Spider-Eating Spiders

Despite the small size of their brain, jumping spiders in the genus Portia *outwit other spiders with hunting techniques that include trial and error*

Robert R. Jackson and R. Stimson Wilcox

In the conventional view, "intelligent" function—complex and flexible behavior, the capacity to innovate and learn—requires the large, highly developed brains of animals such as chimpanzees and dolphins. More primitive creatures, whose behavior is commonly guided by instinct, have small, comparatively simple brains made up of relatively few neurons. A spider's brain, for instance, fits comfortably on a pinhead, and it seems unlikely that such a small collection of neural components could organize complex and flexible behavior. Yet recent work on *Portia*, a genus of jumping spider, illustrates that although a spider may have a small brain, its behavior need not be simple.

The visual capability of jumping spiders sets them apart from other spiders. The eyes of most spiders lack the structural complexity required for acute vision, but jumping spiders have unique, complex eyes with resolution abilities unparalleled in animals of comparable size. A jumping spider has a pair of principal eyes, located front and center on its head, and they provide acute vision. Three pairs of secondary eyes surround the principal ones, and they detect motion. Jumping spiders use their vision when stalking prey. Although many spiders spin a web and wait for something to get captured, most jumping spiders hunt prey without using webs. In general, jumping spiders prey on insects, but *Portia* prefers to hunt other spiders.

Portia is a versatile predator, which means that an individual animal uses a repertoire of disparate predatory tactics, each specific to different circumstances or different types of prey. We shall show that these spiders invade the webs of other spiders, where they use mimicry, detours and deception to capture the resident spider. In addition, they are capable of changing their tactics through trial and error.

Aggressive Mimicry

Although the genus *Portia* includes about 15 species, our knowledge of their behavior comes primarily from studies of five species: *P. africana* and *P. schultzi* from Kenya and Uganda; *P. albimana* from Sri Lanka; *P. labiata* from Malaysia, the Philippines and Sri Lanka; and *P. fimbriata* from Australia, Malaysia and Sri Lanka. Appearance alone suggests that *Portia* is unique. It does not look like a spider at all, or even an animal. Instead, it resembles detritus in a web. Such an appearance may conceal *Portia* from prey that might see it coming, not to mention concealing it from its own visually hunting predators, especially birds.

We have concentrated on another form of mimicry, *aggressive mimicry*, which means that the predator deceives its victim by imitating something desirable. To study this behavior, we watched spiders in the field as well as in laboratory experiments. In addition, one of us (Wilcox) developed a computer-based system for recording and playing back signals on webs, which is rather like listening and talking to spiders in their own language. A transducer—rather like the stylus on an old-fashioned record player—is used to pick up web signals (vibration and movement patterns) from the silk and turn them into electrical signals that can be fed to a computer and analyzed. Signals can be played back by playing signals from the computer through an electric coil to make a magnet on the spider's back force the spider to move in whatever way we choose. Using this system, we found that *Portia* uses aggressive mimicry when pursuing another spider on its web. After entering the other spider's web, *Portia* sends web signals across the silk, and sometimes the resident spider responds as if a small insect were ensnared in its web. When the duped spider approaches, however, *Portia* lunges out and catches it.

Portia makes its web signals by manipulating, plucking and slapping the

Figure 1. Male jumping spider in the genus *Portia* shows two of its crucial characteristics: appearance and vision. Instead of looking like an ordinary spider, it resembles detritus in a web, which helps it approach prey undetected. On the other hand, *Portia* can clearly see its prey with its central pair of principal eyes, and the surrounding secondary eyes detect motion. This combination of camouflage and vision helps *Portia* pursue its favorite prey—other spiders. (All photographs courtesy of Robert R. Jackson.)

