

# PREDATORY BEHAVIOR OF JUMPING SPIDERS

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## ABSTRACT

Salticids, the largest family of spiders, have unique eyes, acute vision, and elaborate vision-mediated predatory behavior, which is more pronounced than in any other spider group. Diverse predatory strategies have evolved, including araneophagy, aggressive mimicry, myrmicophagy, and prey-specific prey-catching behavior. Salticids are also distinctive for development of behavioral flexibility, including conditional predatory strategies, the use of trial-and-error to solve predatory problems, and the undertaking of detours to reach prey. Predatory behavior of araneophagic salticids has undergone local adaptation to local prey, and there is evidence of predator-prey coevolution. Trade-offs between mating and predatory strategies appear to be important in ant-mimicking and araneophagic species.

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## INTRODUCTION

With over 4000 described species (11), jumping spiders (Salticidae) compose the largest family of spiders. They are characterized as cursorial, diurnal predators with excellent eyesight. Although spider eyes usually lack the structural complexity required for acute vision, salticids have unique, complex eyes with resolution abilities without known parallels in animals of comparable size (98). Salticids are the end-product of an evolutionary process in which a small silk-producing animal with a simple nervous system acquires acute vision, resulting in a diverse array of complex predatory strategies.

Here, we begin by discussing how salticid eyes work and then review the predatory strategy of *Portia*—a tropical genus whose members are jacks of all spider trades. In many ways, this spider is the ultimate salticid. Using the exceptionally complex predatory behavior of *Portia* spp. as a baseline, we provide in the second half of the review a survey of the various predatory behaviors of salticid spiders.

## THE SALTICID EYE

Salticids have four pairs of eyes, but it is the pair of very large anterior median eyes (known as the principal eyes) that stare back when you look at the spider's face. Located on either side of the principal eyes are three pairs of smaller secondary eyes, which are highly proficient motion detectors (19, 41, 93, 94). Immediately to either side of the principal eyes are the anterior lateral eyes, which face forward in most species and have binocular overlap in front of the spider. They probably share a role with the principal eyes in range finding and in controlling the pursuit of prey (32, 33, 42). The next pair of secondary eyes, the posterior medians, are very small and apparently degenerate in most salticids, although they are large, well-developed motion detectors in some of the primitive spartaeines and lyssomanines (97, 122, 123). The most rearward-directed secondary eyes, the posterior laterals, have the widest fields of view. With its combination of four, or sometimes six, functional secondary eyes, the salticid's vision covers virtually the entire 360° ambit around the spider (96).

The principal eyes are the most interesting because they provide for acute vision (32, 48, 91, 92), allowing the salticid to identify mates, rivals, and predators from distances of 30 body lengths or more away (71). In typical predatory stalk and leap sequences (16, 18, 30, 33, 34), the salticid turns so its principal eyes face the prey. Next, it stalks the prey until it is a few body lengths away, lowers its body, and slowly crawls forward. Now, worthy of its name, the jumping spider attaches a dragline, raises its forelegs and makes an accurate, visually mediated leap onto the prey. Vision also plays an important role in other aspects of salticid behavior: They display to their image in a mirror (33, 42, 71); discriminate between the images of prey and conspecifics shown on a television screen (10); and respond appropriately to visual cues from motionless mates, rivals, and prey (18, 42, 80).

Salticid eyes, especially the principal eyes, are constructed very differently from the more familiar vertebrate and insect eyes (97). The retinas of the principal eyes have a four-layer, tiered arrangement. Light entering through the corneal lens passes successively through layers 4, 3, and 2 before reaching layer 1, which in cross section has a distinctive boomerang shape. Layer 2 is roughly the same in shape, whereas layers 3 and 4 more closely approximate a circle (91).

Layer 1 forms only an approximate layer, because this set of photoreceptors is not entirely in one plane. Instead, the receptors are arranged in a staircase so that receptors closer to the periphery of layer 1 are closer to the corneal lens; those in the central region are farthest from the lens (1a, 6). A primary function of the tiered arrangement of the retina as a whole, and the staircase arrangement of layer 1 in particular, is apparently to compensate for chromatic aberration and an inability to focus by changing eye tube length (8).

In the central area of layer 1 (the fovea) (1a), receptors are packed especially close together (about 1  $\mu\text{m}$  apart). They appear to be primarily responsible for shape recognition, because this is the only region that can process a sharply focused image (8).

The part of the salticid eye seen from outside is the corneal lens, behind which lies the eye tube. While the tubes of the secondary eyes are shallow and fixed in place, each principal eye has a long eye tube and, because of a set of six attached muscles, is capable of precise, complex rotary and side-to-side movements (92). However, the principal eyes cannot focus images by elongating and shortening the tube. Because of the tiered arrangement of the retina, the salticid principal eye receives a sharp image in the fovea of layer 1 at distances ranging from little more than a body length away to infinity (8). Because the retina of the principal eye is at the end of a long eye tube, the eye has a large focal length, which gives the spider a telephoto lens system. A second lens, just in front of the retina, increases the magnifying power of the eye and turns these eyes into miniature Galilean telescopes (129).

