

- J. Sodroski *et al.*, *Nature (London)* **321**, 412 (1986); M. B. Feinberg, R. F. Jarrett, A. Aldovini, R. C. Gallo, F. Wong-Staal, *Cell* **46**, 807 (1986).
3. L. Philipson *et al.*, *Cell* **13**, 189 (1978); Y. Yoshinaka, I. Katoh, T. D. Copeland, S. Oroszlan, *Proc. Natl. Acad. Sci. U.S.A.* **82**, 1618 (1985); T. Jacks and H. E. Varmus, *Science* **230**, 1237 (1985).
4. H. E. Varmus and R. Swanstrom, in *Molecular Biology of Tumor Viruses*, R. A. Weiss, N. M. Teich, H. E. Varmus, J. M. Coffin, Eds. (Cold Spring Harbor Laboratory, Cold Spring Harbor, NY, 1984), p. 369.
5. F. di Marzo Veronese *et al.*, *Science* **231**, 1289 (1986).
6. M. M. Lightfoote *et al.*, *J. Virol.* **60**, 771 (1986).
7. S. D. Putney *et al.*, *Science* **234**, 1392 (1986).
8. A. J. Berk and P. A. Sharp, *Proc. Natl. Acad. Sci. U.S.A.* **75**, 1274 (1978).
9. R. D. Schiff and D. P. Grandgenett, *J. Virol.* **28**, 279 (1978).
10. N. Tanese, M. Roth, S. P. Goff, *Proc. Natl. Acad. Sci. U.S.A.* **82**, 4944 (1985).
11. M. L. Kotewicz, J. M. D'Alessio, K. M. Driftmier, K. P. Blodgett, G. F. Gerard, *Gene* **35**, 249 (1985).
12. N. Tanese, J. Sodroski, W. A. Haseltine, S. P. Goff, *J. Virol.* **59**, 743 (1986).
13. M. J. Roth, N. Tanese, S. P. Goff, *J. Biol. Chem.* **260**, 9326 (1985).
14. R. A. Kramer *et al.*, *Science* **231**, 1580 (1986).
15. R. Hanecak, B. L. Semler, H. Ariga, C. W. Anderson, E. Wimmer, *Cell* **37**, 1063 (1984).
16. S. Benn *et al.*, *Science* **230**, 949 (1985).
17. HIV polymerase was supplied by M. St. Clair and P. Furman and was purified from pelleted virus ob-

tained from HIV-infected H9 cells. The polymerase was purified by sequential DEAE and phosphocellulose column chromatography essentially as described by J. W. Abrell and R. C. Gallo [*J. Virol.* **12**, 431 (1973)].

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A Sheep in Wolf's Clothing: Tephritid Flies Mimic Spider Predators

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Mimicry where prey resemble predators to avoid predation is unusual. Snowberry flies, *Rhagoletis zephyria* Snow, possess striped wing patterns that resemble the legs of jumping spiders. Observations and comparisons of responses of the jumping spider *Salticus scenicus* (Clerck) to conspecifics, snowberry flies, and other prey flies showed that snowberry flies can avoid predation by jumping spiders through spider mimicry. The mimicry effect was decreased by obliterating snowberry fly wing stripes.

AGGRESSIVE MIMICRY, WHEREIN predators mimic their prey to facilitate prey capture, and Batesian mimicry, wherein harmless species copy coloration patterns of a protected (for example, toxic) species, have been well demonstrated for several biological interactions (1, 2). However, the case in which prey mimic their predators to avoid predation is rarely reported. We investigated the possibility

that tephritid fruit flies mimic one of their predators, jumping spiders. Since jumping spiders are territorial and tend to avoid conspecifics (3), flies mimicking them might avoid predation. The obvious similarity between these flies and jumping spiders arises from wing banding patterns and wing waving behavior common to many tephritid species. The wing banding pattern resembles that of spider legs (Fig. 1) (4).

