Eight-legged Tricksters

Spiders that specialize in catching other spiders

Robert R. Jackson

Spiders are well known as predators of insects, but some even eat their own kind. For most species, eating other spiders appears to be largely an opportunistic occurrence, a larger or faster individual overpowering another in a chance encounter. There are at least a few spider species, however, for which araneophagy (pre-dation on other spiders) is routine (e.g., Jackson and Poulsen 1990). Some of these species employ strategies based on deceit of their spider prey. In this article, I use the images of deception, mimicry, and trickery to convey the functional significance of a predator’s behavior and not to imply cognition.

Use of deceit may be especially important because another spider is a potential predator as well as potential prey.

Aggressive mimicry, where a predator seems beneficial to its prey, is aploy sometimes used by araneophagic spiders. An aggressive mimic might, for example, imitate an insect that is the intended victim’s prey. In this way, an aggressive mimic can gain control over its prey’s behavior. The situation becomes even more complex when an araneo-phagic spider interacts with another spider that is both potential prey and potential predator. Of the araneophagic species, the aggressive mimics are a small minority found only in five distantly related families.

Pirate spiders as aggressive mimics

Although pirate spiders (Mimetidae) are well known as web-invading araneophagic spiders (Foelix 1982), for only a few species from this cosmopolitan family are details known about behavior. Ero furcata, a European mimetid, is a frequently cited example of an aggressive mimic. A member of this species moves onto other spiders’ webs, where it jerks on the web, apparently mimicking the struggles of a trapped insect. It thereby lures the resident spider close enough to be attacked (Bristowe 1941, Gerhardt 1924). Czajka (1963) also described an instance where E. furcata caught a female spider, apparently by mimicking the courtship web vibrations of a male of the victim’s species.

More recently, Mimetus maculosus from Australia and Mimetus sp. from New Zealand (Jackson and Whitehouse 1986) have been shown to catch other spiders by using deceptive vibrating signals (Figure 1). The deceivers ease onto webs, then transmit signals to their intended victims by pulsating their bodies up and down on the web and by plucking and tugging on the silk with their legs in a variety of ways, apparently mimicking struggles of small insects in the web.

The mimetids illustrate several points that apply more generally to aggressive mimic spiders. First, the signaling behavior of aggressive mimics is complex. Mimetids perform several different vibratory behaviors, and, by varying the sequence in which they perform these behaviors and the characteristics of each behavior (e.g., amplitude and speed of leg movement), they can transmit a complex array of vibrations across the web to the host spider (Jackson and Whitehouse 1986).

Second, the basic principles that govern intraspecific communication also govern interactions between species during aggressive mimicry. When animals communicate, one individual (the sender) indirectly manipulates another individual (the receiver) by providing a specialized stimulus (the
signal) to which the receiver responds (see Dawkins and Krebs 1978). In aggressive mimicry systems of spiders, a predator provides another spider species, its prey, with a signal. But in this instance, the predator attempts to elicit a response that benefits itself and not the prey. Whether or not the receiver benefits in a communication system is an important question because the evolution of the receiver’s behavior is easy to account for if it benefits, but more difficult if it does not. The function of the signal, however, refers only to how the signal benefits the sender.

Third, mimetids, like all web-invading aggressive mimic spiders that have been studied in detail, are not limited to using aggressive mimicry (Jackson and Whitehouse 1986). Instead, they are versatile predators (Curio 1976) whose tactics depend on the circumstances (see Dominey 1984), and so the tactics are considered to be conditional predatory strategies. Mimetids, in addition to catching the spiders in their own webs, also steal insects from other spiders’ webs (klep-toparasitism) and open egg sacs to feed on the victim spider’s eggs (oophagy). These behaviors are distinctly different from araneophagic aggressive mimicry because no signaling is associated with them.