The distance between the receptors in the layer 1 fovea ( $\sim 1 \mu\text{m}$ ) appears to be optimal for resolution, given the details of the rest of the optical system. If the receptors were any closer together, then the image obtained would be degraded by quantum effects (8, 97).

The principal eyes appear to be capable of color vision (5, 12, 15, 89, 106, 131), which is most likely dichromatic.

One of the great challenges for future research will be to understand how the salticid's unique eyes enable these spiders to distinguish between different types of prey, webs, and other parts of the environment. The fovea of layer 1 contains at most only a few hundred receptors (8), and an eye with so few components cannot be operating on the same principles as the much larger eye of vertebrates (97).

The principal eye is an active eye, and this is probably the key to understanding shape perception. Yet the only detailed information we have on precisely how the salticid eye tube moves is from Land's (92) work on *Metaphidippus* spp., which described four modes of movement: spontaneous activity, saccades, tracking, and scanning. Scanning, which takes place only after the salticid is oriented so that an image is projected onto the fovea of layer 1, is the most complex movement and should be the target for future studies of shape perception.

## THE COMPLEX PREDATORY STRATEGY OF *PORTIA*

### *Predatory Versatility*

A versatile predator has a conditional strategy consisting of a repertoire of predatory tactics, each specific to different circumstances or different types of

prey (13). The predatory versatility of *Portia* spp. may represent the most pronounced example from arthropods, if not from all nonhuman animals. Five species of *Portia* have been studied (72–74, 76): *P. africana* and *P. schultzi* from Kenya; *P. albimana* from Sri Lanka; *P. labiata* from Malaysia and Sri Lanka; and *P. fimbriata* from Australia, Malaysia, and Sri Lanka. In these species, each spider is a cursorial predator and a web-builder, as well as a predator that invades alien webs, where it uses aggressive mimicry to trick, then catch, the resident spider. In addition, *Portia* spp. prey on the resident spider's eggs and eat insects ensnared in the alien web. The three chapters of the *Portia* predatory strategy—hunting in the open, using its own prey-catching web, and making predatory forays into the webs of other spiders—each features intricate stories of predatory versatility.

In the discussion below, unless otherwise noted, we use the generic name *Portia* to refer to any and all *Portia* species.

### *Web Invasion and Aggressive Mimicry*

The types of webs built by spiders are highly diverse, ranging from sparsely woven three-dimensional webs, to highly organized two-dimensional orb webs, to densely woven sheet webs (115). Some spiders enhance the stickiness of their web by secreting special substances (i.e. glue) onto the structural lines. Cribellate spiders are species that lay a very fine wool of sticky threads across the structural threads of the web. In contrast, some ecribellate spiders string droplets of fluid glue along the structural threads of the web at regular intervals. Generally, cursorial spiders and spiders that build nonsticky webs adhere to sticky webs, and spiders that build ecribellate sticky webs tend to adhere to cribellate webs, and vice versa (RR Jackson, unpublished data). *Portia* is an exception. It spins nonsticky webs, yet it can walk across and capture prey on virtually any type of web, including both cribellate and ecribellate sticky webs (65).

When *Portia* walks onto another spider's web, it enters the other spider's perceptual world, as the web is an extension and critical component of the web-building spider's sensory system (29, 130). On the web, intimate contact with the other spider's sensory system is often dangerous for *Portia*. When the resident spider detects something wrong, instead of fleeing, it may actively defend itself. Then the tables may be turned, and the intended prey becomes the predator.

After entering another spider's web, *Portia* usually does not simply stalk or chase down its victim but instead sends vibratory signals across the silk. The resident spider may respond to these signals in the same way it responds to the vibrations caused by a small insect becoming ensnared in the web. When the duped spider gets close, *Portia* lunges and catches it. A system of this sort,

in which a predator (in the present example, *Portia*) deceives its victim (e.g. a web-building spider) by mimicking prey (e.g. a small insect ensnared in a web) is called aggressive mimicry (28).

For *Portia*, aggressive mimicry involves pronounced behavioral complexity because *Portia* has an exceptionally diverse repertoire of vibratory signals. The spider can make the signals by manipulating, plucking, and slapping the silk with one or any combination of its eight legs and two palps, all of which can be moved in different ways. *Portia* also signals by flicking its abdomen up and down and can combine abdominal movements with virtually any of the appendage movements (72, 73, 86). Many of these signaling behaviors appear to be evolutionary modifications of grooming behaviors (76). The web-building spider has acute abilities to detect and discriminate between vibratory signals transmitted over the silk in its web. How the prey spider interprets these web-borne vibrations varies considerably among species and also with the sex, age, previous experience, and feeding state of the spider (53, 101, 130). Yet *Portia* uses aggressive mimicry to catch just about every kind of web-building spider imaginable, as long as it is about one tenth to twice *Portia*'s size (72, 73; RR Jackson, unpublished data).

The question of how *Portia* chooses, from its large repertoire of signals, the appropriate signals for hunting a particular prey spider has driven a research program at the University of Canterbury, Christchurch, New Zealand, carried out in collaboration with Stimson Wilcox from the State University of New York in the United States. A computer-based system was developed for recording and playing back signals on webs, much as if we could listen and talk to spiders in their own language. This work, which is still in progress, has indicated that the key to the success of *Portia* at victimizing so many different types of spiders is an interplay of two basic ploys (83, 86): (a) the use of specific preprogrammed signals when cues from some of the more common prey species are detected; and (b) the flexible adjustment of signals for different prey species according to feedback from the victims.

