

Disturbance behaviors in the spider *Uloborus glomus* (Araneae, Uloboridae): possible predator avoidance strategies

PAULA E. CUSHING AND BRENT D. OPELL

Department of Biology, Virginia Polytechnic Institute and State University, Blacksburg, VA 24061, U.S.A.

Received May 25, 1989

CUSHING, P. E., and OPELL, B. D. 1990. Disturbance behaviors in the spider *Uloborus glomus* (Araneae, Uloboridae): possible predator avoidance strategies. *Can. J. Zool.* **68**: 1090–1097.

When disturbed, *Uloborus glomus* either remain in position at the hub of their orb webs, jump from the web, move to the edge of the web, or shake the web. Juveniles more frequently exhibited moving and jumping responses, whereas the majority of adults jumped from the web or remained in position. Adults with linear stabilimenta tended to shake their webs in the morning and to jump from their webs in the evening. Juveniles with linear stabilimenta shook their webs in the afternoon and evening, whereas those with circular stabilimenta tended to move to the edge of the web or shake the web during all times of day. Adult females with egg-sac chains were usually aligned with the egg sacs and tended to remain in position when disturbed. Both adults and juveniles lacking stabilimenta or egg-sac chains tended to jump from their webs or move to the edge of their webs. Spiders filmed in a natural setting responded to contact by insects. Predatory wasps repeatedly flew near the spiders without eliciting a response. A tethered predatory wasp held above both juveniles and adults in the laboratory also failed to elicit responses from the spiders. The data agree with the hypothesis that moving to the edge of, shaking, and jumping from the web may be predator avoidance strategies elicited by direct contact.

CUSHING, P. E., et OPELL, B. D. 1990. Disturbance behaviors in the spider *Uloborus glomus* (Araneae, Uloboridae): possible predator avoidance strategies. *Can. J. Zool.* **68**: 1090–1097.

En cas d'alerte, *Uloborus glomus* s'accroche au centre de sa toile, saute hors de sa toile, se déplace vers sa bordure ou la fait vibrer. Les araignées juvéniles ont surtout des réactions de déplacement ou de saut, alors que la majorité des adultes sautent hors de leur toile ou ne bougent pas. Les adultes à stabilimentums linéaires ont tendance à faire vibrer leur toile le matin et à sauter hors de leur toile le soir. Les juvéniles à stabilimentums linéaires font vibrer leur toile l'après-midi, alors que les juvéniles à stabilimentums circulaires ont tendance à se déplacer vers la bordure ou à faire vibrer leur toile en tout temps de la journée. Les femelles adultes qui portent des cocons ovigères se tiennent ordinairement en ligne avec leurs cocons et ont tendance à garder leur position en cas d'alerte. Les adultes et les juvéniles sans stabilimentums ou sans cocons ont tendance à sauter hors de leur toile ou à se déplacer vers sa bordure. Des araignées filmées dans leur habitat naturel ont réagi au contact d'insectes. Des guêpes prédatrices ont volé plusieurs fois vers les araignées sans susciter de réaction. En laboratoire, les araignées juvéniles et adultes sont restées sans réaction en présence d'une guêpe prédatrice attachée et maintenue au-dessus de la toile. Les données corroborent l'hypothèse selon laquelle les déplacements vers la bordure de la toile, le tremblement de la toile ou les sauts hors de la toile constituent probablement des stratégies de fuite en réaction à un contact direct avec des prédateurs.

[Traduit par la revue]

Introduction

Although spiders are important prey items of some wasps, birds, and other spiders (Bristowe 1941; Krombein 1967; Robinson and Valerio 1977; Pyke 1980; Johnsgard 1983; Coville 1987), few studies investigate the defensive mechanisms they use to avoid predation. This study has four objectives: (i) to define more precisely and describe the responses to disturbance shown by an orb-weaving species, (ii) to survey adult and juvenile populations of the species to determine what factors influence the expression of the disturbance behaviors, (iii) to document on film actual encounters between the orb weaver and its natural predators, and (iv) to determine what stimuli (vibratory, visual, or contact) elicit the disturbance behaviors.

We studied the orb weaver *Uloborus glomus* (Walckenaer), family Uloboridae. These horizontal orb weaving spiders are common throughout the eastern United States and are abundant on the shrubbery of the Virginia Polytechnic Institute and State University (VPIU) campus (Cushing 1988). Spiderlings emerge from egg sacs as 2nd instars and reach maturity in the 6th instar. Mature females have a cephalothorax–abdomen length of 10–12 mm. Uloborids build their webs at night, but monitor them and capture prey during both day and night. During the day, both juvenile and adult *Uloborus* hang from the underside of their orb webs in what appears to be a twiglike cryptic posture (Opell and Eberhard 1984) (Fig. 1A). They remain in this posture except when wrapping prey and when feeding at the

web's hub (Fig. 1B). The legs of these spiders display disruptive coloration and the first legs are beset with a setal brush (Fig. 1A).

Mature female *U. glomus* and juvenile spiders often add linear bands of silk stabilimenta to the hubs of their orb webs (Fig. 1B). Some juveniles add a circular stabilimentum platform to the hubs of their webs (Fig. 1D) (Cushing 1988). Mature female *U. glomus* deposit their stellate egg sacs in a chain that extends along a radius from the web's perimeter toward its hub. When an egg-sac chain is present, a female typically positions herself adjacent to the most recently deposited (most centripetal) egg sac where her linear posture makes it very difficult to distinguish spider from egg-sac chain (Fig. 1C). During this time, females continue to feed and maintain their webs. The linear and circular stabilimenta and the linear chain of egg sacs may function as cryptic devices, concealing the spider from visually hunting predators (Hingston 1927; Bristowe 1941; Marson 1947a, 1947b; Marples 1969; Ewer 1972; Eberhard 1973; Tolbert 1975; Levi 1977; Lubin 1980).

