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RESEARCH NOTES

SPIDER VS. SPIDER: *FRONTINELLA PYRAMITELA* DETECTS *ARGYRODES TRIGONUM* VIA CUTICULAR CHEMICALS

Interspecific chemical communication is known among spiders in the contexts of their use of chemotactile information in identifying prey species (e.g., Robinson and Olazarri 1971) and their attraction of prey species with chemical lures (Eberhard 1977, 1981; Horton 1979). We know of no reports, however, of spiders detecting and discriminating among heterospecifics that might, themselves, prey on the spiders doing the chemical sensing.

Several researchers have reported that members of the genus *Argyrodes* (Theridiidae) sometimes prey upon spiders with which they cohabit in an otherwise kleptoparasitic or commensal manner (e.g., Exline and Levi 1962; Lamore 1958). Wise (1982), in an experimental field study, showed that the predatory (i.e., host-killing) behavior of *Argyrodes trigonum* (Hentz) is more common than was previously realized, at least when the host is relatively small. Predation on larger spiders such as the agelenid *Agelena limbata* Thorell is also known (Tanaka 1984), and Larcher and Wise (1985) have shown that some of the relationships between *A. trigonum* and its host species can be quite complex.

One of the common hosts of *A. trigonum* in the northeastern United States is the bowl and doily spider, *Frontinella pyramitela* (Walckenaer) (Linyphiidae). The relationship between these two species is frequently kleptoparasitic but is also predatory. Archer (1946) reported *A. trigonum* preying on *F. pyramitela*, and more recently Suter (1985) reported the same phenomenon. Whatever the character of the interaction between the two species, it is certainly intense: during part of the summer, the kleptoparasite/predator inhabits about 20% of all bowl and doily webs and causes the departure or death of many of the hosts (Suter 1985). Moreover, indirect evidence suggests that the two species have interacted frequently and over a long period of time: female bowl and doily spiders, though larger than their mates, permit males to capture prey on the females' webs, and the function of that permissiveness may be to deflect (onto the males) the risk of being captured by *Argyrodes* and other prey-mimicking spiders (Suter 1985).

In the work reported here, we sought to determine whether physical contact between a bowl and doily spider and its kleptoparasite/predator was chemically informative from the host's perspective, and whether the information gained was predator-specific.

Female bowl and doily spiders and the kleptoparasitic *A. trigonum* were captured on *F. pyramitela* webs in Poughkeepsie, NY, during June, 1985. Juvenile instars of a crab spider, *Misumenoides* sp. (Thomisidae) that were approximately the same size as adult *A. trigonum* were also captured in June. These eventually served as a check on whether the responses of *F. pyramitela* to contact with the kleptoparasites' carcasses were species specific. The bowl and doily spiders were maintained in the laboratory using methods described elsewhere (Suter 1985). Soon after their capture, both *A. trigonum* and *Misumenoides* sp., as well as several *F. pyramitela*, were killed by freezing and stored frozen until they were prepared for testing.

A. trigonum carcasses were either left intact (not chemically modifed) or washed in hexane for 30 minutes. Because of our experience with the cuticular pheromones of *F. pyramitela* (Suter et al. 1987), we expected that treatment with hexane would remove behaviorally active chemicals found on the surfaces of the carcasses.

The assay arena consisted of the web of an adult female bowl and doily spider with the carcass of another spider cemented to it. The carcass was cemented with droplets of Testor's paint (behaviorally neutral after drying) near the center of the underside of the bowl in the location normally occupied by the owner of the web. Several hours later, the completed arena was used in behavioral tests. At the start of a test, we released a female bowl and doily spider onto the bowl of a web that contained a heterospecific or a conspecific female carcass. Oriented search behavior (Suter 1984) usually brought the assay female into contact with the carcass after less than 30 seconds. The first contact with the carcass began the behavioral assay, which ended 5 minutes later. The initial contact and subsequent behaviors were videotaped from above while a voice record of the behaviors visible from the side of the web was made on one of the tape's audio channels. We analysed both immediate post-contact behavior and later behaviors, though we did not consider any behaviors that took place >5 minutes after initial contact.

Apart from normal locomotion, three distinct behaviors followed the assay spider's contact with a carcass: *flinch*—the rapid withdrawal of the first two pairs of legs from the immediate vicinity of the carcass without displacement of the assay spider's body; *touch-retreat*—a rapid leap away from the carcass resulting in displacement of the assay spider's body and a change in the orientation of the body relative to the carcass; and *feeding*—the insertion of the assay spider's fangs into the body of the carcass and the beginning of ingestion.

Contact with the four classes of test carcasses (intact *F. pyramitela*, intact and washed *A. trigonum*, and intact *Misumenoides* sp.) resulted in different arrays of behaviors from the assay spiders (Table 1). Contact with an intact carcass of the predatory kleptoparasite, *A. trigonum*, nearly always elicited touch-retreats from the assay spider whereas contact with *F. pyramitela* carcasses seldom did and contact with hexane-washed *A. trigonum* and with *Misumenoides* sp. never did. The assay spiders rarely fed on the carcass of an intact *A. trigonum* but often fed upon the carcasses of the other three classes of spiders.

During the five minutes of any particular test, the number of touch-retreats reflected the identity of the carcass: the host species elicited significantly fewer touch-retreats ($N = 35$, median = 0) than did the kleptoparasitic predator ($N = 71$, median = 3; 1-tailed Mann-Whitney test, $Z = -6.09$, $P < 0.001$). The orientation of the assay spider immediately after a touch-retreat also reflected, though less strongly, the identity of the carcass: following a touch-retreat, the assay spider was significantly more likely to be facing away from the carcass if the carcass was *A. trigonum* ($N = 70$, median = 120°) than if it was *F. pyramitela* ($N = 16$, median = 97°; 1-tailed Mann-Whitney test, $Z = -1.96$, $P < 0.025$). (Note that in the

Table 1.—Incidences of behaviors performed by female *F. pyramitela* during the 5 minutes immediately following contact with the carcass of a conspecific or heterospecific spider. Decimals indicate the fraction of trials during which a particular behavior was performed.

