate sticky webs, eventually freeing itself after biting at threads and pulling forcefully with its legs.

Nests

The spider never built a nest unless it had access to two dead leaves, with their surfaces only a few millimetres apart, between which to spin. A thick layer of silk was spun against the surface of each leaf. On each of two opposing sides, a more sparsely woven sheet connected the two thick sheets and held the leaves together. The resulting nest had the shape of a flattened tube, $c. 10$ mm long, 7 mm wide and 2 mm deep and open at both ends. Two to six rivets (bands of silk $c. 2$ mm long, 0.5–1.0 mm wide, strung between the leaves) were widely spaced about the nest. The two leaves were very tightly bound by the silk of the rivets and the sides of the nest.

Predatory behaviour

Although *Drosophila* were pursued only occasionally (vestigial: 9 or 16 tests; Oregon: 3 of 12 tests), *P. comosus* readily pursued salticids (6 of 9 tests). However, essentially the same predatory behaviours occurred with both prey-types. *Dolomedes* were ignored by the *P. comosus* (8 tests).

P. comosus usually began to approach its prey, in its usual rocking gait, from 25–35 mm away; and its rocking movements became progressively slower and of lower amplitude as it got closer, especially as it came to within 5–10 mm. There was no tendency for *P. comosus* to behave differently depending on prey orientation. Generally, *P. comosus* did not wave its palps while pursuing its prey.