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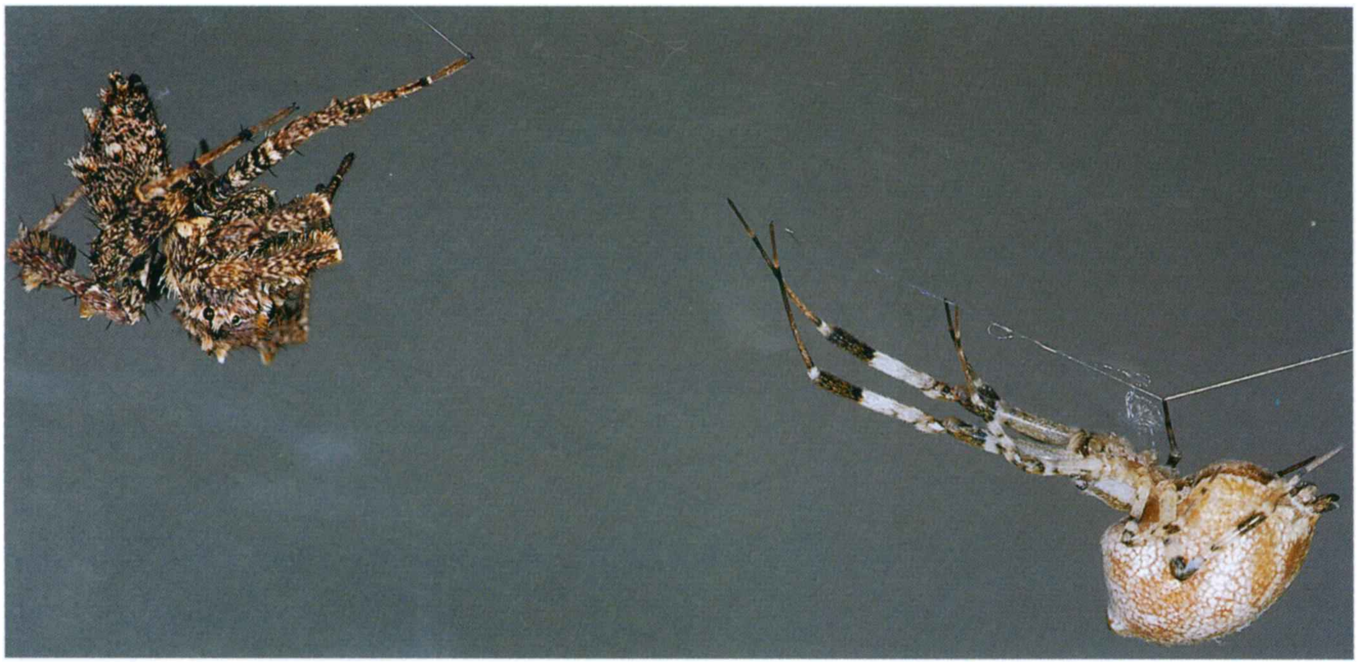

Figure 2. Aggressive mimicry helps *Portia* capture other spiders. This juvenile female *(left)* flexes her legs to generate a vibration on the web that catches the attention of a larger orb-weaving spider (*Zosis genicularis*) *(right)*. In many cases, a resident spider responds to such a vibrational signal as if a small insect got ensnared in its web. When the spider approaches to investigate, *Portia* attacks and kills it. This is called aggressive mimicry: The predator mimics something desirable that attracts the prey.

silk with any one or any combination of its eight legs and two *palps*, relatively small appendages near the mouth. Each appendage can be moved in a great variety of ways, and the movements of any one appendage can be combined with different movements of any number of the other appendages. In addition, *Portia* makes signals by flicking its abdomen up and down, and this can also be combined with virtually any of the appendage movements. Consequently, *Portia* can make an apparently unlimited number of different signals on the web of another spider.

Instead of relying on vision, typical web-building spiders detect and interpret web signals. *Portia* needs to vary the web signals that it makes because different species interpret them differently. How a spider interprets a web signal may also vary with its sex, age, previous experience and hunger level. Despite that variability, we have observed *Portia* using aggressive mimicry to capture just about any kind of web-building spider, from about one-tenth to twice its own size.

Tuning the Trembles

How does *Portia* generate an effective web signal for each victim? We think that the spider relies on two basic ploys: using preprogrammed tactics and deriving signals by trial and error. Using preprogrammed tactics is consistent with the popular portrayal of spiders as animals governed by instinct. For instance, *Portia* makes specific web signals when hunting a specific species of spider. Trial and error, on the other hand, is an unexpectedly flexible behavior for a spider.