We formulated three hypotheses: (i) the disturbance behaviors shown by *U. glomus* are predator avoidance strategies and will be expressed at different frequencies throughout the day, reflecting changes in predatory pressure; (ii) the stabilimenta and egg-sac chains are functioning as cryptic devices and spiders that have these structures and are aligned with them are less likely to show active avoidance behaviors when disturbed; and (iii) because these disturbance behaviors protect spiders

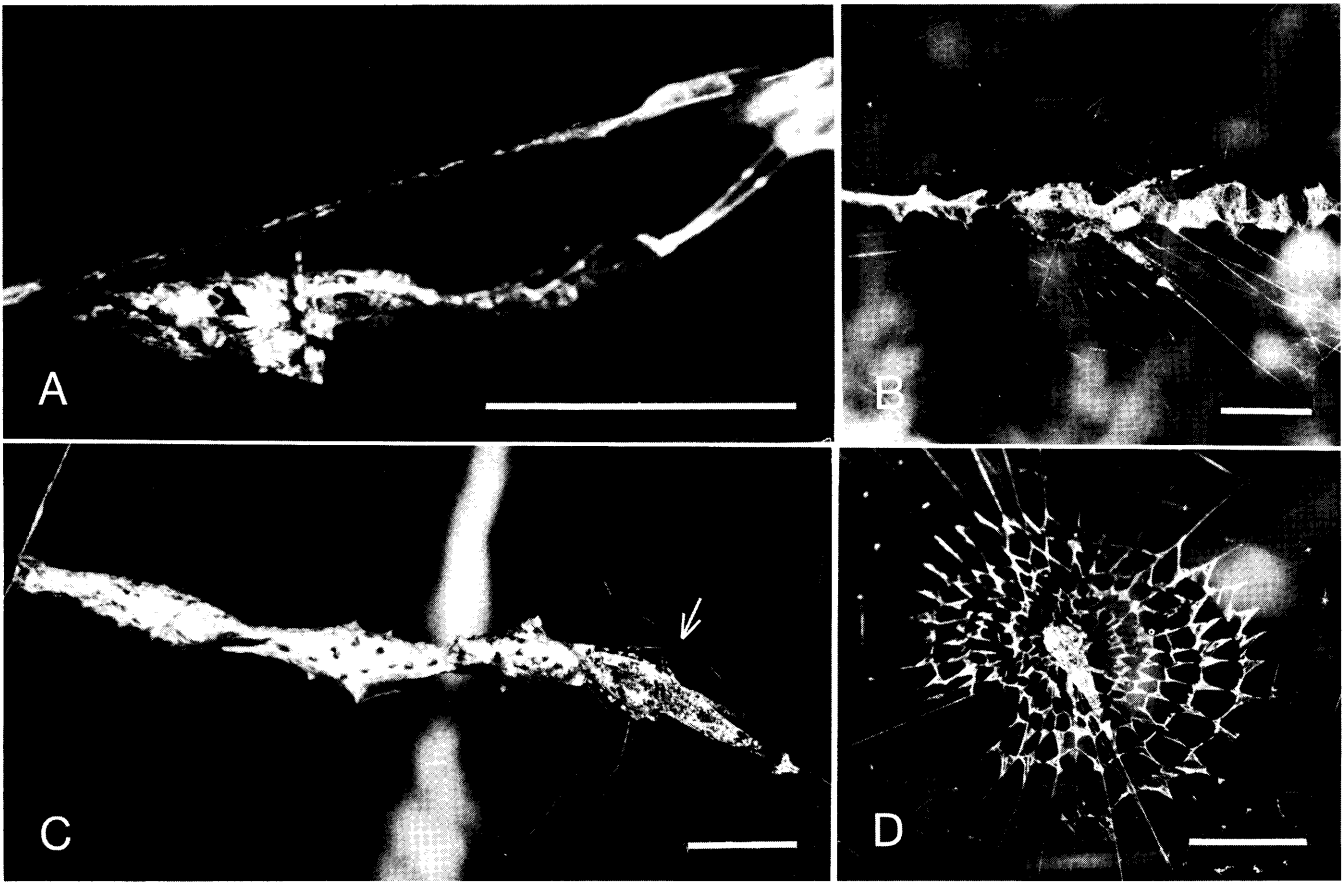


FIG. 1. (A) Adult female *U. glomosus* in a cryptic posture. (B) Female feeding at the hub of a web aligned with a linear silk stabilimentum. (C) Female aligned with an egg-sac chain (arrow points to the spider). (D) Circular stabilimentum platform of a juvenile web. Bar, 5 mm.

from hunting wasps, they are elicited by the vibratory stimuli of a flying wasp.

Methods

Description of the behaviors

To more precisely define and describe the disturbance behaviors, we collected adult females on campus and established them on frames in a greenhouse where we filmed them with a Super 8 mm movie camera as they jumped from and shook their webs in response to contact stimuli (the tip of a finger). Since uloborids often shake their webs during prey capture, we also filmed the shaking behavior of an adult female when fruit flies were placed in her web.

Survey of adults

Adult spiders living in shrubbery at three sites on the VPI&SU campus were studied during June and July, 1986. We made 222 observations during the morning (08:00–10:00), 227 during the afternoon (12:00–14:00), and 146 during the evening (17:00–19:00) for a total of 595 observations. Since adult male *U. glomosus* do not build typical capture webs (Opell 1979), we used only adult females in this survey. Temperature was inadvertently recorded during only one of three mornings during which observations were made (25.9°C) and two of three afternoons (mean = 35.6°C, SD = 2.62). The mean evening temperature was 28.5°C (SD = 0.38, $n = 3$).

Four variables were recorded during the adult survey: (i) time of day, (ii) the presence of a stabilimentum or of an egg-sac chain, called stab sac, (iii) alignment of the spider with either stabilimentum or egg-sac chain, and (iv) response of the spider to disturbance. Each variable had several categories, each assigned a number for the analysis (Table 1).