### *Trial-and-Error Behavior*

The first ploy, using preprogrammed tactics, is consistent with the popular image of spiders as animals that are hard-wired and governed by instinct, but the second ploy is based on the use of trial and error to derive signals, an unexpectedly flexible behavior for a spider (see 105). To illustrate how trial and error works, let us look at what happens when *Portia* goes into the web of a species of web-building spider for which it does not have a preprogrammed tactic. *Portia* first presents the resident spider with a range of different vibratory signals. When one of these signals eventually elicits an appropriate response from the victim (e.g. it behaves as though *Portia* were a small insect caught

in the web), *Portia* ceases to vary its signals and concentrates on producing the signal that elicits the response (86). However, communication between predator and prey is often more subtle.

Aggressive mimicry for *Portia* is a dangerous way to make a living, especially when facing a large and powerful spider in a web, and simply to pretend to be prey and provoke a full-scale predatory attack would probably not be a successful tactic. Instead, *Portia*'s strategy appears geared toward finely controlling the victim's behavior (59, 65–69). *Portia* may make signals that draw the victim in slowly. In contrast, the signals may keep the victim calm while *Portia* moves in slowly for the kill. Calming effects appear to be achieved through monotonous repetition of a habituating signal (RR Jackson & RS Wilcox, unpublished data), as though *Portia* were putting its victim to sleep with a vibratory lullaby derived from trial and error.

When using trial and error, *Portia* associates success with a particular signal and remembers to keep using it. This is at least a simple kind of learning (see 105). Learning is not unique to *Portia*. Some typical insectivorous salticids learn to avoid ants, and some appear to improve with practice their performance of the stalk-and-leap routine against their normal insect prey (18, 26, 31, 42, 100). Salticids will also acquire aversion to models paired with electric shock (18).

However, *Portia*'s trial-and-error behavior is not only an example of learning: The wide range of signals generated and the ability to identify and remember successful ones in a variety of contexts gives these salticids problem-solving capabilities (39).

### *Smoke-Screen Behavior*

Another example of flexibility in *Portia*'s predatory strategy is the smoke-screen tactic. In the field, investigators have noticed that whenever the wind blows, movement of the web masks nearly all other signals going across the silk. Interestingly, when the wind blows, *Portia* is most likely to walk rapidly toward the spider in the web. Laboratory experiments using fans to generate artificial wind demonstrated that *Portia* deliberately chooses to approach its victim when a breeze provides a vibratory "smoke screen" to hide behind (128a). Also, if the wind does not blow, *Portia* can make its own vibratory camouflage. While walking across the web, *Portia* masks the faint vibrations caused by its steps by adding large-scale vibrations that simulate a breeze (128a; RS Wilcox & RR Jackson, unpublished data). *Portia* is selective; it uses opportunistic and self-generated smoke screens when hunting spiders, but not, for instance, when stalking insects caught in the webs or preying upon the eggsacs of other spiders when masking would be irrelevant (RS Wilcox & RR Jackson, unpublished data).

### Detouring

In the field, sometimes *P. fimbriata* stops, looks at a web, then turns and walks away, only to approach the web later from another direction. This behavior is especially distinct on webs of the Queensland spider *Argiope appensa*, which builds orb webs on tree trunks. Walking straight from the tree into the web would seem easy for *P. fimbriata*, but *A. appensa* has a dramatic defense. This spider is exceedingly sensitive to anything foreign touching its web, and hence it rarely gives *P. fimbriata* time to enter the web and start signaling. If *A. appensa* is sure the intruder is an insect prey, it attacks; otherwise, it pumps the web fibers (79) by rapidly, repeatedly flexing its legs. It thus sets the web in motion, which either drives or throws *P. fimbriata* off (67).

In its natural environment, the rain forest, *P. fimbriata* often walks up the tree trunk toward *A. appensa*, stops, looks around, then goes off in a different direction, later reappearing above the web. Vines and other vegetation, which usually grow near the tree, often extend out above the web. After looking at the web, the vine, and the neighboring vegetation, *P. fimbriata* sometimes moves away, perhaps to where the web is completely out of view, crosses the vegetation, and comes out on the vine above the web. From above the web, *P. fimbriata* drops on its own silk line alongside, but without touching, the web of the *A. appensa*. Then, when parallel with the spider in the web, *Portia* swings in to make a kill (67, 84).

In the laboratory, experimental evidence shows that *P. fimbriata* makes deliberate, planned detours (116, 117). For example, if presented with a choice of two routes on artificial vegetation, only one of which leads to a prey spider, *P. fimbriata* consistently walks past the inappropriate path to take the appropriate one, even when that path initially leads away from the prey to where the prey is temporarily out of view (117; MS Tarsitano & RR Jackson, unpublished data).

### Predation by Queensland's *P. fimbriata* on Cursorial Salticids

The habitat of *P. fimbriata* in Queensland, Australia, is unique in that it has a superabundance of cursorial salticids (73). The predatory behavior of this *Portia* species appears to be specially adapted to this locally abundant prey.