Fourth, the characteristics of the invaded web largely determine how effective an aggressive mimic is at catching the web’s resident. Spider webs vary greatly in shape and design, from two-dimensional orb webs to sparsely spun three-dimensional space webs to thickly woven sheet webs (Foelix 1982). Some spiders, called cribellates, build sticky webs by coating structural lines with fine threads from the cribellum, a specialized spinning plate with minute spigots. Other spiders, called ecribellates, build sticky webs by secreting from spigots on the spinnerets adhesive fluid to form glue droplets along the threads. Webs without either form of glue are referred to as nonsticky, although all spider silk may be adhesive to some extent (Hallas and Jackson 1986).

Mimetids are most effective when invading the space and orb webs created by ecribellates (Jackson and Whitehouse 1986); they do not adhere to the glue on these most frequently invaded webs. They do, however, adhere to cribellate webs and are less efficient as predators there. Some other aggressive mimics are more effective when invading ecribellate webs than when invading cribellate webs. How mimetids and other web-invading spiders avoid adhering to sticky webs is not known.

Except for salticids, which will be discussed later, spiders do not have acute vision. Typical web-building spiders rely primarily on web-borne vibrational cues to detect and locate prey. A web invader, also without acute vision, relies on vibrational cues in the alien web. But because webs may differ significantly in their vibrational characteristics due to structural diversity, web invaders are limited as to the range of web types they can exploit. This sensory factor apparently limits most aggressive mimics to being effective as predators on a restricted range of web types (Jackson 1986).

Both a web builder and a web invader

Research on Pholcus phalangioides (Jackson and Brassington 1987) illustrates that an individual spider may be both a web builder and a web invader. *P. phalangioides* is a cosmopolitan pholcid that builds a nonsticky dome-shaped web and, like other pholcids, has legs that are especially long relative to the body. When prey contacts the web, *P. phalangioides* uses its long legs to wrap the prey up with silk while keeping its body distant and out of harm’s way.

However, *P. phalangioides* is not simply a predator that uses its own web. Like *Mimetus*, *P. phalangioides* invades alien webs and practices aggressive mimicry and also eats the resident spider, insects in the alien web, and the victim spider’s eggs (Jackson and Brassington 1987).

Unlike *Mimetus*, *P. phalangioides* adheres to both cribellate and ecribellate sticky webs. Therefore, *P. phalangioides* is more efficient at catching prey on nonsticky than on sticky webs, and most efficient of all when on its own web (Jackson and Brassington 1987). Nevertheless, *P. phalangioides* can catch prey on both types of sticky webs. With its long legs, *P. phalangioides* appears to tip-toe across the sticky web, minimizing contact with the sticky threads (Figure 2). Also, by grooming its legs frequently, *P. phalangioides* can remove any sticky silk that accumulates. Another key to *P. phalangioides*’ success at invading sticky webs ap-
pears to be its own silk. While in alien sticky webs, *P. phalangioides* spins, laying its own nonsticky silk over the other spider’s sticky silk, thereby making a nonsticky walkway for itself.

**Web builder and prey stealer**

Most spiders in the family Theridiidae build sticky ecribellate space webs and use these webs to catch prey, generally staying out of other spiders’ webs. However, certain species of *Argyrodes*, a large cosmopolitan genus of small-bodied theridiids, also routinely enter the webs of other spiders. The best known species of web-invading *Argyrodes* are kleptoparasites in the webs of much larger host spiders (e.g., Vollrath 1979a).

Besides taking insect prey from the host spider’s web, some species of *Argyrodes* also feed with the host, on the same prey item. After detecting web vibrations made by the host while wrapping prey (Vollrath 1979b), *Argyrodes* moves stealthily into position to take its meal from close to the host’s mouth (Figure 3). *Argyrodes* can also modify its style of stealing prey in response to changes in conditions such as prey size and host spider behavior (Cangialosi 1991).

In addition to kleptoparasitism, araneophagy appears to be an important part of the predatory strategy of some species of *Argyrodes* (Vollrath 1984). The most details are known for *Argyrodes antipodiana*, a New Zealand species with pronounced predatory versatility (Whitehouse 1986), even though it feeds primarily by practicing various forms of kleptoparasitism.