As a stimulus, we lightly touched the venter of each spider through the web with a 13 mm diameter rubber pipette bulb on the end of a 45 cm long dowel rod. Using the dowel rod minimized the influence of

the observer's presence. The rubber bulb was considered an approximately standardized stimulus, similar in size to the rubber pencil eraser used by Tolbert (1975) in his study of predator avoidance behaviors. This stimulus was assumed to simulate the sudden contact of an attacking predator. The data were analyzed using a log-linear analysis designed for multivariate categorical data (Bishop *et al.* 1975; Fienberg 1987).

Survey of juveniles

During August and September 1987, we conducted a similar survey of juvenile *U. glomosus* in the field. To determine the stadia of juvenile spiders we collected every 10th individual and measured the length of its carapace and first femur. We compared these data with the values used by Opell (1987) to assess the stadia of *U. glomosus* from the same population.

This survey differed from the adult survey in four ways. (i) As juvenile *U. glomosus* males spin typical capture webs, this survey included both males and females. As male and female uloborids cannot be easily distinguished until they enter the penultimate (5th) instar, the sex of the individuals tested could not be determined. (ii) Being juveniles, these spiderlings never had egg-sac chains in their webs and some individuals had circular rather than linear silk stabilimenta. (iii) The stimulus used for this juvenile survey was a 4 mm diameter plastic sphere affixed to the end of a 15 cm long wooden applicator stick. Relative to spider size, this stimulus was approximately the same size as that used in the adult survey. Although predators probably feed on both adult and juvenile spiders, the smaller stimulus used for juveniles allowed us to better observe their responses. (iv) Morning, afternoon, and evening subsurveys were conducted at different bushes within the limits of each site, ensuring that no individual was tested more than once. Adults and juveniles from the different sites on campus were assumed to be samples from a single population, although dispersal distances for these spiders have not been determined.

TABLE 1. Categories of each of the four variables used in the log-linear analyses

Variable	Category
Time	1. Morning 2. Afternoon 3. Evening
Stab sac	1. Linear silk stabilimentum 2a. Egg-sac chain (adults) 2b. Circular stabilimentum (juveniles) 3. Neither
Alignment	1. Aligned* 2. Not aligned† 3. No web structure to align with
Response	1. Jumped from the web 2. Moved to the edge of the web 3. Remained in position 4. Shook the web

*Long axis of the spider's body aligned with the web structure.

†Long axis of the spider's body not aligned with the web structure or the spider away from the hub.

There were 1800 total observations in this survey: 600 each during the morning, afternoon, and evening. At the times observations were made, the mean morning temperature was 20.2°C (SD = 3.24, $n = 9$); the mean afternoon temperature was 25.3°C (SD = 2.09, $n = 10$); and the mean evening temperature was 24.3°C (SD = 3.07, $n = 8$).

As in the adult survey, at each site we recorded time of day, presence of a silk stabilimentum, alignment with the stabilimentum, and disturbance behavior shown by the spiderling. These data were also analyzed using a log-linear analysis.

Predatory encounters

We used a VHS (video home system) camera to obtain qualitative information on the adaptive value of these behaviors as predator avoidance strategies. The camera was set up on a tripod on the open porch of a farmhouse in rural Montgomery County, VA, that supported a natural population of *U. glomosus*. An adult *U. glomosus* female was allowed to build a web within a 22 × 22 cm square horizontal frame constructed of wooden dowel rods. This frame was then hung from the rafters of the porch directly beneath an active mud dauber nest (*Trypoxylon* sp.). When a spider disappeared or refused to build a web for several days, it was replaced with another adult female. Each day after filming, spiders were fed with fruit flies (*Drosophila* sp.) blown into their webs. Eight females were filmed for approximately 50 days from about 08:00 to 19:00, from late June through August, 1987. We used 6-h VHS videocassette tapes to minimize disturbance during the filming episodes and reviewed them in fast-forward mode.

Stimulus experiment

We established fourteen 2nd- and 3rd-instar spiderlings (reared in the laboratory from a single egg sac) and nine adult females in an experimental room with an average temperature of 22.3°C (SD = 3.13, $n = 12$). Each spiderling was placed in a 10.5 × 10.5 × 8.5 cm plastic freezer container with wooden applicator sticks glued inside for web attachment. Each adult was placed in a 31 × 16.5 × 9 cm plastic shoebox with wooden dowel rods glued inside.

We used a tethered spider-hunting wasp of the family Pompilidae to test the combined effects of visual and vibratory stimuli. A long piece of thread was glued to the wasp's thorax and inserted through a clear plastic drinking straw so that the wasp could be controlled without impairing its wing movement.

To test the responses of the spiders to a contact stimulus, we dropped water on the venter of each using Pasteur pipettes. This stimulus was suggested by W. G. Eberhard (personal communication), as it is more easily standardized than touching spiders with a probe. Preliminary observations showed that spiders responded similarly to a water drop as

to contact by a probe. Pipettes used for juveniles had an average tip diameter of 0.51 mm and those used for adults, 1.20 mm. Several days after testing for the effects of the contact stimulus, we tested for the effects of visual and vibrational stimuli by slowly lowering the buzzing wasp over each spider until its legs were within 1–3 cm of the spider. Several days later, we again tested all 23 spiders for their responses to contact with a water droplet. The data were analyzed using two-way contingency table analyses.

To determine the wingbeat frequency of tethered spider-hunting Sphecidae wasps and of the Pompilidae wasp used in this experiment, we made direct recordings on a Sona-Graph 7029-A sound spectrograph.