Although strictly cursorial salticids do not spin prey-catching webs, they do spin shelters out of silk (nests) that are usually densely woven, tubular, and not much larger than the resident spider. A salticid that finds a conspecific inside a nest may court or threaten the resident spider by making vibratory signals on the silk (66, 112). *P. fimbriata* responds to nests of nonconspecific salticid spiders with vibratory signals (nest probing), to which the resident reacts by poking its front out of the nest, only to be grabbed and eaten (73).

*P. fimbriata* also catches salticids out in the open, away from their nests,

by using a special type of trickery, known as cryptic stalking (72), which capitalizes on the unusual appearance of *Portia* spp. Markings, tufts of hairs, and long, spindly legs give *Portia* the appearance of detritus in a web (120), which presumably protects it from visually hunting predators. Normally, *Portia* locomotion consists of a slow, choppy gait that renders the genus difficult to recognize even when moving. When inactive in a web, *Portia* adopts a special posture, the cryptic rest posture, with palps retracted beside the chelicerae and legs retracted beside and under the body. This positioning blurs the outlines of these appendages into the contours of the body (72).

When cryptically stalking a salticid away from webs, *P. fimbriata* moves even more slowly than usual, often remaining undetected until too late for the victim to escape. However, as salticid secondary eyes are excellent movement detectors, sometimes the victim suddenly swivels around to see what is coming up on it. The Queensland *P. fimbriata* compensates: It freezes in its tracks and stays motionless until the salticid turns away again. When the salticid takes a look, it apparently perceives a piece of detritus. Another consistent component of cryptic stalking by *P. fimbriata* is that it retracts its palps, as in the cryptic rest posture. Experiments have confirmed that hiding the outlines of palps is important because these outlines are cues by which the salticid can recognize *P. fimbriata* as a predator (SD Pollard & RR Jackson, unpublished data).

Interactions between *P. fimbriata* and *Euryattus* (species undetermined) illustrate the evolution of a prey-specific predatory behavior for use against a single species. *Euryattus* sp. is sympatric with *P. fimbriata* in Queensland but is not known to be sympatric with other populations of *Portia*. *Euryattus* females are unusual salticids because, instead of making a tubular silk nest, they suspend a rolled-up dead leaf by heavy silk guylines from a rock ledge, tree trunk, or the vegetation in the rain forest and use this as a nest (51). *Euryattus* males go down guylines onto leaves and court by suddenly flexing their legs and making the leaf rock back and forth. *Euryattus* females then come out of their leaves to mate with or drive away conspecific males. Unlike any other *Portia* studied, *P. fimbriata* from Queensland also goes down guylines onto the leaves and makes the leaf rock by suddenly flexing legs, apparently simulating the courtship behavior of *Euryattus* males (83). *Euryattus* females that come out of their leaves when "courted" by *P. fimbriata* are attacked and eaten.

### *Coevolution of P. fimbriata and Euryattus sp.*

The Queensland *P. fimbriata* is not always successful at deceiving and catching *Euryattus* sp. Sometimes the strategy fails because the *Euryattus* female detects an approaching *P. fimbriata* and drives it away, either before or after it reaches the leaf. To drive *P. fimbriata* away, the *Euryattus* spider comes out of the



rolled-up leaf, then suddenly and violently strikes, leaps at, or charges toward the *Portia* individual. Sometimes *Euryattus* sp. leaps and bangs into *P. fimbriata* (usually head-on) and knocks it away, after which *Euryattus* sp. swings down on its dragline, then climbs back to the leaf. Once attacked, the *Portia* spider flees and the *Euryattus* survives (83).

Observations of thousands of interactions between *P. fimbriata* and many different species of salticids (72, 73; RR Jackson, unpublished data) have shown that *Euryattus* sp. is more effective than other salticids at recognizing and defending itself against a stalking *Portia*. Frequent predation by *P. fimbriata* on *Euryattus* sp. has apparently resulted in *Euryattus* sp. evolving special abilities to recognize and defend itself against *P. fimbriata*, which suggests coevolution between these two species.

Interpopulation variation in *Euryattus* behavior supports the coevolution hypothesis. *P. fimbriata* is absent from a second *Euryattus* habitat sampled about 15 km away from the location where *Euryattus* sp. and *P. fimbriata* are sympatric. In tests using laboratory-reared spiders, allopatric *Euryattus* sp. only rarely evaded or attacked stalking *P. fimbriata*, and *P. fimbriata* hunted allopatric more efficiently than sympatric *Euryattus* sp. (85).

## SPARTEAINE SALTICIDS, A PRIMITIVE GROUP

Behaviorally, the Spartaeineae, the subfamily to which *Portia* belongs, is a collection of unusual salticids. This subfamily of primarily tropical African, Asian, and Australasian species is of special interest because of morphological characters (i.e. presence of female palpal claws and unreduced posterior medial eyes) that are regarded as plesiomorphic for salticids (114, 123, 128). Most strikingly, retinal ultrastructure of the principal and especially the secondary eyes of spartaeineae tends to be less organized than that of typical salticids. Findings from extensive comparative and ontogenetic studies consistently indicate that the eyes of the Spartaeineae (and Lyssomaninae: see below) represent a remarkable series of plesiomorphic states leading up to the condition prevailing in advanced salticids (1a–4, 7, 8).