Although *A. antipodiana* builds a web of its own, it appears to use its web only infrequently as an insect snare. Instead, its web seems to be used primarily as a base from which to make forays onto the host spider’s web. *A. antipodiana* usually minimizes contact with the host’s web, staying primarily on its own silk lines, which extend from its own to the host’s web. In this way, *A. antipodiana* might reduce risk of detection by the host spider. Sometimes, however, *A. antipodiana* enters alien webs and catches small spiders (e.g., juveniles of the host species in the host species’ web) by using vibratory aggressive mimicry. *A. antipodiana* is more effective as a web invader (kleptoparasite and araneophagic predator) when on sticky ecribellate space or orb webs and is less effective on other types of webs.

**Web builder and prey stalker**

A recent study of *Taieria erebus* (Jarman and Jackson 1986), a New Zealand gnaphosid, illustrates that an araneophageic web-invading spider can be both a web builder and a cursorial predator. Most gnaphosids are insectivorous hunters. *T. erebus*, like typical gnaphosids, generally hunts prey in the open, completely away from webs. However, an individual *T. erebus* may also build a nonsticky web and, in addition, invade the webs of other spiders.

While in an alien web, *T. erebus* practices aggressive mimicry by making vibratory signals (Figure 4), and it may also steal prey or eat eggs. Unlike mimetids and *Argyrodes*, *T. erebus* gets stuck on ecribellate sticky webs. *T. erebus* is most efficient at catching prey on cribellate sheet webs, a type of web on which the previously discussed web invaders are especially inefficient.

*T. erebus* has yet another trick, one that is unknown among other web invaders. After killing and eating the resident spider, *T. erebus* often stays in the funnel webs of one of its common victims, *Segestria* (species undetermined), and uses the web to catch additional prey (Jarman and Jackson 1986).

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**Figure 2.** Long-legged *Pholcus phalangioides* (right) tiptoeing across sticky cribellate web of *Badumna longinqua* (lower left) on which it preys. Both spiders are from New Zealand.

**Figure 3.** *Argyrodes antipodiana* (arrow), a small kleptoparasitic spider, feeds beside the mouth of its much larger host, *Eriophora pustulosa*, on an insect captured and wrapped up by the host. Both spiders are from New Zealand. Photo: Simon Pollard.
Web-invading jumping spiders

Most spiders, having small eyes with simple retinas, have poor eyesight. Jumping spiders (Salticidae) are exceptions. With their large eyes and complex retinas (Figure 5), salticids have acute vision (Blest 1985). All salticids appear to be cursorial insectivores, but some species are also araneophagic web invaders.

Numerous salticids are known to leap or walk into webs (e.g., Robinson and Valerio 1977). But only ten species of salticids (from four genera), all from the subfamily Spartaeinae (Wanless 1984), are known to practice vibratory aggressive mimicry (Table 1). Each of these ten salticid aggressive mimics is a versatile predator that catches prey outside of webs by cursorial hunting, invades webs where it uses aggressive mimicry and catches the resident spider species (Figure 5), and also takes insects (Figure 6) and the resident spider’s eggs from the alien web. Each species of Portia also builds a nonsticky prey-capturing web.

Each web-invading spartaeine salticid catches prey efficiently on all of the different types of webs exploited by the nonsalticid web invaders (Jackson and Hallas 1986). There appear to be three reasons why the web-invading spartaeine salticids are not restricted to certain web types as are the nonsalticid aggressive mimics.

First, the spartaeines are versatile in locomotion. Unlike other web-invading spiders and apparently uniquely among spiders, the spartaeines can walk across both cribellate and ecribellate sticky silk without getting stuck (Jackson 1986). Second, the spartaeines, having acute vision, are not restricted to interpreting web vibrations to detect, identify, and locate prey on webs as are the nonsalticids (Jackson and Blest 1982).

Third, the spartaeines have a complex and finely tuned predatory strategy. Compared to nonsalticid web invaders, the spartaeines seem to be capable of producing a greater variety of effective signals for tricking different victim species. They combine and vary signals more extensively than do other aggressive mimic spiders. The signal output variation may enable an aggressive mimic to finely control the responses of each particular victim spider.