Analysis

To evaluate the association between the variables recorded during the surveys, we fitted the data to a log-linear model using the BMDP statistical software package (Bishop *et al.* 1975; Fienberg 1987; Dixon 1981). This analysis is designed for multidimensional contingency tables. The log-linear analysis provides a model that describes the entire data set, defining any associations (two-way and higher order associations) between variables. Using this analysis, the magnitude of the interaction among the categories of the associated variables in the chosen model can also be assessed by calculating ratios of the log-linear parameter estimates to the standard errors.

Parameter estimates are calculated under the assumption of normality. Therefore, ratio terms $> |1.96|$ (corresponding to p values < 0.05 in a normal Z-table) indicate categories that contribute significantly to the association between the variables (Bishop *et al.* 1975; Kennedy 1983). Positive and negative ratios indicate a positive and negative association between the categories, respectively.

Results

Description of the behaviors

The Super-8 films showed that jumping behavior has several distinct elements. (i) The spider propels itself off the web anteriorly, at an angle of approximately 16° to the vertical. (ii) It releases a variable length of dragline silk attached to the web's hub and hangs at the end of this dragline in a cryptic posture. Both at the hub and at the end of the dragline, the spider maintains an approximately horizontal orientation, although at the hub the long front legs are bent at the tibiae–metatarsus joint about 80°, whereas at the end of the dragline the legs are bent at this joint only about 25°. (iii) After an interval of a few seconds to 20 min, the spider swings upward and grasps the dragline with the first two pairs of legs. It uses these legs to ascend the dragline to the web's hub. (iv) The spider stops from one to five times on its ascent. At each stop, it reassumes the cryptic posture, orienting itself vertically rather than horizontally, with the long first legs directed toward the web and bent at the tibiae–metatarsus joint about 90°.

The shaking behavior, induced by touching the spider's venter, consists of rhythmic oscillations that continue for several seconds. It also has unique features: the spider alternately flexes and extends its long front legs and, to a lesser extent, the second pair of legs. These sudden flexion–extension sequences result in the rhythmic movement of the spider's body and set up web oscillations.

Super-8 films showed that the shaking behavior prior to prey wrapping consists of a different set of movements, resulting principally from alternate flexion and extension of the third pair of legs and from alternate lowering and raising of the abdomen. The fourth pair of legs primarily serves to hold onto the web.

Frequency of avoidance behaviors

Tables 2 and 3 present the observed frequencies of adult and juvenile behaviors permitting comparisons with the behavioral

TABLE 2. Survey of adult responses to contact stimuli (total number of observations was 595)

Stab sac	Alignment	Time	Responses			
			Jumped	Moved	Remained	Shook
Linear	Yes	Morning	30	7	3	5
		Afternoon	19	12	5	1
		Evening	21	7	1	0
	No	Morning	4	2	0	0
		Afternoon	8	0	1	0
		Evening	11	1	0	0
Egg sac	Yes	Morning	37	1	74	4
		Afternoon	23	3	57	1
		Evening	16	6	38	0
	No	Morning	1	0	2	0
		Afternoon	6	0	1	0
		Evening	5	0	0	1
Neither	—	Morning	32	11	7	2
		Afternoon	58	17	7	8
		Evening	28	9	0	2
Total			299	76	196	24
%			50	13	33	4

TABLE 3. Survey of juvenile responses to contact stimuli (total number of observations was 1800)

Stab sac	Alignment	Time	Responses			
			Jumped	Moved	Remained	Shook
Linear	Yes	Morning	90	121	13	40
		Afternoon	85	124	7	82
		Evening	114	156	17	119
	No	Morning	8	20	0	7
		Afternoon	25	42	1	19
		Evening	14	27	4	27
Circular	Yes	Morning	9	23	3	6
		Afternoon	13	23	0	14
		Evening	8	13	2	12
	No	Morning	0	0	0	2
		Afternoon	0	0	0	0
		Evening	0	0	0	1
Neither	—	Morning	63	152	11	32
		Afternoon	34	79	3	49
		Evening	22	37	4	23
Total			485	817	65	433
%			27	45	4	24

tendencies suggested by log-linear analyses (below). The majority of adults jumped from their webs in response to contact and most of the spiders that remained in position had egg-sac chains in their webs. The majority of juveniles moved to the edge of the web in response to contact and very few remained in position.

Survey of adults

Spiders that had neither silk stabilimenta nor egg sacs in

their webs had no web structures with which to align. Therefore, the data for these spiders were analyzed separately. A two-way contingency table analysis comparing the association between the time of day and the response variables indicated independence between the two variables ($G^2 = 9.94$, $p = 0.1273$, $df = 6$). Therefore, a log-linear analysis fitted these data to a model that treated the time and the response variables separately (i.e., two-way or higher order association terms were omitted from the model).

TABLE 4. Ratio terms (Z-values) for the response $\times$ time, response $\times$ stab sac, response $\times$ alignment, time $\times$ alignment, and stab sac $\times$ alignment associations of adults with linear stabilimenta and adults with egg-sac chains

	Response				Alignment	
	Jumped	Moved	Remained	Shook	Yes	No
Time						
Morning	-0.785	-2.879*	-0.733	2.432*	2.733*	-2.733*
Afternoon	-0.321	0.817	0.703	-0.564	-0.946	0.946
Evening	0.864	1.819	-0.056	-1.149	-2.168*	2.168*
Stab sac						
Linear	1.839	4.674*	-7.856*	0.967	-2.117*	2.117*
Egg sac	-1.839	-4.674*	7.856*	-0.967	2.117*	-2.117*
Alignment						
Yes	-2.711*	0.726	1.886	-0.482	—	—
No	2.711*	-0.726	-1.886	0.482	—	—

* $P < 0.05$.

The ratio of the log-linear parameter estimate to its standard error showed that spiders with no web structures tend to jump from their webs when disturbed (ratio = 10.979), tend not to remain in position (ratio = -3.379), and tend not to shake the web (ratio = -3.852). For this and all other models in which the time and response variables were analyzed separately, only the ratios of the response variable are reported, since the ratios of the time variable simply reflect sampling patterns which do not affect the results of the response analysis.