Among salticids, only ten species (in four genera) are known to use vibratory aggressive mimicry in conjunction with araneophagic web invasion, and all of these are spartaeineae. Besides the five studied species of *Portia*, this group includes *Brettus adonis*, *Brettus cingulatus* (75), and *Gelotia lanka* (60) from Sri Lanka; *Cyrbia algerina* (61, 75) from southern Europe; and *Cyrbia ocellata* (61) from Australia, Kenya, Sri Lanka, and Thailand.

*Brettus* spp., *Cyrbia* spp., and *G. lanka* have not been studied as thoroughly as *Portia* spp., but all these genera exhibit some aspects of aggressive mimicry in common. None of these spiders are exclusively web invaders; each also catches prey away from webs. *G. lanka*, like *Portia*, not only invades webs,

but also builds them. Like *Portia*, the other spiders are armed with large repertoires of vibratory signals, and preliminary evidence (60, 61, 75) indicates that each uses a trial-and-error tactic similar to that of *Portia*.

Behavioral studies have been carried out on another three spartaeine genera. *Cocalus gibbosus*, from Queensland, invades webs and eats spiders in addition to catching prey away from webs, but does not practice aggressive mimicry (62). *Phaeacius malayensis* and *Phaeacius wanlessi*, from Singapore and Sri Lanka, respectively, are specialized ambush predators that neither build nor invade webs (75, 63). *Spartaeus spinnimanus* and *Spartaeus thailandica*, from Singapore and Thailand, respectively, are web-building, but not web-invading, salticids (78).

Although *Brettus*, *Cocalus*, *Cyrba*, and *Phaeacius* spp. do not build webs, they do build aberrant, web-like silk edifices in which to molt and oviposit (60–63, 75). These structures contrast with the tightly woven tube-like nests typically built by salticids (53). Also, the way that all spartaeine species attack their prey is atypical for salticids. All spartaeines studied do not perform the typical stalk-and-leap sequence and usually lunge at rather than leap upon their prey. *G. lanka* and *Portia*, *Brettus*, *Cocalus*, and *Cyrba* spp., the web invaders, all have cuticles that do not adhere to sticky webs; they differ from the nonspartaeine web-invading salticids in this respect. All of the web-invading spartaeines prey not only on the resident spider, but on its eggs as well, and also take insects from the other spider's web (65).

These odd salticids appear to be evolutionary experiments that branched off in the early history of the family, before the majority of salticids got locked into a path toward becoming insect hunters. However, the spartaeines are not the only unusual salticids. Another salticid subfamily, Lyssomaninae, also exhibits a predominance of plesiomorphic morphological characters. This subfamily contains seven genera and about 85 species of primarily tropical salticids (36, 122). *Chinoscopus* and *Lyssomanes* are New World genera, whereas *Asemonea*, *Goleba*, *Macopaeus*, *Onomastus*, and *Pandisus* are Old World genera. Details concerning predatory behavior are available for species from four of the genera: *Lyssomanes*, *Asemonea*, *Goleba*, and *Onomastus*.

Compared with the spartaeines, the lyssomanines do not appear to have diversified very much in their predatory behavior. For instance, no evidence supports web invasion. Yet like the spartaeines, these spiders are quite unusual. They do not adopt typical stalk-and-leap sequences, and they usually make contact with the prey by lunging instead of leaping. Although the lyssomanines do not build large prey-catching webs comparable to the webs of *G. lanka*, *Spartaeus*, and *Portia* spp., neither do they build tightly woven silk nests comparable to those of the majority of salticids. Instead, they spin flimsy sheets under leaves, which they use for rudimentary webs. When an insect contacts the silk, the lyssomanine rushes out and grabs it (40, 52, 64).

## PREDATORY VERSATILITY IN NONSPARTAEINE WEB-BUILDING SALTICIDS

*Simaetha paetula* and *Simaetha thoracica*, from tropical Queensland, resemble *Portia* spp. in that they are versatile predators, but they have some interesting idiosyncrasies. *Simaetha* spp. build a large prey-catching web. However, spiders of this genus, unlike *Portia* spiders, often also build a typically salticid tube-like nest. Nests and webs may be built alone or the nest may be incorporated into the web (52).

Besides building their own prey-catching webs, *Simaetha* spp. often live within the colonies of a social web-building cribellate spider, *Phryganoporus* (formerly *Badumna*) *candidus* (17). *Simaetha* spp. glean insects from the edges of the alien webs and incorporate their own nest, web, or web-nest combination within the alien communal web. Although cribellate silk adheres to their cuticles, *Simaetha* spp. avoid becoming prey of the social spiders by moving carefully along vegetation and old, no-longer-sticky silk mixed in among the fresh, sticky silk of the web.