When *Portia* enters a web of a species for which it lacks a preprogrammed tactic, it makes a vast array of web signals. If one of these signals has an appropriate effect—such as enticing the resident spider to approach as if *Portia* were a small insect ensnared in the web—then *Portia* stops varying its signals and concentrates on producing the signal that worked. Nevertheless, aggressive mimicry can be dangerous for *Portia*, especially when the resident spider is large and powerful. By pretending to be prey and provoking a full-scale attack, *Portia* runs a risk of becoming what it pretends to be. *Portia* compensates for that danger by gaining fine control over the victim's behavior. For example, *Portia* may make signals that slowly draw in a dangerous spider. Alternatively, *Portia* may move in slowly for the kill while using a monotonous web signal that keeps the victim calm. Sometimes, *Portia* entices its victim into a particular orientation before attacking. Interactions with pholcids, spiders with very long legs, illustrate this. If *Portia* hits a pholcid's leg first, the pholcid defends itself and sometimes kills the would-be predator. So *Portia* uses trial and error to generate a web signal that coaxes the pholcid into a position that offers a clear shot at the body.

Even when *Portia* has a preprogrammed tactic for a spider, trial and error remains relevant. Often the preprogrammed tactic simply gets a predatory sequence off to a good start, after which *Portia* finishes the job by trial and error. For instance, the victim spider might start approaching slowly but then lose interest, become distracted or begin approaching too fast. At that point, *Portia* might switch from a preprogrammed tactic to trial and error.

Deception and Detours

In most cases, *Portia* very slowly stalks a spider in a web. In some circumstances, especially when the wind blows, *Portia* might walk rapidly toward an intended victim. We used fans to generate artificial wind in laboratory experiments that showed that *Portia* opportunistically chooses to approach its victim when wind provides a vibratory "smokescreen." This tactic works because wind-generated movement of the silk masks most web signals, including the faint signals from *Portia* stalking across it.

In still conditions, *Portia* can make its own vibratory smokescreen. That is, while stalking across the web, *Portia* can mask the faint vibrations it makes by producing smokescreen signals that mask forward motion as well as simulate the vibrations made when twigs and leaves hit a web. Perhaps surprisingly, *Portia* only uses opportunistic and self-generated smokescreens against spiders, not when it stalks insects ensnared in webs or the egg sacs of another spider—targets for which masking is irrelevant.

If *Portia* cannot get close to intended prey through deception, it might use a detour, as it often does in pursuit of *Argiope appensa*, a spider that builds orb webs on tree trunks. Although it might appear that *Portia* could simply walk straight from the tree trunk to the web, *A. appensa* is exceedingly sensitive to anything foreign touching the web and rarely lets *Portia* enter unchallenged. If an insect prey is detected, *A. appensa* attacks. If a potential predator is detected, it uses a specialized defense called "pumping," or rapidly flexing its legs over and over again. That sets the web in motion and either drives or throws *Portia* out of the web.

Portia often walks up the tree trunk toward *A. appensa* and then stops, looks around, goes off in a different direction and reappears above the web. If there is a vine over the web, for example, *Portia* seems to look at the web, the vine and the neighboring vegetation before moving away, perhaps going to where the web is completely out of view, crossing the vegetation and coming out on the vine above the web. From above the web, *Portia* drops on a silk line alongside but not touching the intended victim's web. Then, when parallel with the spider in the web, *Portia* swings in to make a kill.

In laboratory experiments with Michael Tarsitano (then Jackson's graduate student), we found that *Portia* consistently takes detours to reach prey, and these detours often appear to be planned ahead of time. For example, if presented with a choice of two routes on artificial vegetation, only one of which leads to prey, *Portia* consistently takes the appropriate path even when this means initially going away from the prey and losing visual contact.

Getting to Know the Locals

Portia can also adapt to local prey. For instance, a population of *Portia fimbriata* in Queensland, Australia, evolved predatory tactics against local cursorial jumping spiders, which are exceptionally abundant there.

Although jumping spiders that are strictly cursorial do not spin prey-capture webs, they do spin silk shelters, or nests, which are usually densely woven, tubular in shape and not much larger than the resident spider. When a spider of the same species but opposite sex finds a jumping spider inside a nest, the intruder might court the resident by making vibratory signals on the silk. If *P. fimbriata* finds an occupied nest, it uses vibratory signals that often cause the resident to poke its front end out, only to be grabbed and eaten.