A log-linear model selected for adults with linear stabilimenta or egg-sac chains in the hubs of their webs indicated that there were two-way associations between the following five pairs of variables: time and response, time and alignment, response and alignment, response and stab sac, and stab sac and alignment ($G^2 = 30.99$, $p = 0.1892$, $df = 25$). Adding the two-way associations between time and stab sac did not improve the fit of the model. No higher order associations (i.e., three-way) contribute significantly to the fit of the model.

This model indicated that adults with egg-sac chains exhibit different behaviors when disturbed than do females with linear stabilimenta and that they are aligned with their egg sacs far more often than spiders with linear stabilimenta are aligned with these structures (Table 4). Only 6% of the spiders with egg-sac chains were not aligned, whereas 20% of spiders with linear stabilimenta were not aligned. This is a significant difference ($G^2 = 7.92$, $p < 0.005$, $df = 1$). Because of these findings and because Cushing (1988) found that females remaining aligned with their egg sacs actively protected them against parasitoid wasps, we deemed it inappropriate to equate the functional significance of egg-sac chains and linear stabilimenta. Therefore, we analyzed the data for spiders with linear stabilimenta separately from the data for spiders with egg-sac chains.

The log-linear model selected for adults with linear stabilimenta in the hubs of their webs indicated two pairwise associations among the variables ($G^2 = 12.40$, $p = 0.1344$, $df = 8$): one between time and response and another between time and alignment. Adding a two-way association term between response and alignment or a three-way term among time, response, and alignment did not significantly increase the fit of the model. This model indicated that, in the morning, spiders with linear stabilimenta tend not to move to the edge, but do tend

TABLE 5. Ratio terms (Z-values) for the time $\times$ response and time $\times$ alignment associations of adults with linear stabilimenta

	Time		
	Morning	Afternoon	Evening
Response			
Jumped	-1.939	-1.942	2.119*
Moved	-2.178*	-1.119	1.829
Remained	-1.488	0.000	1.488
Shook	2.169*	1.580	-2.031*
Alignment			
Yes	1.724	-0.075	-1.862
No	-1.724	0.075	1.862

* $P < 0.05$.

to shake the web. In the evening, these spiders tend to jump from the web and tend not to shake the web (Table 5).

Of 276 adults with egg-sac chains in the hubs of their webs, only 16 (6%) were not aligned with those web structures. Therefore, the data for all 276 spiders was analyzed regardless of alignment. A two-way contingency table analysis comparing the association between the time of day and the response variables did not indicate association between the two variables ($G^2 = 9.27$, $p = 0.1590$, $df = 6$). A log-linear analysis fitted these data to a model that treated the time and response variables separately (i.e., the two-way association term was omitted).

The ratio terms indicated that adults with egg-sac chains show a strong tendency to remain in position when disturbed (ratio = 11.954) or to jump from the web (ratio = 6.845). They tend neither to move to the edge of the web (ratio = -4.331) nor to shake the web (ratio = -5.152).

We also conducted a two-way contingency table analysis comparing the responses of females with linear stabilimenta to those without stabilimenta or egg-sac chains. The responses of spiders was independent of the presence of linear stabilimenta ($G^2 = 0.84$, $p = 0.8409$, $df = 3$). Both spiders with and without stabilimenta tend to jump (ratio = 14.724) or move to the edge (ratio = 2.353) when disturbed and tend not to remain in position (ratio = -4.318) or shake the web (ratio = -5.402). Spiders also tend not to build stabilimenta (ratio = -2.400).

TABLE 6. Ratio terms (Z-values) for the time $\times$ response association of juveniles with no stabilimenta and for the time $\times$ response and time $\times$ alignment associations of juveniles with linear stabilimenta

	Time		
	Morning	Afternoon	Evening
No stabilimentum			
Response			
Jumped	0.463	-0.130	-0.246
Moved	1.696	0.540	-1.850
Remained	1.103	-1.491	0.703
Shook	-3.752*	2.850*	0.575
Linear stabilimentum			
Response			
Jumped	1.094	0.798	-2.112*
Moved	1.004	1.241	-2.535*
Remained	1.280	-1.987*	1.072
Shook	-4.004*	2.268*	2.279*
Alignment			
Yes	2.695*	-3.917*	0.619
No	-2.695*	3.917*	-0.619

* $P < 0.05$.

Survey of juveniles

Carapace length and first femur length measurements indicated that all juveniles were in either the 3rd or 4th stadia.

Because spiderlings with neither linear nor circular stabilimenta in their webs had nothing to align with, their responses were analyzed separately. A two-way contingency table analysis comparing the association between time of day and response indicated that responses of the spiderlings with no stabilimenta in their webs vary depending upon the time of day ($G^2 = 24.46$, $p = 0.0004$, $df = 6$). This model indicated that spiderlings with no stabilimenta do not tend to shake their webs in the morning, but do tend to shake them in the afternoon (Table 6).

Of the 1800 spiderlings observed, 129 (7%) had a circular stabilimentum at the hub of their webs. Unlike a linear stabilimentum, which follows a single radial line, a circular stabilimentum covers the entire hub (Fig. 1D). Of these 129 spiderlings, only 3 (2%) were not positioned beneath this silk platform. Since a spiderling could be oriented in any direction and still be beneath this stabilimentum, we considered this orientation different than the alignment of adults or juveniles with a linear stabilimentum or an egg-sac chain. Therefore, the data for these 129 spiderlings were analyzed separately, regardless of "alignment" beneath the stabilimentum.

A two-way contingency table analysis of spiderlings with circular stabilimenta indicated that response to disturbance was independent of the time of day ($G^2 = 8.84$, $p = 0.1825$, $df = 6$). To detect which responses were most likely to be shown, we conducted a log-linear analysis that fitted these data to a model that treated the time and response variables separately (i.e., the two-way association term was omitted). The ratio terms indicated that, when disturbed, spiderlings with circular stabilimenta tend to move to the edge of the web (ratio = 5.696) or to shake the web (ratio = 2.215). They tend not to remain in position (ratio = -4.527).