Female *Euryattus* sp., the leaf-hanging salticids preyed on by *P. fimbriata* in Queensland (see above), are not the only unusual members of this species. The juveniles are also unusual because they build prey-catching webs (51). The webs of *Euryattus* and *Simaetha* spp. are nonsticky, three-dimensional space webs that lack the funnel shape of webs of *Portia* spp. and are not as densely spun as the sheet web of *Spartaeus* spp. However, another salticid builds a dense sheet web. *Pellenes arciger*, from southern France, builds a large silk sheet in the vegetation (99). The predatory behavior of this species has not been studied, but the large web it spins is probably used as a prey-capture device.

The spinning of *Plexippus paykulli* illustrates the blurry distinction between a nest and a web. The nest of this species is a tube surrounded by a dense tangled array of silk that forms a sticky layer over the tube. Insects, such as grasshoppers, coming into contact with nests of *P. paykulli* tend to become stuck for several seconds, or even minutes. *P. paykulli* responds to ensnared insects by coming out of the nest and leaping onto the prey or by walking across the nest and over to the insect to attack it (77).

All of the web-building salticids studied are versatile predators that not only use webs for predation, but also catch prey cursorially.

## PREY-SPECIFIC PREDATORY BEHAVIOR OF ANT-EATING SALTICIDS

Most salticids avoid ants, which generally bite, sting, and taste bad, but an interesting minority routinely eat these heavily defended prey. The most thor-

oughly studied are three euophrynes, *Corythalia canosa*, *Habrocestum pulex*, and *Zendora* (formerly *Pystira*) *orbiculata* (14, 24, 81), and six heliophanines, *Chrysilla lauta*, *Siler semiglaucous*, *Natta rufopicta*, and another three undescribed species of *Natta* (82).

Predatory behavior used against ants varies among the species. The six heliophanines are remarkably similar to each other but differ from each of the three euophrynes. Among the euophrynes, *Z. orbiculata* differs considerably in behavior from *C. canosa* and *H. pulex*. *C. canosa* and *H. pulex* usually maneuver to attack ants head on. Heliophanines also often attack head on, but they attack from directly behind as well. *Z. orbiculata* attacks ants from just about any orientation. However, this species, unlike the other ant-eating salticids, also frequently positions itself facing down on ant-infested tree trunks and ambushes ants by lunging down on them instead of actively pursuing them. *C. canosa* usually holds its cephalothorax elevated while pursuing, attacking, and starting to feed upon ants. The heliophanines, in contrast, tend to hold the first pair of legs, but not their cephalothoraxes, elevated. When the euophrynes attack, they usually hold on, but the heliophanines often stab ants then back away (81, 82).

Although the ant-eating heliophanines and euophrynes are behaviorally specialized on ants, their diet is not restricted to ants. They attack other prey in typical salticid stalk-and-leap sequences (81, 82).

## SUBTLE PREDATORY VERSATILITY IN *PHIDIPPUS*

*Phidippus* is a genus of common, sometimes large (e.g. *Phidippus regius* can reach 22 mm in body length) salticids in North America. At least one species, *Phidippus audax*, is an important insect predator in agroecosystems (132). In studies of predatory behavior, *Phidippus* spp. have generally been described as typical insectivorous salticids, but there is more to these spiders than the usual stalk-and-leap routine.

In nature, the studied species of *Phidippus* appear to prey opportunistically on a diverse assortment of arthropods, but these spiders' diets seem to be biased especially toward caterpillars and flies (49, 124, 126). Although not so striking as the predatory versatility of *Portia* spp., the predatory behavior of *Phidippus* spp. apparently consists of two different prey-specific strategies (25, 26, 35). Each appears to be especially efficient for catching particular prey.

*Phidippus* spp. approach the two types of prey differently and leap on them from different distances, stalking closer to caterpillars than to flies before attacking. Typically, upon seeing a moving caterpillar, a *Phidippus* spider approaches rapidly to within 10–12 mm, then pauses and watches it. If the caterpillar continues to move, the spider circles until it is directly in front, stalks forward a few millimeters, then leaps and pins the caterpillar's head

down. In interactions with flies, *Phidippus* spp. approach by walking rapidly, pause when 25–30 mm away, then leap. Attacks on flies are initiated from just about any direction, but regardless of the direction of attack, the spiders almost always capture the flies by biting their thoraxes near the wing bases (25, 26). Also in *Phidippus* spp. and some other salticids, the spider's approach and method of attack are influenced by the size and speed of the prey (16, 18, 32, 35, 37, 47). These salticids move around and attack large prey from the rear, but attack small prey from any orientation. Prey that is stationary or moving only slowly is stalked slowly, but rapidly moving prey is chased.

Observations of the predatory behavior of *Phidippus* spp. suggest that prey-specific predatory behavior may be more common than previously supposed. Perhaps when we compare salticids interspecifically, the question to ask is not whether the species exhibits predatory versatility, but instead how pronounced that versatility is. The same lesson may apply to the individual behavioral flexibility demonstrated by the detours taken by *Portia* spp. to reach prey. *Phidippus* spp. have not been seen to undertake detours as long as those of *Portia* spp. However, the length of *Portia*'s detours makes sense as a hunting strategy against web-building spiders, because these are sedentary victims. An active insect is unlikely to stay put long enough to allow for a long detour, but *Phidippus* spp. do undertake short detours to reach insect prey (45). A common European insectivorous salticid, *Evarcha blancardi*, also takes short detours to reach prey (42), which suggests that detouring may be a widespread ability in the salticids.