For catching jumping spiders out in the open, *P. fimbriata* uses *cryptic stalking*, a special type of trickery that capitalizes on its unusual, detritus-mimicking appearance. *Portia* normally walks in a slow, choppy gait, but during cryptic stalking the Queensland *P. fimbriata* moves even more slowly, often going undetected until it is too late for the victim to escape. If the stalked spider suddenly turns around, the Queensland *P. fimbriata* freezes in its tracks, and the hunted spider apparently perceives nothing more than a piece of detritus. In addition, the Queensland *Portia* pulls in its palps during cryptic stalking, which makes it look even less like a spider. Other species of *Portia* also pull in their palps when they are quiescent in a web. We know that palp outlines are cues by which jumping spiders recognize *Portia* as a predator, making it all the more interesting that the Queensland *Portia* hides this cue when stalking other jumping spiders.

Another example of local adaptation exists between the Queensland *P. fimbri-*

Figure 3. Trial and error often helps *Portia* find the right web signal to cause the desired effect. This proves especially important against this green pholcid spider, which has spun its flimsy—and here invisible—web on the surface of a leaf. If the hunting *Portia* touches one of the pholcid's long legs it will attack and possibly kill *Portia*. So *Portia* drums on the web with its palps, small appendages near its mouth, until it makes a signal that happens to make the pholcid turn to give *Portia* a clear shot at its body. Eventually, *Portia* caught this pholcid and ate it and its eggs.

ata and another local jumping spider, *Euryattus*, which is not known to coexist with any other population of *Portia*. The female *Euryattus* is unusual because, instead of making a tubular silk nest, she uses heavy silk guylines to suspend a rolled-up dead leaf from a rock ledge, tree trunk or vegetation. *Euryattus* males go down guylines onto rolled-up leaves and court by suddenly flexing their legs and making the leaf rock back and forth. Then the *Euryattus* female comes out on the leaf surface to mate with or drive away the male. Unlike other *Portia* studied, the Queensland *Portia* mimics the courtship of a male *Euryattus*. When the "courted" female comes out, the Queensland *Portia* attacks and eats her.

Euryattus is not defenseless. Either before or after *Portia* reaches the leaf, *Euryattus* may come out and make sudden, violent leaps or charges toward the invader, sometimes making head-on collisions with the predator and knocking it away. Once attacked, *Portia* always flees. *Euryattus* is exceptionally effective at recognizing and defending itself against a stalking *Portia*. This appears to be a local adaptation. At Davies Creek, only about 15 kilometers away from the habitat where *Euryattus* and *P. fimbriata* live together, there is another population of *Euryattus* living in the absence of *Portia*. When tested in the laboratory, Davies Creek *Euryattus* only rarely evaded or attacked stalking *Portia*, and the Queensland *Portia* readily caught the Davies Creek *Euryattus*.

Figure 5. *Euryattus*, a common jumping spider in Queensland, suspends a rolled-up leaf as a nest and the female crawls inside. A male climbs down the guylines that hold the leaf and then signals his presence to the female by rocking his legs one way *(left)* and then the other *(right)*. On detecting that signal, the female comes out to either mate with or drive away the male.

Mate or Meal?

Some of the most unpredictable behavior in *Portia* involves mating. An apparent mate may become a meal, and what appears to be a mating tactic may also be a predatory or defensive tactic. In general, male jumping spiders approach females in rapid stop-and-go spurts of activity, punctuated with displays, such as stiffly extending the first two pairs of legs and waving or shaking them in front of the female. Most female jumping spiders scrutinize the male's displays and occasionally display back. Conversely, *Portia* females often initiate intersexual interactions by displaying first. Once the interaction begins, the female is exceptionally active in displaying back to the displaying male. *Portia*'s intersexual interactions may take place in or outside of webs, with the female tending to display, move away a short distance and then turn back and look at the male. In this way, the female moves steadily to higher ground at the top of a web or up in the vegetation, with the courting male close behind.

Figure 4. Detours help *Portia* capture some spiders. One orb weaver, *Argiope appensa*, challenges *Portia* if it enters the web. So *Portia* moves around to a position above the web, drops down on a line of silk and attacks the unsuspecting spider.