To detect associations between the time, alignment, and response variables for juveniles with linear stabilimenta, the data were fitted to a log-linear model. This model indicated two-way associations between time and response and between

TABLE 7. Ratio terms (Z-values) for the response $\times$ stab sac association of juveniles with linear stabilimenta and those with no web structures

		Response			
		Jumped	Moved	Remained	Shook
Stab sac	Linear	1.393	-2.824*	-0.161	1.360
	Neither	-1.394	2.824*	0.161	-1.361

* $P < 0.05$.

time and alignment ($G^2 = 11.22$, $p = 0.2609$, $df = 9$). Adding a three-way association term among time, response, and alignment, or a two-way term between response and alignment did not significantly increase the fit of the model. This model indicated that, in the morning, spiderlings with linear stabilimenta do not tend to shake their webs and tend to be aligned with their stabilimenta; in the afternoon, they do not tend to remain in position, do tend to shake their webs, and do not tend to be aligned with the stabilimenta; and in the evening, they do not tend to either jump from the web or move to the edge of the web, but do tend to shake the web (Table 6).

We also conducted a two-way contingency table analysis comparing the responses of spiderlings with linear stabilimenta to those without stabilimenta. The responses of juveniles varied depending upon the presence of linear stabilimenta ($G^2 = 16.09$, $p = 0.0011$, $df = 3$). When disturbed, spiderlings with linear stabilimenta tend not to move to the edge of the web whereas those without stabilimenta do (Table 7).

Predatory encounters

During approximately 280 h of filming, three mature female *U. glomosus* responded 15 times to contact. All responses occurred between 11:45 and 19:00 and were exhibited by females without egg sacs or stabilimenta. One female jumped from her web in response to contact by the long antennae of a grasshopper (suborder Ensifera) that walked along the dowel frame, and another jumped to escape an unquestionable wasp attack. At about 14:50, this female was resting in a cryptic posture at the hub of the web when a wasp flew toward the spider, momentarily hovered a short distance above her, and then dropped, contacting the spider's venter. The spider jumped, successfully eluding the wasp; then, approximately 20 s later, she began ascending her dragline to the hub. The attacking wasp was not a *Trypoxylon*; however, we were unable to identify it with certainty from the film (perhaps Sphecidae or Pompilidae).

One female propelled herself to another part of the web seven times in response to contact by insects (ants and a grasshopper) and two times to unobserved stimuli. In other females, we noted three instances of web shaking, one in response to an insect approximately 3 mm long contacting the web and two in response to unknown stimuli. On 16 occasions, wasps flew within 3 cm of spiders without eliciting defensive behaviors. On one occasion, a wasp crawling from its nest along the ceiling contacted the spider, causing her to move from the hub to the edge of the web.

Stimulus experiment

A spider's response to visual-vibratory and contact stimuli was recorded as either active (jumped from, moved to the edge of, or shook the web) or as remaining in position (Table 8). Four two-way contingency table analyses were conducted to deter-

TABLE 8. Responses of juveniles and adults to contact by water droplets and to a tethered wasp; active responses include jumping from, moving to the edge of, and shaking the web

Response	Stimulus			Total
	Droplet (initial)	Wasp	Droplet (subsequent)	
Active				
Juvenile	10	2	14	26
Adult	7	0	7	14
Total	17	2	21	40
Remain in position				
Juvenile	4	12	0	16
Adult	2	9	2	13
Total	6	21	2	29

mine if spiders exhibited different frequencies of active responses to the water drop stimulus and the stimuli produced by the tethered wasp. The comparisons analyzed were initial drop versus wasp and wasp versus subsequent drop (for juveniles and for adults in both comparisons). Yates correction for small sample sizes was applied to all the frequency data (Sokal and Rohlf 1981). All four analyses resulted in G^2 values greater than 7.52, p values smaller than 0.01, and df values equal to 1. For both adults and juveniles, the wasp (i.e., the visual and vibratory stimuli) elicited significantly fewer active responses than the contact stimulus.

Sceliphron (Sphecidae) wingbeat frequency ranged from 75 to 275 Hz, *Trypoxylon* (Sphecidae) from 200 to 300 Hz, *Chalybion* (Sphecidae) had a frequency of 70 Hz, and the pompilid wasp produced frequency values between 136 and 480 Hz.

Discussion

We found that time of day, presence of a web structure (stabilimentum or egg-sac chain), and alignment with the web structures each influence the disturbance behaviors shown by *U. glomosus* adults and juveniles. However, adults and juveniles (3rd and 4th stadia) are affected differently by these factors. The majority of adults jump from the web when disturbed, whereas the majority of juveniles move to the edge of the web. Time of day and the presence of stabilimenta also affect adults and juveniles differently. These results agree with the hypotheses that (i) the disturbance behaviors are predator avoidance strategies influenced by time of day and (ii) the egg-sac chains function as cryptic devices that make spiders aligned with them less likely to show active avoidance behaviors when disturbed.

Although these results do not exclude alternative hypotheses, several lines of evidence suggest that the observed disturbance behaviors are distinct predator avoidance strategies. Both shaking and jumping behaviors are characterized by elements not found in the spiders' primary activities of web monitoring and prey capturing. The active responses (jumping, shaking, and moving to the edge of the web) are exhibited by members of other orb-weaving and non-orb-weaving spider families and have often been reported as responses to predator attacks, usually by wasps or hunting spiders (Pekham and Pekham 1887; Marples 1969; Eberhard 1970, 1973; Robinson and Robinson 1970, 1978; Ewer 1972; Edmunds 1974; Tolbert 1975; Levi 1977; Hoffmaster 1982). The video filming in this study shows that

jumping from the web can protect a spider from visually hunting predators.