Portia, the most thoroughly studied spartaeine genus, makes signals on its victim’s web by plucking, striking, fluttering its legs and palps (Figure 7), and twitching its abdomen up and down. Duration, rate, amplitude, and combinations of these behaviors vary, with almost any combination of the spider’s eight legs and two palps moving at the same time.

R. S. Wilcox and I have worked together in the field and the laboratory to record the different vibrations Portia makes when using these various behaviors and to demonstrate that these vibrations are responsible for the prey spider’s response to Portia.1 We detect web vibrations with a galvanometer connected by a stylus to a web, record these vibrations on an FM tape recorder, and, after analog-to-digital conversion, analyze the signals with a computer. Signals are played back from the computer through a power amplifier to a coil to control the movement of a small magnet positioned on the web. This methodology is analogous to the system Wilcox has used in communication studies of

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Table 1. Salticids that practice vibratory aggressive mimicry (Jackson 1990a,b, Jackson and Hallas 1986a,b).

<table>
<thead>
<tr>
<th>Species</th>
<th>Location</th>
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<tbody>
<tr>
<td>Brettus adonis</td>
<td>Sri Lanka</td>
</tr>
<tr>
<td>Brettus cingulatus</td>
<td>Gelotia</td>
</tr>
<tr>
<td>Cyrba algerina</td>
<td>Southern Europe</td>
</tr>
<tr>
<td>Cyrba ocellata</td>
<td>Sri Lanka, Australia, Kenya, and Thailand</td>
</tr>
<tr>
<td>Portia africana</td>
<td>Kenya</td>
</tr>
<tr>
<td>Portia schultzi</td>
<td>Sri Lanka</td>
</tr>
<tr>
<td>Portia albimana</td>
<td>Sri Lanka and Malaysia</td>
</tr>
<tr>
<td>Portia labiata</td>
<td>Sri Lanka, Malaysia, and Australia</td>
</tr>
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water striders, aquatic insects that make specialized ripple signals on the water surface (Wilcox 1979).

In encounters with some of their more common victim species, Portia appear to use certain signals. But for many of their other victims, they appear to use trial and error. After successively trying different signals, Portia species continue to use only those that elicit an appropriate response from the potential victim. An appropriate response from the victim might be localized movements (e.g., pivoting and using forelegs to tug on the web) or a slow approach toward the signaling Portia; to move away or to approach too rapidly would be inappropriate response. No other spiders have been shown to use trial and error, and there are only a few other examples of an invertebrate using learning as part of a system of deceiving, then catching, prey (see Mitchell 1986).

Specialized araneophagy away from webs

Studies of T. erebus and P. fimbriata illustrate that web-invading spiders may also use trickery to catch spiders away from webs. Both of these spiders are specialists at catching cursorial salticids (Jackson and Hallas 1986a, Jarman and Jackson 1986). Strictly cursorial salticids do not spin prey-catching webs, but they do spin silk shelters (nests), which are usually densely woven, tubular in shape, and not much larger than the spider inside.

A salticid that finds a conspecific inside a nest may court or threaten the resident spider by making vibratory signals on the silk (Jackson 1982a). T. erebus and P. fimbriata respond to the nests of salticids by making vibratory signals (nest probing; Figure 8). They then grab their prey when it pokes its front end out of the nest. T. erebus may also enter the nest to attack a pacified female salticid.

P. fimbriata has a special method for catching salticids out in the open, away from their nests. This trickery, known as cryptic stalking, is not an example of aggressive mimicry. The predator capitalizes on its unusual appearance; its markings, tufts of hairs, and long, spindly legs make this spider resemble detritus. This cryptic appearance, enhanced by a slow,
choppy gait, probably helps protect P. fimbriata against its own visually hunting predators and conceals Portia from its potential prey. In cryptic stalking, P. fimbriata moves especially slowly, pulls its palps back and out of its prey’s view (Figure 9a), and freezes if the salticid turns to face it (Figure 9b). Eventually, P. fimbriata approaches the salticid from behind, then swoops down to kill it (Figure 9c). P. fimbriata stalks no other prey in this way.