The principal species of our study was the snowberry fly *Rhagoletis zephyria*, the mimic, and the common zebra spider *Salticus scenicus*, the model and predator. *Rhagoletis zephyria* is found throughout North America where snowberry, *Symphoricarpos albus*, bushes grow. The characteristic wing markings are common to all species in its sibling species complex (5). When disturbed by an approaching object, individuals within this species complex adopt a characteristic defensive display. Wings are brought slightly forward and a jerky side-to-side dance, similar in appearance to the gait of a jumping spider, is performed. Generally, the display will proceed until the approaching object withdraws or the fly leaves its position. The display dance is also employed in courtship and agonistic encounters between conspecific flies (6).

Zebra spiders are common throughout North America, where they inhabit walls, fences, bushes, and trees and pursue prey that include flies, moths, stinkbugs, and aphids; these can vary in size from a fraction of to more than twice a spider's size (7).

Jumping spiders capture their prey by first stalking those that they encounter within their visual field (8). Stalking spiders crouch and crawl "cat-like" toward their prey and, once within striking range, pounce upon and immobilize them.

To conduct our studies, snowberry flies were obtained from naturally infested snowberry bushes during 1985 (9), and zebra spiders were collected from building walls, wooden railings, and fence posts around the Simon Fraser University campus from May to August 1986. After capture, each spider was fed a single onion fly, *Hylemya antiqua*, housed in a glass jar and then starved for 2 days before testing.

To test whether or not snowberry flies mimic jumping spiders we performed a series of observational experiments within plexiglas arenas fitted with Plexiglas "observation domes" that confined prey and isolated them within view of the spiders. The domes were of sufficient size to allow prey to move freely within them and apparently provided a clear view of prey to the predator spiders (Fig. 2).

Individual spiders were released in arenas harboring single prey that were held within the observation dome. The behavior of each predator spider was recorded for up to 5 minutes or until it vacated a "reactive" zone that surrounded the observation dome. Based upon preliminary observations, we arbitrarily defined a reactive zone of 7 cm in diameter. When jumping spiders become aware of potential prey or conspecifics, they generally cease movement and then orient toward the object. Following this, stalking behavior begins (8) or the spiders either turn away and leave, or flee in an attempt to escape (7). The latter response is common during encounters with conspecifics, particularly since first inhabitants of territories, regardless of size, are dominant (3). Occasionally, when close encounters do occur,

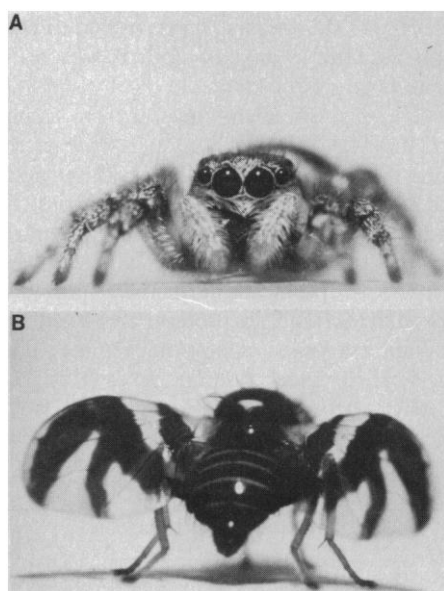


Fig. 1. (A) Front view of zebra spider *Salticus scenicus* and (B) posterior view of snowberry fly *Rhagoletis zephyria*. Note similarity between spider legs and fly wing markings.

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Table 1. Comparison of jumping spider responses to different potential prey held within the experimental arena. For comparisons between flee and pounce responses, Scheffe's multiple comparison tests were used; different letters in columns show statistically significant differences ($P < 0.05$). Comparisons of mean time (\pm SEM) spent in reactive zone employed Kruskal-Wallis analysis of variance tests ($P < 0.005$).