Some spider-hunting predators, such as wasps and birds, more actively hunt in the afternoon and evening (Bristowe 1948; Stiles and Wolf 1979; Coville 1987) whereas others, such as hunting spiders, are active throughout the day (Anderson 1970; Gardner 1965; Abraham 1983). The effect of time of day upon the responses exhibited by both adult and juvenile *U. glomosus* is consistent with the hypothesis that the activity patterns of spider predators have influenced the spiders' behaviors. The alternative explanation that temperature affects these behaviors is not supported in *U. glomosus* (Cushing and Opell 1990).

The results are also consistent with the hypothesis that an adult female aligned with an egg-sac chain is concealed from visually hunting predators, as these spiders tend to remain aligned with their egg sacs when disturbed (Fig. 1C). However, Cushing (1988) found that *U. glomosus* females aligned with their egg sacs also exhibit unique, apparently defensive behaviors in response to parasitoid wasps walking on their egg sacs.

The majority of juveniles with circular stabilimenta were positioned beneath the stabilimentum, suggesting that they may utilize the cryptic potential of these web structures (Fig. 1D). However, spiderlings with circular stabilimenta still tended to actively respond when disturbed. This tendency to position themselves beneath the stabilimenta may, instead, be an artifact of their usual tendency to monitor their webs from the hub, as this is the position from which spiders can best detect and respond to prey intercepted anywhere in the orb web (Barth 1982). At the hub, juveniles with circular stabilimenta may be oriented in any direction and still be hidden by this structure.

This study does not support the hypothesis that the vibrational and visual stimuli produced by a wasp elicits disturbance behaviors in *U. glomosus*. The experiment comparing spiders' responses to a contact stimulus and to the combined vibratory and visual stimuli of a tethered wasp indicated that the contact stimuli used in both the adult and the juvenile surveys were appropriate disturbance stimuli. In both adult and juvenile spiders, contact is required to elicit disturbance behaviors. The wingbeat frequencies of the examined sphecids and pompilid wasps are all within the range detectable by trichobothria, the long sensory hairs that adorn the legs of uloborids (Opell 1979) and detect airborne vibrations (Barth 1982). The wasp used in the stimulus experiment was held within the visual field coverage of *U. glomosus* (Opell and Ware 1987). Therefore, the spiders were probably able to perceive the wasp hovering above them.

Spiders may conserve their energy resources when faced with ambivalent or harmless stimuli, such as a large insect flying near them, but readily react to potentially life-threatening stimuli posed by direct contact, or they may remain in position to avoid detection until it is clear they have been discovered. This may be why adults and juveniles aligned with linear stabilimenta also tended to show active avoidance behaviors when disturbed. Alternatively, these disturbance behaviors may have evolved in response to a spider predator other than wasps.

The different frequencies of disturbance behaviors exhibited by adults and juveniles may reflect ontogenetic changes, differences in predation pressure, and (or) differences in the energetic or strategic costs of each behavior. For example, 50% of adult spiders jumped from the web when disturbed, but only 27% of the juveniles showed this behavior. Juveniles are both more clustered and more densely distributed than adults (P. E. Cushing and B. D. Opell, personal observation). Because adults and 3rd- and 4th-stadia juveniles have little temporal overlap

(P. E. Cushing and B. D. Opell, personal observation), any intraspecific interactions occur between similar age (size) classes. Therefore, it may be more costly for juveniles to jump from the web, since under their relatively crowded conditions, they have a greater risk of intercepting a neighbor's web and being treated as prey. *Uloborus glomosus* spiderlings do cannibalize each other in captivity (P. E. Cushing and B. D. Opell, personal observation) and may do so in nature as well.

Crane (1952) defined seven distinct defensive mechanisms in invertebrates: crypsis, active escape, startle response, withdrawal into protected position, attack, unpalatability, and chemical concealment. *Uloborus glomosus* exhibit the first four of these mechanisms. (i) These spiders have cryptic coloration and posture. They also enhance their morphological crypsis by incorporating silk stabilimenta and egg-sac chains into their webs. (ii) When disturbed, some spiders actively escape by jumping from their webs. (iii) Others shake the web, which probably serves to blur the outline of the spider or to startle an attacking predator (Edmunds 1974). (iv) Some *U. glomosus* withdraw to the edge of the web, where they are probably concealed from attack by surrounding vegetation. These mechanisms are common to many different web-weaving spiders.

Acknowledgments

We are grateful to Richard D. Fell, Thomas A. Jenssen, and David A. West for their advice and input. We thank William G. Eberhard and Terry E. Christenson for commenting on an earlier draft of this manuscript. The Statistics Consulting Center of VPISU provided advice on the use and interpretation of the analyses. This project was supported by two grants from Sigma Xi and matching funds from the Biology Department of VPISU.