Whether *Phidippus* spp. undertake longer detours when the prey are web-building spiders has not been tested. This question is appropriate because *Phidippus* spp. are, in fact, web-invading araneophagic spiders (90, 119). However, rather than practice aggressive mimicry like *Portia* spp., *Phidippus* spp. leap into the web to catch the spider. Similar leaping attacks on web-building spiders may be widespread among salticids (9, 27, 51, 56–58, 113).

Givens (38) demonstrated that *P. audax* males feed less often and take smaller prey than do females. *Portia* spp. appear to exhibit a similar male-female trend (73), which may be widespread in the Salticidae.

## PREDATORY STRATEGY OF MYRMARACHNE

*Myrmarachne* is a large genus of predominantly tropical ant-like species (121). Generally these species do not eat ants, but instead, like the majority of salticids, feed on a wide range of arthropod prey. However, their prey-catching methods are unusual (54, 87).

In a typical predatory sequence, a *Myrmarachne* spider runs up to the prey, taps it with the first pair of legs, then attacks it by lunging rather than leaping (54, 87). These sequences are unique among salticids that have been studied

(112) and appear especially appropriate for an ant-mimicking species because, by adopting this style of predation, the spider can usually capture prey with only a minor disruption in its ant-like walking gait. Ants often tap each other and other animals with their antennae, and *Myrmarachne* spp. may tap their prey to maintain Batesian mimicry (21) during predatory sequences: If *Myrmarachne* spp. did not tap their prey, the spiders' predators might more readily recognize them. However, is there a cost? Does tapping alert potential prey or give them an opportunity to flee before being attacked?

How serious the disadvantage of warning the prey might be to *Myrmarachne* spp. probably varies considerably with the type of prey, and this variation may have influenced the natural diet of *Myrmarachne* spp. These spiders apparently feed on a wide range of arthropod prey, including other salticids, but they seem to prefer insects that are slow to take flight, such as moths (87). Interestingly, whether tapping alarms the prey is not clear. It may even have a calming effect. Moths, and even salticids, sometimes stay more or less stationary when tapped by *Myrmarachne* spp.

*Myrmarachne* spp. also feed on a prey item that cannot flee—the eggs of other spiders. *G. lanka* and *Portia*, *Brettus*, and *Cyrra* spp. also eat spider eggs. *Myrmarachne* adults get at eggs by using their fangs to tear open nests of cursorial spiders, especially those of other salticids, including other *Myrmarachne* spp. Small juveniles of *Myrmarachne* spp. enter nests of other spiders and feed on eggs one at a time (54, 87). This tactic is also used by adults of *Phycates comosus* (55), a minute, highly cryptic salticid from Sri Lanka. Other salticid species feed on insect eggs (43, 44, 88, 103, 104, 125, 127). Nectar is another stationary, but energy-rich, salticid food source (22, 108, 111; SD Pollard & RR Jackson, unpublished data).

## SEXUAL DIMORPHISM AND TRADE-OFFS BETWEEN MATING AND PREDATORY STRATEGIES IN *MYRMARACHNE* AND *PORTIA*

In salticids, as in insects (118), intrasexual competition for access to potential mates has probably been the primary selection pressure responsible for the evolution of secondary sexual characteristics in males. In males of *Myrmarachne* spp., we find some of the most dramatic examples of these often bizarre and, from the perspective of survival, incongruous features, which are usually exaggerated forms of structures found on conspecific females.

In *Myrmarachne plataleoides*, one of the most sexually dimorphic species in this genus, the differences in male and female predatory behavior can be attributed to enlarged chelicerae in males (109, 110). In this species, the female's chelicerae hang down at right angles to the horizontal plane, as in most salticids. The male's chelicerae are about five times longer than the

female's and project forward, parallel with the body's horizontal plane. During intrasexual conflict, males first spread apart the elongated basal segments of their chelicerae to expose their extra-long fangs, then approach, make contact, and push against each other in contests of strength, as described in detail in another sexually dimorphic *Myrmarachne* species, *M. lupata* (50). The male and female *M. plataleoides* are both convincing mimics of weaver ants (*Oecophylla smaragdina*). Juvenile *M. plataleoides* males have short chelicerae like those of females. During the final molt, the male emerges sexually mature, equipped with fully elongated chelicerae (102). Mature females and juveniles of both sexes are armed with venom-injecting glands, but the male's fangs have no openings (109, 110). The venom glands are at the base of each chelicera, close to the spider's eyes, and in males, a continuous duct from there to the tips of the fangs would have to be about five times longer than the ducts in females. Even if the male could organize an intact duct of this length in its final molt, it is unlikely that it could generate, by squeezing the venom glands, sufficient pressure to eject venom from the distant fang tips.

*M. plataleoides* males have apparently made evolutionary adjustments in prey capture to compensate for the inability to envenomate. Unlike females, males hold prey down while making repeated stabs with the long fangs. This method is less effective than the female's venom-based style of prey capture, and many prey manage to escape before males can stab them to death (54, 87). In addition, the modified male chelicerae reduce the effectiveness of feeding on captured prey. *M. plataleoides* females puncture prey with their fangs, then suck nutrients out from the holes. However, the male's long fangs push through both sides of the prey's body so that the tips point back into the spider's mouth. The male then sucks from the large holes in its skewered prey. Potential nutrients can leak out of the prey's body, and the viscera that remain in place increase in viscosity through evaporative fluid loss (see 107). Consequently, males take longer to feed compared with females and extract less food (SD Pollard, unpublished data).