Prey	Sample (n)	Flee (%)	Pounce (%)	Time in reactive zone
Spider	40	47.5 a	5.0	32.9 \pm 7.2
House fly	40	2.5 b	60.0	77.9 \pm 12.1
Snowberry fly	76	32.8 ac	20.0	58.4 \pm 8.7
Blackened-wing snowberry fly	33	12.1 bc	38.0	95.7 \pm 17.15

obvious agonistic behaviors ensue, including leg waving and erect posture. Thus, the behaviors recorded for each trial were: stop, stalk, pounce, and flee (10). In addition, we recorded the length of time each spider spent within the reactive zone. No predator spider was tested more than twice, usually once, and all prey only once. Both sexes of spiders and snowberry flies were used.

We hypothesized that predatory jumping spiders would treat snowberry flies as if they were spiders. Thus, we compared the frequencies of spider behaviors (10) when released in arenas containing domes harboring either snowberry flies or conspecific spiders. As a control to ensure that similar spider response to spiders and snowberry flies was not an artifact of the experimental design, we ran trials in which house flies, *Musca domestica* (prey that neither possess wing stripes nor perform defensive display dances), were held in the observation domes. Here, we predicted that spiders would recognize such flies as prey and thus respond differently than they would to spiders in domes. As a further control to confirm that it is the wing stripes that cause spiders to treat snowberry flies as if they were spiders, we obliterated fly wing stripes with marking pen ink (11).

We analyzed our results by comparing the proportions of those spiders that either fled from or pounced at the four prey types. The results show that zebra spiders treated snowberry flies as if they were conspecifics (Table 1). Not only did spiders flee from snowberry flies at rates similar to those from which they fled from conspecific spiders, but also they fled at higher rates than from house flies (Table 1). Thus, house flies were pounced at much more often than snowberry flies or other spiders. In addition, the lengths of time spiders spent before vacating reactive zones when placed in arenas with different prey support the assumption that spiders spend more time with prey than with conspecifics or prey that mimic conspecifics (Table 1).

Results from our trials employing flies with obliterated wing stripes indicate that such markings are important in the mimicry

process. Spiders fled from those flies at far lower rates than from spiders but at rates intermediate to those from nonmanipulated snowberry flies and house flies (Table 1). That these markings are an essential but only partial component of the mimicry phenomenon can be shown by comparing spider response to normal striped-wing snowberry flies that displayed to approaching spiders with flies that did not. We found that spiders fled displaying flies more often than from nondisplayers (Table 2). A similar comparison of spider response to displayers and nondisplayers, each with obliterated wing stripes, showed no statistically significant differences (Table 2). Thus, we conclude that both wing markings and the manner in which wings are displayed are important components of the mimicry effect.

The ultimate test of the effectiveness of any supposed mimicry lies in the relative survivorship of mimics. We tested the hypothesis that snowberry flies lacking wing stripes would be more prone to spider predation than normally striped-wing flies by releasing two individuals of each type into a Plexiglas arena with a single zebra spider. We then recorded which fly type was captured first. Out of 27 such trials, flies with obliterated wing stripes were captured first 21 times ($P < 0.05$, G test). It is not likely that the higher mortality of these flies was due to the obliteration process (12).

Our results provide strong evidence that

Table 2. Comparison of jumping spider responses to displaying and nondisplaying snowberry flies with and without blackened wings. Comparisons employed G tests.

Snowberry fly	Spider response	
	Sample (n)	Flee (%)
Nondisplaying	31	9.7*
Displaying	45	46.6*
Nondisplaying, blackened wings	11	0.0†
Displaying, blackened wings	21	19.0†

* $P < 0.01$. †Not statistically significant.