Although several populations of five species of Portia have been studied, no population other than P. fimbriata in Queensland, Australia, practices these two special salticid-catch methods (nest probing and cryptic stalking). The habitat in which this particular Portia lives is unique among those studied in having a superabundance of cursorial salticids. Apparently, the Queens-land P. fimbriata’s predatory behavior is specially adapted to a locally abundant prey.

A behavior specific to a single prey

A study of the interactions between P. fimbriata and Euryattus (species unknown) illustrates that an araneophagous spider may evolve a prey-specific predatory behavior for use against even a single species. Euryattus is sympatric with P. fimbriata in Queensland but is not known to be sympatric with other populations of P. fimbriata or the other species of Portia studied.

Euryattus females are unusual salticids because, instead of making a tubular silk nest, they suspend a rolled-up dead leaf by heavy silk guylines (Figure 10a) from a rock ledge, tree trunk, or the vegetation in the forest and use the leaf as a nest (Jackson 1985). Euryattus males (Figure 10b) 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 the males.

Unlike any other Portia studied, P. fimbriata from Queensland (Figure 10c) also goes down guylines onto the leaves and makes the leaf rock by suddenly flexing its legs, apparently simulating the courtship of Euryattus males (Jackson and Wilcox 1990). We call this behavior suspension nest probing. Euryattus females that come out of their leaves when courted by P. fimbriata are eaten.

Nest probing, cryptic stalking, and suspension-nest probing by the Queensland P. fimbriata do not depend on prior experience with salticids as prey. Naive, laboratory-reared P. fimbriata perform these behaviors immediately when tested for the first time with salticid prey, and Portia from other populations and species never perform these behaviors, even if they are reared in the continual presence of salticid prey (Hallas 1988, Jackson and Wilcox 1990).

Cannibalism

For most spiders, the notion that male courtship behavior functions primarily as a defense against predatory conspecific females does not stand up to close scrutiny (e.g., Jackson and Pollard 1990). Females of some species have become behaviorally specialized at catching conspecific males. For example, Araneus pallidus spins a prey-capture web and usually feeds on insects, but females are also skillful at catching males during mating (Grassholf 1964). The male is smaller than the female, and he must move under the female’s abdomen to mate. While the male mates with her, the female slowly pulls out a band of silk
Figure 9. a. Queensland Portia fimbriata (right) cryptically stalking another salticid (left). Note that the Portia’s palps are pulled back. b. The Portia freezes when the salticid turns around. The salticid, apparently not recognizing Portia as a predator, later turns and walks slowly away. c. The Portia (facing right) feeds on salticid after cryptically stalking it, moving over it from behind, then swooping down to grab it. Portia’s chelicerae are around the posterior dorsal carapace of prey.

Behavioral complexity

When discussing ants, E. O. Wilson (1971) suggested that “a group of species sharing common descent can be said to have truly radiated if one or more species is a specialized predator on others” (p. 2). By this criterion, spiders have truly radiated: an assortment of spider species has evolved specialized methods of preying on other spiders. Among the most striking characteristics of araneophagic spiders are behavioral complexity, variable signal output, and pronounced predatory versatility, generally more complex predatory repertoires than are known among other spiders.

Some web-invading spiders also prey on conspecifics. The females of two species of web-invading salticids, P. labiata and P. schultzi, for example, are known to have predatory behavior specific to courting and mating conspecific males (Jackson and Hallas 1986a). When salticids mate, the male usually mounts the female. All species of Portia studied are unusual in that the female usually drops on a dragline after the male mounts and the pair mates while suspended in mid-air. While suspended, P. labiata and P. schultzi females attack males with one of her rear legs, then suddenly wraps up and eats the male.

Males do not appear to be willing victims. Instead, P. labiata and P. schultzi males are exceedingly skittish suitors compared with most salticids, being prone to run and leap away when the female moves even slightly. Interestingly, P. fimbriata females do not twist lunge, and P. fimbriata males are not especially prone to run and leap away from females (Jackson 1982b).