Although *M. plataleoides* males are less efficient than females at catching active prey, they appear as efficient at oophagy (87). In fact, the male's large chelicerae might be an asset when it removes silk from egg sacs and reaches into the nest for the eggs.

The elongated chelicerae of males of *Myrmarachne* spp. have apparently not jeopardized their ability to mimic ants. *M. plataleoides* is especially interesting. Weaver ant colonies have major workers that forage and minor workers that care for the eggs and larvae inside the nest. Major workers commonly carry minors from one subnest to another by holding the smaller ants' abdomens in their mandibles. The minor worker being carried holds its legs against the side of its body (46). Remarkably, the *M. plataleoides* male,

with chelicerae that simulate the minor worker, closely resembles this duo. The ability of *M. plataleoides* males to maintain the illusion of being ant-like, by mimicking ants carrying nest mates, may have facilitated evolution of large chelicerae. In fact, *M. plataleoides* may be only an extreme example of how *Myrmarachne* males generally resemble ants carrying nest mates, food, or other objects.

The behavior of ant-eating salticids (see above) supports this hypothesis. These salticids prefer to attack ants that are carrying something in their mandibles (RR Jackson & SD Pollard, unpublished data), presumably because such ants cannot readily use their mandibles for defense. Also, the ant-eating salticids more readily stalk *Myrmarachne* males than females, which suggests that the ant-hunters initially mistake *Myrmarachne* males for ants with occupied mandibles. Stalked *Myrmarachne* spp. of both sexes, however, usually escape unharmed because, by briefly displaying to the ant-hunter, they communicate that they are really salticids and risky prey to attack.

Perhaps not only secondary, but also primary sexual characters have had evolutionary effects on the foraging behavior of salticid males. In spiders, the males' palps, being gonopods (i.e. primary sexual structures, or genitalia), are considerably enlarged compared with the females' palps (29). Palps of salticid males may also have secondary characters—conspicuous hairs and markings that are absent from the females'. In Queensland *P. fimbriata*, the males' palps appear to have a foraging cost in relation to cryptic stalking, the tactic by which this population of *Portia* catches cursorial salticids (72). Cryptic stalking depends primarily on concealment, and one of its consistent components is for *P. fimbriata* to pull back its palps so that their outlines blur into the contours of the body. However, the male of the Queensland *P. fimbriata* is less effective at catching salticids, apparently because his enlarged palps reveal him as a predator to his visually competent prey. Moreover, in experiments where the males' palps were removed, their capture efficiency became indistinguishable from that of females (SD Pollard & RR Jackson, unpublished data). Evidently, in this population of *Portia*, primary sexual characters compromise a predatory tactic. We know the secondary characters (i.e. markings) are not responsible for the males' failures because juvenile males, which have enlarged palps but not the markings, are also less effective than females (adult and juvenile) at catching salticids. Also, primary sexual characters are usually not exaggerated sufficiently to have costs comparable to those of secondary sexual characters (20). However, a combination of the spider's method of sperm transfer, the relation of intersexual selection in salticids to visual displays, and the acute vision of both the cryptically stalking predator and its prey appears to have resulted in a unique adaptive trade-off in males of Queensland *P. fimbriata*.



## CUES FOR PREDATORY DECISIONS

The cues typical salticids use for distinguishing between their insect prey and other objects such as mates, rivals, enemies, and irrelevant stimulation have been investigated extensively. Shape, symmetry, presence of legs and wings, size, and style of motion (short, jerky movements) are some of the more important features by which these salticids appear to recognize their prey (12, 18, 23, 32, 34, 42). Appreciating predatory versatility forces us to go beyond the question of how the salticid recognizes prey, but for salticids with complex predatory strategies, we have little information about the cues that influence the different components of the strategy. Most of what we know concerns the cues that govern *Portia*'s decisions about whether to enter a web, whether to make signals once in a web, and whether to persist at signaling (70).

In eliciting web entry, visual cues are effective, but volatile chemicals from the web are not. Seeing a spider in a web increases *Portia*'s inclination to enter the web. After web entry, cues from webs of prey spiders are sufficient to elicit signaling behavior, even in the absence of other cues coming directly from the prey. In contrast, volatile chemical cues from prey spiders are not important. Once *Portia* is on a web and signaling, seeing a moving spider and detecting vibrations on the web encourage it to persist in signaling. On the basis of visual cues alone, *Portia* can distinguish between quiescent spiders, insects, and eggsacs (70).

These studies of cues highlight how far we remain from fully understanding the functioning of the salticid visual system. Although salticid eyes are large and complex for a spider, this animal is no primate (95). The principal eye lens is only a few millimeters in diameter. The numbers of receptors in the salticid eye and neurons in the salticid brain are limited. How so small a visual system, with so few components, can perform these perceptual feats is currently a mystery.

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