	Incidence of			
	Touch/ Retreats	Flinches	Feeding	*N*
A. trigonum	0.96	0.18	0.04	*28*
Washed *A. trigonum*	0	0.20	0.30	*20*
F. pyramitela	0.27	0.10	0.32	*30*
Misumenoides sp.	0	0.10	0.50	*20*
χ^2	68.11	1.57	9.45	
P	<0.001	>0.50	<0.01	

preceding analysis of orientation, circular statistical tests could not legitimately be applied because the data were semicircular.) Finally, although the post-contact orientation of the assay spider and the retreat distance were positively correlated ($r = 0.373$, $P < 0.01$) over all touch-retreats, the retreat distance did not vary significantly with carcass identity.

Our results indicate that female bowl and doily spiders respond differentially to contact with the surfaces of conspecific females and two different taxa of heterospecifics. Because the major differences are eliminated after *Argyrodes trigonum* carcasses are washed in hexane, we conclude that the relevant differences are chemical rather than structural.

Because 1) the carcasses of the theridiid and the thomisid are treated very differently by *F. pyramitela* and 2) responses to carcasses of the kleptoparasitic predator are least like responses to the two other types of intact spiders, we further conclude that the assay spiders respond to the *A. trigonum* carcasses in a way that is specific to the genus or species of the carcass. The validity of this conclusion would be suspect if it were not for the apparent appropriateness of the host spider's response to contact with the kleptoparasitic predator. We know that contact with a living *A. trigonum* is sometimes fatal to the host (references above) and thus is to be avoided. We should expect, then, to find that chemotactile recognition of *A. trigonum* would be followed immediately by flight or other rapid withdrawal, and that is exactly what the data show. Because feeding requires intimate contact between the host and the carcass, we should also expect feeding on *A. trigonum* to be suppressed, and it apparently is.

The ability of bowl and doily spiders to discriminate among potential predators based on chemical information is not surprising given their similar abilities in the realm of intraspecific communication (Suter et al. 1987 and references therein). Because the detection of predators' chemicals by prey is well documented in other arthropod taxa (e.g., ants; Carlin and Johnston 1984), the near absence (Tretzel 1959) from the literature of other examples of spider-to-spider interspecific chemical communication suggests that the phenomenon demonstrated here is either rare or has been rarely sought.

The specificity and appropriateness of *F. pyramitela*'s responses to contact with *A. trigonum* carcasses suggests that the two species have interacted intensely over relatively long periods of time. The same logic suggests that one might expect to find interspecific communication of a specific and appropriate nature whenever two spider species are known to have interacted frequently over the course of many generations. Because such relationships are probably rare, the accompanying communication may also be found only infrequently.

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LITERATURE CITED

Archer, A. F. 1946. The Theridiidae or comb-footed spiders of Alabama. Alabama Mus. Nat. Hist. Papers, 22:1-67.

Carlin, N. F. and A. B. Johnston. 1984. Learned enemy specification in the defense recruitment system of an ant. Naturwissenschaften, 71:156-157.

Eberhard, W. G. 1977. Aggressive chemical mimicry by a bolas spider. Science, 198:1173-1175.

Eberhard, W. G. 1981. The single line web of *Phoroncida studo* Levi (Araneae, Theridiidae): A prey attractant? J. Arachnol., 9:229-232.

Exline, H. and H. W. Levi. 1962. American spiders of the genus *Argyrodes* (Araneae, Theridiidae). Bull. Harvard Mus. Comp. Zool., 127:75-204.

Horton, C. C. 1979. Apparent attraction of moths by the webs of araneid spiders. J. Arachnol., 7:88.

Lamore, D. H. 1958. The jumping spider, *Phidippus audax* Hentz, and the spider *Conopistha trigona* Hentz as predators of the basilica spider, *Allepeira lemniscata* Walckenaer in Maryland. Proc. Ent. Soc. Washington, 60:286.

Larcher, S. F. and D. H. Wise. 1985. Experimental studies of the interactions between a web-invading spider and two host species. J. Arachnol., 13:43-59.

Robinson, M. H. and J. Olazarri. 1971. Units of behavior and complex sequences in the predatory behavior of *Argiope argentata* (Fabricius):(Araneae: Araneidae). Smithson. Contrib. Zool., 65:1-36.

Suter, R. B. 1984. Web tension and gravity as cues in spider orientation. Behav. Ecol. Sociobiol., 16:31-36.

Suter, R. B. 1985. Intersexual competition for food in the bowl and doily spider, *Frontinella pyramitela* (Araneae, Linyphiidae). J. Arachnol., 13:61-70.

Suter, R. B., C. M. Shane and A. J. Hirscheimer. 1987. Communication by cuticular pheromones in a linyphiid spider. J. Arachnol., 15:157-162.

Tanaka, H. 1984. Rate of predation by a kleptoparasitic spider, *Argyrodes fissifrons*, upon a large host spider, *Agelena limbata* (Araneae). J. Arachnol., 12:363-368.

Tretzel, E. 1959. Zum Begegnungsverhalten von Spinnen. Zool. Anz., 163:194-205.

Wise, D. H. 1982. Predation by a commensal spider, *Argyrodes trigonum*, upon its host: an experimental study. J. Arachnol., 10:111-116.

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