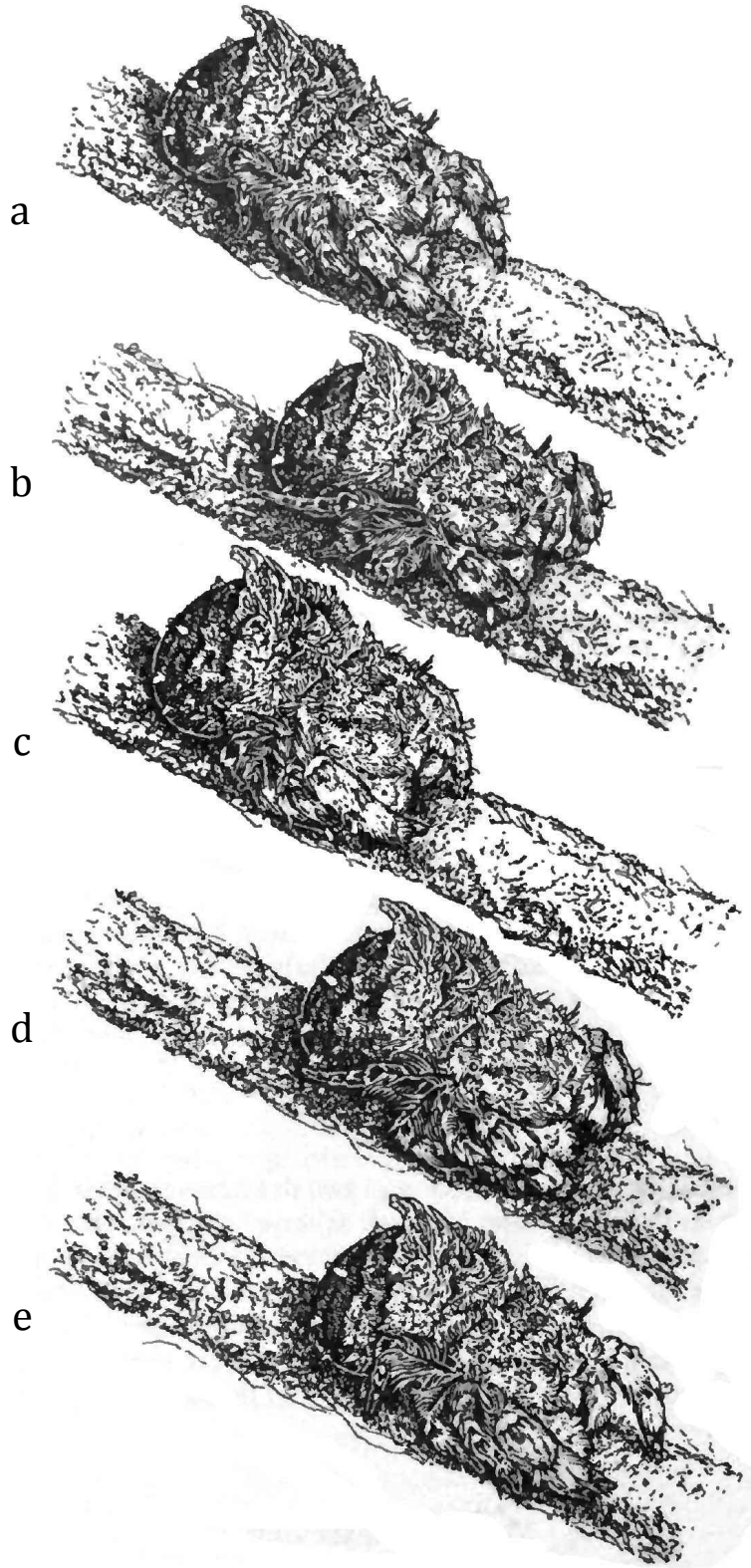


Fig. 1. *Phycas comosus* Simon. Walking pattern on a stem: (a) Initial position as begins to rock body forward. (b) Maximum forward position before begins to rock backward. (c) Maximum rearward position before starting to move forward again. This position is slightly forward of the initial position. (d) Maximum forward position at the end of the second rock forward. This position is slightly beyond the maximum forward position during the first motion. Barely perceptible shifting of legs across the substrate occurred as the spider rocked forward and backward. (e) Legs are shifted forward as the spider prepares for the next bout of rocking.



Fig. 2. *Phyaces comosus* Simon eating an egg of a much larger salticid (*Bavia aericeps* Koch). Its fangs are piercing the chorion of the egg. The eggs are almost equal in size to the *P. comosus*.

When $\frac{1}{2}$ –1 body length away, *P. comosus* stood inactive for 1–10 s, occasionally longer, then suddenly lunged forward and grasped its prey. There were no evident preliminaries to lunging (legs were not lifted, etc.). Prey was grasped with chelicerae alone. *P. comosus* was observed to capture a *D. melanogaster* only twice (vestigial winged in both cases), but all pursued salticids were captured.

P. comosus never entered webs voluntarily and never attacked juvenile web spiders (24 tests), eggs (4 tests), or ensnared *Drosophila* (10 tests). If it accidentally contacted the edge of a web, it moved away immediately (2 tests).

P. comosus always responded distinctively to the nests of cursorial spiders, whether occupied (8) or vacant (3). *P. comosus* intermittently chewed (opened and closed its chelicerae against the silk) or tugged (lifted its cephalothorax once or twice while holding onto the silk with its chelicerae) and gradually made a hole into which it placed legs I. The hole was slowly enlarged as *P. comosus* burrowed its way into the interior of the nest (time elapsing from initial contact with

the nest: 0.2–3 h). The 4 small juvenile salticids tested left their nests as *P. comosus* entered, but there were no evident responses by the 3 adult salticids and the one adult clubionid tested. If no eggs were present in the nest, the *P. comosus* eventually left (maximum latency: 4h); but *P. comosus* fed if eggs were present. Additional layers of silk separated eggs from the inner chamber of the nest; and to feed, *P. comosus* burrowed through this layer then walked on to and pierced an egg with its fangs. After feeding, *P. comosus* remained in the nest near or on the eggs for up to 6 days, sometimes feeding on one or two additional eggs. Host spiders were 8–14 mm in body length, and their eggs were almost as large as the *P. comosus* (Fig. 2).

Discussion

Crypsis

As a result of its specialized locomotory behaviour and its unusual morphology and posture, *P. comosus* is a decidedly cryptic spider, closely resembling small particles of detritus that are common on the ground and on leaves in the understory of the Sri Lankan rain-forest. By choosing dead, dried leaves for nest sites, *P. comosus* is able to move out on to a background against which it is maximally concealed when it ventures forth from its nest.

Locomotion

Functionally, the locomotory behaviour of *P. comosus* is comparable to that of *Portia* and many other highly cryptic, leaf-mimicking and stick-mimicking arthropods (Robinson, 1969). Locomotion occurs in a manner that minimizes the extent to which the animal's specialised camouflage is sacrificed, but there are major differences in the motor patterns employed. The legs and palps of *Portia* move in a unique 'choppy' fashion; *P. comosus* steps in a completely different forward-and-backward rocking gait.