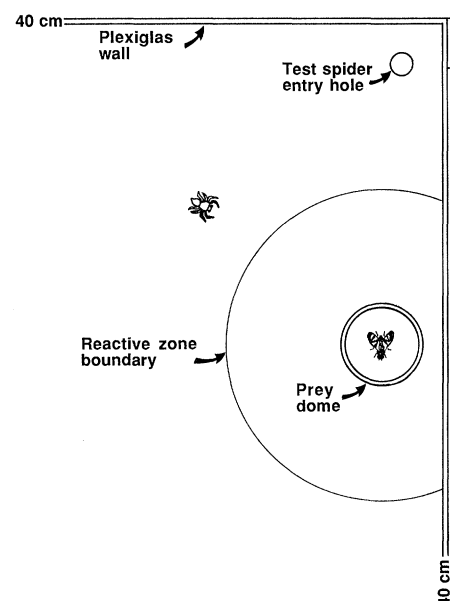


Fig. 2. Plexiglas arena in which spider reactions were observed. The floor was covered with orange cardboard to provide a visible surface. At the center of one side of the box, we placed a petri dish, 3 by 1 cm, facedown. The dish provided a dome to house the prey and allowed them to move about freely within a controlled position.

zebra spiders are deceived by snowberry fly wing patterns. Since many species of jumping spiders and tephritid flies have overlapping ranges and live in similar habitats, this form of mimicry may be widespread. Because jumping spiders use a wide range of prey species, there is probably little need for them to distinguish tephritid flies from conspecifics as long as their encounters with the flies are relatively infrequent. Whether spiders can learn to discriminate between conspecifics and mimics and to what degree mimicry might be effective at different mimic to model densities, is still to be determined.

REFERENCES AND NOTES

1. J. V. Z. Brower, *Evolution* **12**, 32 (1958).
2. J. E. Lloyd, *Science* **187**, 452 (1975); T. Eisner, K. Hicks, M. Eisner, *ibid.* **199**, 790 (1978).
3. A. R. Jacques and L. M. Dill, *Am. Nat.* **116**, 899 (1980).
4. L. G. Monteith, *Can. Entomol.* **104**, 257 (1972); T. Eisner, *Nat. Hist.* **11**, 112 (1984).
5. G. L. Bush, *Evolution* **23**, 237 (1968).
6. R. J. Prokopy and B. D. Roitberg, *Am. Sci.* **72**, 41 (1984).
7. A. N. Freed, *Zool. Soc. London* **203**, 49 (1984).
8. L. M. Dill, *Can. J. Zool.* **9**, 1284 (1975).
9. *Rhagoletis zephyria* maggot-infested-fruit were collected during September 1985 at Vancouver. The berries were placed on hardware cloth suspended over sand. Soon after, larvae dropped to the sand and pupated. The pupae were held at 5°C until the experiment began.
10. The spider behaviors recorded were (i) stop, the spider would abruptly cease movement and orient in the direction of the prey; (ii) stalk, the spider approached the dome, often with a flattened stance; (iii) pounce, the spider jumped directly at the dome; (iv) flee, the spider abruptly turned away from the dome and ran in the opposite direction to the dome; and (v) leave, the spider walked from the observation zone.
11. We obliterated the wing stripes by coloring the

wings with a black felt-tipped marker. Flies were first immobilized by chilling them at -10°C for about 30 seconds.

12. To determine that pen markings on the wing do not directly cause increased mortality, we maintained 20 flies, 10 of which we marked, within a Plexiglas cage. Mean age at death for each group did not differ (Mann-Whitney U test). Further, observations confirmed that flies did not behave differently after

marking, nor was their ability to flee spiders hampered.

13. This study was supported by an NSERC Canada operating grant to B.D.R. We thank L. Dill, R. Ydenberg, and R. Smith for reviewing the manuscript. We also thank L. Dill and B. Lalonde for advice and B. Lalonde for photographs.

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A Tephritid Fly Mimics the Territorial Displays of Its Jumping Spider Predators

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The tephritid fly *Zonosemata vittigera* (Coquillett) has a leg-like pattern on its wings and a wing-waving display that together mimic the agonistic territorial displays of jumping spiders (Salticidae). *Zonosemata* flies initiate this display when stalked by jumping spiders, causing the spiders to display back and retreat. Wing transplant experiments showed that both the wing pattern and wing-waving displays are necessary for effective mimicry: *Zonosemata* flies with transplanted house fly wings and house flies with transplanted *Zonosemata* wings were attacked by jumping spiders. Similar experiments showed that this mimicry does not protect *Zonosemata* against nonsalticid predators. This is a novel form of sign stimulus mimicry that may occur more generally.