There may also be elements of aggressive mimicry during the courtship sequences of P. labiata and P. schultzi (Jackson and Hallas 1986a). Females of these species, unlike the females of most salticids, have distinct displays by which they solicit a male. Recently mated females are unlikely to mate again; nevertheless, they readily perform these displays. Even subadult females, which cannot mate, perform these displays, apparently mimicking receptive adult females in these instances. If a male mounts a subadult female, she also may try to kill the male while he attempts to copulate.

Males of a few species, such as Araneus diadematus, may even feed themselves deliberately to their mates. In this way, the mother of the male’s future offspring gets a meal and, by providing this meal, the male may contribute to his progeny’s well-being. Therefore, these males may behave in a way that facilitates, rather than defends against, cannibalism (Elgar and Nash 1988; but see Gould 1984).

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All of the aggressive mimic spiders studied take spiders ranging from smaller than to considerably larger than themselves. The special problems facing a spider that attempts to prey on another spider, especially a spider of similar or larger size, may help account for the complexity of the behavioral repertoires: the tables may be turned and the araneophagic predator may become its intended meal’s own meal. The fine control of variable signals may be crucial in enabling the aggressive mimic to gauge its attack before it is itself attacked by the intended victim.
Aggressive mimics are only one among many predators for the victimized spiders; other enemies such as birds and parasitoid wasps (Bristowe 1941) are probably more important for most species. It may be important that spiders practicing aggressive mimicry do not prey too heavily on any particular prey species. Otherwise, prey species might have evolved efficient means of avoiding predatory deceit and exploitation.

Is there any evidence that prey species have evolved defenses against aggressive mimics? The best example may be from interactions between *P. fimbriata* and *Euryattus* (Jackson and Wilcox 1990). While *P. fimbriata* is approaching, *Euryattus* females sometimes come out of their rolled-up leaves, and they suddenly and violently strike, leap at, or charge toward *P. fimbriata*. *Euryattus* may bang head on into *Portia* and knock *P. fimbriata* away at the end of a leap; after this encounter, *Euryattus* swings down on its dragline, then climbs back to the leaf. Once attacked, *P. fimbriata* always gives up, and *Euryattus* survives.

From observing thousands of interactions between *P. fimbriata* and many different species of salticids (Jackson and Hallas 1986a), it is evident that *Euryattus* is more efficient than other salticids at recognizing and defending itself against a stalking *P. fimbriata*. Laboratory tests provided corroborative data: *P. fimbriata* caught *Jacksonoides queenslandica*, another Queensland salticid on which it is known to prey, more efficiently than it caught *Euryattus* (Jackson and Wilcox 1990). Frequent predation by *P. fimbriata* on *Euryattus* appears to have resulted in *Euryattus* evolving special abilities to recognize and defend itself against this predator, suggesting that these two species may have been involved in a coevolutionary arms race (Abrams 1986).

Recent studies are consistent with coevolution. *P. fimbriata* is absent, but *Euryattus* present, in a second Queensland habitat which is only approximately 15 km away from the habitat where *Euryattus* and *P. fimbriata* are sympatric. In tests using laboratory-reared spiders, allopatric *Euryattus* only rarely evaded or attacked stalking *P. fimbriata*, and *P. fimbriata* caught allopatric more efficiently than sympatric *Euryattus*.1

The notion that it is advantageous for aggressive mimics not to prey too heavily on particular prey species has parallels in discussions of Batesian mimicry. A Batesian mimic is a palatable species that derives protection from potential predators by resembling aposematic species, which are consciously marked and unpalatable. Batesian mimics are apparently successful only if relatively rare (Turner et al. 1984).

Perhaps behavioral complexity is an important way for aggressive mimic spiders to appear rare to their prey. Because the prey spider receives different stimuli from the predator at different times, it might not perceive accurately the predator’s abundance. Also, by using a variety of signals and feeding methods, the aggressive mimic spider can exploit a wide spectrum of prey, reducing the frequency of interaction with any one prey species.

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**References cited**