The normal locomotion of most salticids is rapid and agile, and leaps across barriers are made readily. *Portia* and especially *P. comosus* are reluctant to leap. *Portia*, however, unlike *P. comosus*, is quite capable of moving agilely and rapidly if stressed. Although it walks faster and abandons its bouncy gait when chased vigorously, *P. comosus* continues to move atypically slowly for a salticid. *P. comosus*, like African chameleons (Guppy & Davison, 1982) seems to be incapable of running. It is difficult to understand the evolution of an inability to retreat rapidly from predators. Perhaps crypsis is so extreme in *P. comosus* that rapid escape is rarely required. It would be interesting to look for structural or physiological constraints which might hinder rapid movements by *P. comosus*.

Predatory behaviour

The predatory behaviour of *P. comosus* consists primarily of using its normal locomotory gait to approach the prey, slowing down when close, and making a sudden lunge from close range. The manner in which *P. comosus* stalks prey, like its specialized gait during normal locomotion is consistent with crypsis and most probably maintains its concealment from visually hunting predators; but it is inefficient as a means of capturing motile insects (*Drosophila*). It is efficient, however, against a type of prey which is itself a visually hunting predator, namely other salticids. Both *P. comosus* and *Portia fimbriata* have a pronounced tendency to pursue salticids and a relatively weak tendency to pursue insects, suggesting that salticids are a primary prey of *P. comosus*. Crypsis most probably evolved initially as an antipredatory rather than a predatory adaptation, antipredatory crypsis possibly preadapting both species as specialized predators on salticids. Compared to *P. comosus*, the behaviour used by *P. fimbriata* when pursuing a salticid as prey is more discrete from normal locomotion and from predatory behaviour used against other types of prey. With its shorter legs and more hirsute body, *P. comosus* may be a more thoroughly cryptic spider than *P. fimbriata*. Thus it might have less to gain by 'refinements' of the types used by *P. fimbriata*. Also the normally larger salticid prey of the larger (c. 10 mm) *P. fimbriata* may

tend to have vision of greater acuity than the minute salticids with minute eyes preyed on by the small *P. comosus* in the dimly lit understory of the forest (Blest, in press).

Considering the differences in the behaviour of *P. fimbriata* and *P. comosus* when pursuing salticids and the disparate taxonomic placements of these two species, specialized stalking of salticids most likely evolved convergently. Cursorial salticids are extraordinarily abundant in the Queensland habitat of *P. fimbriata*, and this may have been a major factor favouring the evolution of specialized predation on salticids by this species. Salticids did not seem comparatively abundant in the habitat of *P. comosus*, although small salticids easily could have been overlooked. *P. comosus* and *P. fimbriata* have another behaviour in common, which is shared by all studied *Portia*: feeding on the eggs of other spiders. Differences in the oophagic behaviours of *Portia* and *P. comosus* are evidently related to differences in the sizes of these spiders. *Portia* either bites into the egg sac and eats out its contents as a single entity, or it opens up egg sacs, rakes out the eggs, and feeds on them one at a time. The much smaller *P. comosus* bores into egg sacs, stands on the eggs, and eats them one at a time.

Salticids and clubionids will attack if they detect intruders at the nest (Eberhard, 1974; Jackson, 1976; Pollard, 1983). However, with its small size, stealthy movements, and cryptic morphology, *P. comosus* avoids attracting the attention of and eliciting attacks from the maternal spider. As a distinctly araneophagic spider, *Portia* is in frequent proximity of spider egg sacs, and this was probably an important factor in the evolution of oophagy in this genus. Oophagy probably evolved independently in *P. comosus*, crypsis and small size being important preadaptations. Each egg of a large spider is almost as large as the *P. comosus*, and the egg mass in a single egg sac is a veritable bonanza. The adaptive advantage of oophagic behaviours for *P. comosus* are readily apparent.

Evolutionary implications

To evaluate the proposal that the unique combination of behaviours that occurs in *Portia* is partially a reflection of salticid ancestry, it will be important to ascertain the distribution of these behaviours within the Salticidae. Detritus mimicry, oophagy and specialized predation on salticids are three unusual characteristics that probably evolved independently in *P. comosus* and *Portia*. However, web-building and web-invading with the use of aggressive mimicry, which were proposed as characteristics of salticid ancestors, do not occur in *P. comosus*, suggesting that these are evolutionarily conservative characters, as implied by the Jackson & Blest hypothesis.

A more exhaustive study of *Phyaces* would be interesting; but the prospects for this are dim because of the remoteness, for most arachnologists, of the natural habitats of these spiders and the considerable difficulty of locating *Phyaces* in the field, which is at least partly due to its mimicry of detritus and its small size.

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