MOST FORMS OF MIMICRY, SUCH as cryptic coloration or Batesian and Müllerian systems, confer protection against a wide array of predators (1). We describe a novel form of mimicry in which an organism mimics its major predator and thereby reduces the risk of being eaten by it. A tephritid fly, by mimicking the stereotyped aggressive behavior of one family of spiders, can escape from spiders of this family but not from other predators.

The fly *Zonosemata vittigera* (Diptera: Tephritidae) is purported to mimic jumping spiders (Araneae: Salticidae) (2, 3). Both sexes have dark wing bands, which resemble spider legs, and false eyespots on the end of the abdomen. When disturbed, these flies hold their wings perpendicular to the body and wave them up and down (Fig. 1A); this resembles the agonistic leg-waving behavior typical of the jumping spiders. However, there have been no experimental demonstrations that *Zonosemata* is a spider mimic.

Many flies have dark wing markings and wing-flicking displays, so *Zonosemata* might fortuitously resemble jumping spiders, but not gain protection from predators by these features. If *Zonosemata* is in fact a jumping spider mimic, it is not clear what types of predators are deterred. Since salticids are quick and have a poisonous bite, it has been suggested that a salticid mimic may be shunned by many vertebrate and arthropod predators (3).

Another possibility, which had not been suggested, is that *Zonosemata* displays may specifically mimic salticid territorial displays, and be effective only against salticid predators (4). Many salticids defend "privacy spheres" around themselves. When two meet they usually initially perform agonistic displays (which may turn into courtship displays depending upon sex and species) (5). These displays can be performed by juveniles and adults of both sexes and occur within and between species. Although the

precise details of these stereotyped behavioral displays vary intraspecifically, salticid agonistic displays generally commence with leg-waving (6).

To test the effect of the wing pattern and the wing-waving display on the behavior of jumping spiders and other potential predators, we transplanted wings between house flies (*Musca domestica*) and *Zonosemata* flies (7). House fly wings are the same general size and shape as *Zonosemata* wings, but they lack pattern. After this operation, the flies retained complete movement of their wings, and could display and fly normally (Fig. 1B).

Behavioral trials between jumping spiders and flies were conducted for 5 minutes in a glass-topped arena (8). Jumping spiders were collected on or around *Zonosemata* host plant (silver leaf nightshade, *Solanum elaeagnifolium*). Twenty jumping spiders representing 11 species (9) were each presented with five treatments: normal *Zonosemata*, *Zonosemata* with other *Zonosemata* wings (sham operation), *Zonosemata* with house fly wings, house flies with *Zonosemata* wings, and normal house flies. Each spider was presented with these treatments in a random order. All jumping spiders were hungry when tested: they were given water but no food for 2 days before the trial. Individual spiders were never tested more than twice in one day.

The wing pattern had a profound effect upon jumping spider behavior (Fig. 2). Normal *Zonosemata* and the sham-operated control flies were attacked or killed less frequently than flies in the three remaining treatments (10). There was no statistically significant difference in the jumping spiders' responses to the normal *Zonosemata* flies and the sham-operated control flies (homogeneity test, $G = 3.28$, $P > 0.1$), indicating that the operation itself did not affect spider responses. Jumping spiders began stalking these flies within seconds after the trial began. When the spider approached to within about 5 cm, *Zonosemata* flies usually began a vigorous wing-waving display. In response, the jumping spiders abruptly stopped stalking and waved their legs at the flies. The flies backed away in a zigzag fashion while waving their wings and flew off. Most jumping spiders made no further stalking attempts during the remaining 5 minutes. Jumping spiders were repelled from both the front and back of the flies. In



Fig. 1. (A) A female *Zonosemata vittigera* beginning its wing-waving display toward a stalking jumping spider (*Phidippus apacheanus*). The jumping spider stopped stalking, waved its legs at the fly, and then retreated. (B) A *Zonosemata vittigera* fly with transplanted house fly wings. Such flies can display normally and fly.

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