The distinction between mating and predation blurs in the Sri Lankan *P. labiata* and the Kenyan *P. schultzi*. Females of these two species drum—pounding on the silk with their two palps—and tug—making sharp pulls on the silk with their forelegs—solely in interaction with males of the same species. Once a female has been mounted by a male, she drops on a dragline with the male on board. A risky mating takes place with the pair suspended on thread. During or just after mating, while still suspended, females almost always swing around violently with fangs extended, in sometimes successful attempts to impale and eat their unfortunate suitors. Other times, the male does not mate at all because, as he approaches, the female suddenly and violently lunges forward, spears him with her fangs and eats him.

The twisting and forward lunges of *P. labiata* and *P. schultzi* females appear to be prey-specific predatory tactics designed to catch courting males—prey that deliberately approaches. By killing the male after he starts copulating, the female chooses him as both a sperm donor and a meal. If she kills and eats him before mating, she rejects him as a mate but accepts him as a meal. In some cases, females might encourage

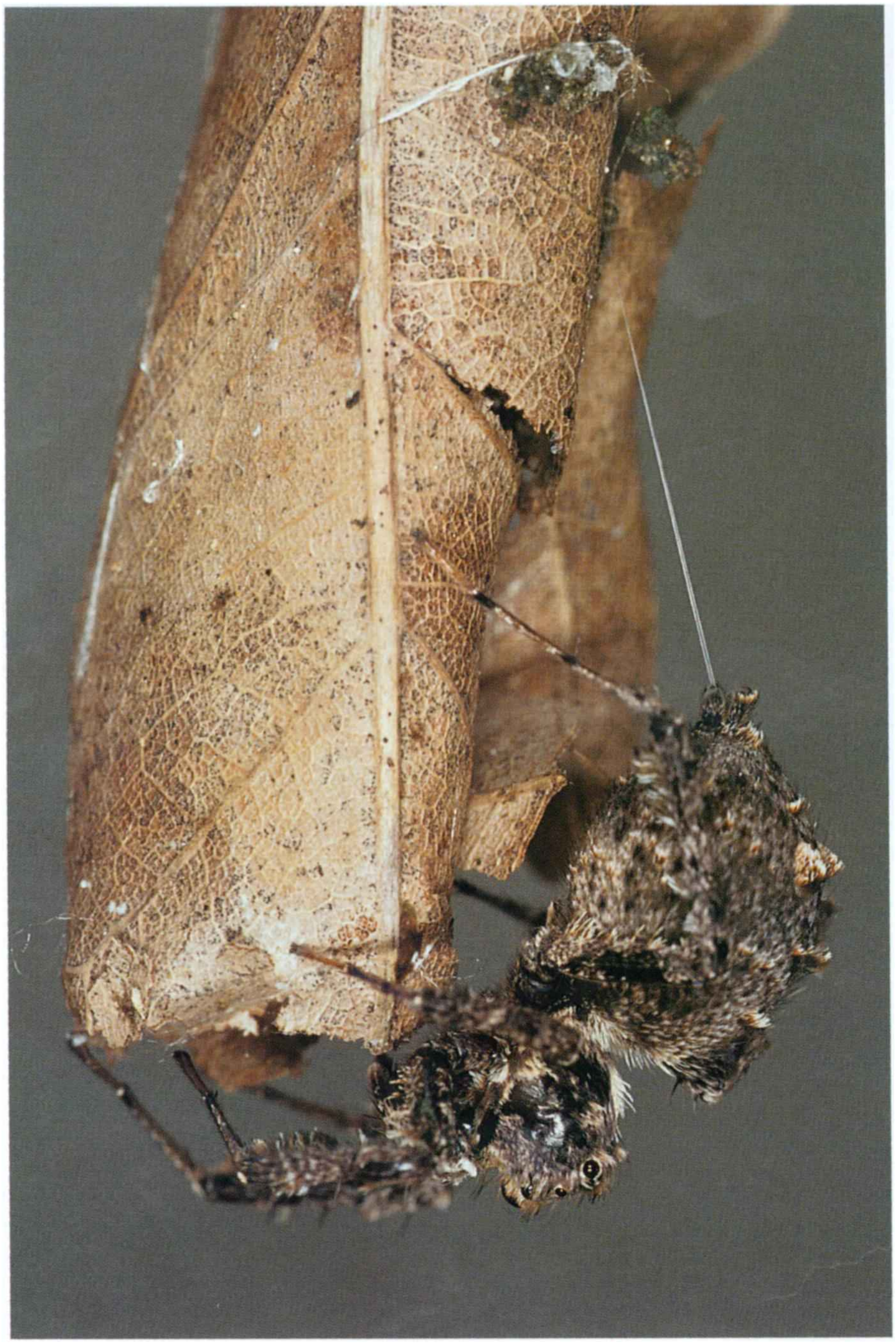

Figure 6. *Portia fimbriata* has adapted to the habits of *Euryattus* in some parts of Queensland. This female *P. fimbriata* climbed down to a leaf nest, intermittently simulated the courtship of a male *Euryattus* and then moved the nest opening to wait for the female *Euryattus* to emerge, where she was eventually captured and eaten.

males under false pretenses. If eating is a female's only interest in a male, then she is using aggressive mimicry against her own species.

The implication of feminine deceit is less ambiguous when *P. labiata* and *P. schultzi* females are immature and cannot mate. Males appear unable to distinguish a large juvenile from an adult female, and juvenile females drum and tug, apparently as a ploy to lure a male in for the kill. Often a male mounts and performs futile and dangerous pseudocopulations while suspended from the juvenile female's dragline. By twisting and lunging, the juvenile often makes a meal of the frustrated male. Chemical deceit may also be part of the juvenile's game. Pheromones from adult *Portia* females attract males and prime them to court, and juvenile females release similar, if not identical, chemical signals.

Portia females also react violently toward other females. Female-female interactions can become fights to the death in which the spiders fight over 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 a rival. Moreover, another *Portia* female is also a potential predator and prey because cannibalism is a frequent outcome of female-female interactions.

Vision and Beyond