- ABRAHAM, B. J. 1983. Spatial and temporal patterns in a sagebrush steppe spider community (Arachnida: Araneae). *J. Arachnol.* **11**: 31–50.
- ANDERSON, J. F. 1970. Metabolic rates of spiders. *Comp. Biochem. Physiol.* **33**: 51–72.
- BARTH, F. G. 1982. Spiders and vibratory signals: sensory reception and behavioral significance. In: *Spider communication: mechanisms and ecological significance*. Edited by P. N. Witt and J. S. Rovner. Princeton University Press, Princeton. pp. 67–122.
- BISHOP, Y. M. M., FIENBERG, S. E., and HOLLAND, P. W. 1975. *Discrete multivariate analysis: theory and practice*. M.I.T. Press, Cambridge.
- BRISTOWE, W. S. 1941. The comity of spiders. *Ray Society*, No. 128, London.
- . 1948. Notes on the habits and prey of twenty species of British hunting wasps. *Proc. Linn. Soc. London*, **160**: 12–37.
- COVILLE, R. E. 1987. Spider hunting sphecids wasps. In *Ecophysiology of spiders*. Edited by W. Nentwig. Springer-Verlag, Berlin. pp. 309–318.
- CRANE, J. 1952. A comparative study of innate defensive behavior in Trinidad mantids (Orthoptera: Mantoidea). *Zoologica (NY)*, **37**: 259–293.
- CUSHING, P. E. 1988. A study of disturbance behaviors in *Uloborus glomosus* (Araneae: Uloboridae) as possible predator avoidance strategies. M.S. thesis, Virginia Polytechnic Institute and State University, Blacksburg, VA.
- CUSHING, P. E., and OPELL, B. D. 1990. The effect of time and temperature on disturbance behaviors shown by the orb-weaving spider *Uloborus glomosus* (Uloboridae). *J. Arachnol.* **18**. In press.
- DIXON, W. J. 1981. *BMDP statistical software*. University of California Press, Berkeley.
- EBERHARD, W. G. 1970. The predatory behavior of two wasps, *Agnoideus humilis* (Pompilidae) and *Sceliphron caementarium* (Sphecidae), on the orb weaving spider *Araneus cornutus* (Araneidae). *Psyche*, **44**: 243–251.
- . 1973. Stabilimenta on the webs of *Uloborus diversus* (Araneae: Uloboridae) and other spiders. *J. Zool.* **171**: 367–384.
- EDMUNDS, M. 1974. *Defense in animals: a survey of antipredator defenses*. Longmans, Essex.
- EWER, R. F. 1972. The devices in the web of the West African spider *Argiope flavipalpis* J. Nat. Hist. **6**: 159–167.
- FIENBERG, S. E. 1987. *The analysis of cross-classified categorical data*. 2nd ed. M.I.T. Press, Cambridge.
- GARDNER, B. T. 1965. Observations on three species of *Phidippus* jumping spiders (Araneae: Salticidae). *Psyche*, **72**: 133–147.
- HINGSTON, P. W. G. 1927. Protective devices in spiders' snares, with a description of seven new species of orb-weaving spiders. *Proc. Zool. Soc. London*, 1927(18): 259–293.
- HOFFMASTER, D. K. 1982. Predator avoidance behaviors of five species of Panamanian orb-weaving spiders (Araneae: Araneidae, Uloboridae). *J. Arachnol.* **10**: 69–73.
- JOHNSGARD, P. A. 1983. *The hummingbirds of North America*. Smithsonian Institution Press, Washington, D.C.
- KENNEDY, J. J. 1983. *Analyzing qualitative data: introductory log-linear analysis for behavioral research*. Praeger Scientific, New York.
- KROMBEIN, K. V. 1967. *Trap-nesting wasps and bees: life histories, nests, and associates*. Smithsonian Institution Press, Washington, D.C.
- LEVI, H. W. 1977. The American orb-weaver genera *Cyclosa*, *Metazygia* and *Eustala* north of Mexico (Araneae: Araneidae). *Bull. Mus. Comp. Zool.* **148**: 61–127.
- LUBIN, Y. D. 1980. The predatory behavior of *Cyrtophora* (Araneae, Araneidae). *J. Arachnol.* **8**: 159–185.
- MARPLES, B. J. 1969. Observations on decorated webs. *Bull. Br. Arachnol. Soc.* **1**: 13–18.
- MARSON, J. E. 1947a. Some observations on the ecological variation and development of the cruciate zigzag camouflage device of *Argiope pulchella* (Thor.). *Proc. Zool. Soc. London*, **117**: 219–227.
- . 1947b. Some observations on the variations in the camouflage devices used by *Cyclosa insulana* (Costa), an Asiatic spider, in its web. *Proc. Zool. Soc. London*, **117**: 598–605.
- OPELL, B. D. 1979. Revision of the genera and tropical American species of the spider family Uloboridae. *Bull. Mus. Comp. Zool.* **148**: 443–549.
- . 1987. Changes in web-monitoring forces associated with reduction in the spider family Uloboridae. *Can. J. Zool.* **65**: 1028–1034.
- OPELL, B. D., and EBERHARD, W. G. 1984. Resting postures of orb-weaving uloborid spiders. *J. Arachnol.* **11**: 369–376.
- OPELL, B. D., and WARE, A. D. 1987. Changes in visual fields associated with web reduction in the spider family Uloboridae. *J. Morphol.* **192**: 87–100.
- PEKHAM, G. W., and PEKHAM, E. G. 1887. Some observations on the mental powers of spiders. *J. Morphol.* **1**: 383–419.
- PYKE, G. H. 1980. The foraging behaviour of Australian honeyeaters: a review and some comparisons with hummingbirds. *Aust. J. Ecol.* **5**: 343–369.
- ROBINSON, M. H., and ROBISON, B. 1970. The stabilimentum of the orb web spider *Argiope argentata*: an improbable defense against predators. *Can. Entomol.* **102**: 641–655.
- . 1978. Developmental studies of *Argiope argentata* (Fabricius) and *Argiope aemula* (Walckenaer). *Symp. Zool. Soc. London*, **42**: 31–40.
- ROBINSON, M. H., and VALERIO, C. E. 1977. Attacks on large or heavily defended prey by tropical salticid spiders. *Psyche*, **84**: 1–10.
- SOKAL, R. R., and ROHLF, F. J. 1981. *Biometry*. W.H. Freeman, San Francisco.
- STILES, F. G., and WOLF, L. L. 1979. Ecology and evolution of lek mating behavior in the long-tailed hermit hummingbird. *Ornithol. Monogr.* **27**: 1–78.
- TOLBERT, W. W. 1975. Predator avoidance behaviors and web defensive structures in the orb weavers *Argiope aurantia* and *Argiope trifasciata* (Araneae, Araneidae). *Psyche*, **82**: 29–51.