Many other investigators have shown that typical jumping spiders distinguish between prey and nonprey through various optical cues, including shape, symmetry, presence of legs and wings, size and style of motion. Beyond using its visual skills, *Portia* seems to be making decisions to control the many components of its predatory strategy. Most of what we know so far concerns the cues that govern *Portia*'s decisions on whether to enter and stay in a web, whether to make signals once in a web and whether to persist at signaling.

Many cues influence *Portia*'s behavior. Seeing a web drives *Portia* to enter it. Seeing a spider in a web increases *Portia*'s inclination to enter. As far as we know, volatile chemical cues from webs or prey spiders appear to be unimportant. After entering a web, cues from the web largely control signaling behavior, but seeing a prey spider or detecting vibrations on the web make *Portia* more prone to signal by vibrating the web. Working with our colleagues, we have also shown that, with optical cues alone, *Portia* can distinguish between quiescent spiders, insects and egg sacs, as well as between different kinds of spiders, but we do not know precisely what cues they are using to make such distinctions.

Although *Portia*'s eyes are large and complex for a spider, this is no primate. The principal eye lens is only a few millimeters in diameter, and there are only about 100 photoreceptors in the fovea of a jumping spider's principal eye. How does *Portia* do so much with so little?

If there is a lesson to learn from *Portia*'s predatory strategy, it might be that we should not underestimate the potential for complex behavior in a small and seemingly simple animal. There were good reasons to expect less from *Portia*. How an eye with so few components can achieve *Portia*'s feats of visual discrimination is only part of the mystery.

Figure 7. Mating can also lead to a meal for a female *Portia*. This male spider *(left in upper photograph)* displays to the female by stiffly extending and shaking his forelegs. The female *(right in upper photograph)* responds by drumming and tugging on the web on this leaf, as a female commonly does before mating. When the male approaches, however, the female lunges and kills him *(left)*. In other cases, a female might mate first and then kill the male. In some species of *Portia* a female lets a male mount her and then she drops on a dragline with the male on board, where she may swing around and eat him. So *Portia* uses trickery to capture and eat all kinds of spiders, including members of its own species.

Portia's tiny central nervous system somehow supports a predatory strategy more similar to what we would expect in a cat or a dog than in a spider. Much more work must be done to find out how a brain so small orchestrates such complex and flexible behavior.

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Links to Internet resources for further exploration of "Spider-Eating Spiders" are available on the *American Scientist* Web site:

http://www.amsci.org/amsci/articles/98articles/jackson.html