THE EFFECT OF TIME AND TEMPERATURE ON DISTURBANCE BEHAVIORS SHOWN BY THE ORB-WEAVING SPIDER *ULOBORUS GLOMOSUS* (ULOBORIDAE)

Paula E. Cushing and Brent D. Opell

Department of Biology
Virginia Polytechnic Institute and State University
Blacksburg, Virginia 24061 USA

ABSTRACT

When disturbed, *Uloborus glomosus* 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. The time of day influences which of these behaviors is expressed. Spiders tend to jump in the afternoon and the evening but not in the morning. In the morning they tend to move to the edge of the web or remain in position. The tendency to shake the web is approximately the same throughout the day. Ambient temperature appears not to be the principal factor explaining the differences in jumping, moving to the edge, and remaining in position. Historical differences in the activity patterns of various spider predators may have influenced the time-related expression of disturbance behavioral patterns.

INTRODUCTION

Many orb-weaving spiders show predictable responses when disturbed. Some run to a retreat or to surrounding vegetation, others move to the edge of the web, others shake the web and others jump from the web (Pekham and Pekham 1887; Levi 1968; Marples 1969; Eberhard 1970, 1973; Robinson and Robinson 1970; Robinson 1978; Ewer 1972; Edmunds 1974; Tolbert 1975;, Levi 1977; Hoffmaster 1982; Cushing and Opell in press). These behaviors are thought to be predator avoidance strategies. The jumping and shaking responses have been cited as responses to a variety of predators including both spider-hunting wasps and salticid spiders (Richards and Hamm 1939; Eberhard 1970; Coville 1976; Hoffmaster 1982; Cushing and Opell in press).

When the spider *Uloborus glomosus* (Walckenaer) (Uloboridae) is disturbed while resting beneath the hub of its horizontal orb-web, it may show one of four responses: jumping from the web, shaking the web, moving to the edge of the web, or remaining in position (Cushing and Opell in press). Many factors, including time of day, evidently influence the expression of the behaviors. The objectives of this study are to determine how time of day influences the disturbance behaviors shown by these spiders and if temperature mediates these behavioral patterns.

METHODS

Forty-nine adult female *Uloborus glomosus* were collected from shrubbery at various locations on the V. P. I. and S. U. campus (Blacksburg). When collected no spiders had eggsacs, although many subsequently produced eggsacs, a factor not considered in the analyses. Twenty-five spiders were collected in mid-July, 1987 and assigned to Group I. Others collected in late July were in Group II. All spiders were maintained in an outdoor study enclosure in a wooded area of Blacksburg.

Spiders in Group I were marked for identification by applying small dots of green and red enamel paint to their dorsal abdominal surfaces. The dots were observed by holding a long-handled dental mirror beneath a spider on its orb web. Group I spiders were established on six frames, each providing a vertical series of 25 wooden dowel rods spaced 12 cm apart. Each rod was 8 mm in diameter and 50 cm long. Spiders chose their own web attachment sites and were maintained at a density of one to four spiders per frame. Frames were kept in a 3 × 3 × 3 m screened enclosure to prevent dispersal away from the study area. Group II spiders were kept in 31 × 16.5 × 9 cm plastic shoeboxes covered with mosquito netting and placed under a plastic roof just outside the screened enclosure housing Group I spiders. We began testing Group I on 13 July, and Group II 7 days later. Group I spiders were removed and the experiment terminated after 19 days of testing. Group II spiders were tested for 36 days.

As a disturbance stimulus we dropped water on the venter of each spider from a Pasteur pipette with an average tip diameter of 1.20 mm held 1 cm above the spider. The water was kept in the enclosure to maintain it at ambient temperature. This stimulus was suggested by W. G. Eberhard (pers. comm.) as it is more easily standardized than touching the spider with a probe. A water drop was considered to approximate the sudden ventral contact by an attacking predator such as a wasp or a hunting spider. Since *U. glomosus* does not respond to the visual or vibratory stimuli produced by a tethered wasp held directly above the spider (Cushing and Opell in press), visual and vibratory stimuli were considered inappropriate disturbance stimuli. After stimulating a spider, we recorded its response to this disturbance as either: jumping out of the web, moving to the edge of the web, remaining in position, or shaking the web. Preliminary observations showed that the spiders responded similarly to a water drop as to contact by a small probe.

Temperature was recorded at the time observations were begun. It took approximately 30 minutes to test all of the spiders' responses. For both groups, we tested all spiders in the morning (0800-1000 hours) of day 1 of the tests and recorded their behaviors. On day 2, we tested all the spiders in the afternoon (1200-1400 hours) and on day 3 we tested them in the evening (1600-1800 hours). These times corresponded to the times used by Cushing and Opell (in press). Spiders were not disturbed on day 4 to ensure 24 hours between tests. This 24 hour testing sequence was a cautionary measure chosen to diminish any degeneration of the behaviors that might result from too frequently disturbing the spiders. On day 5, the 3-day cycle, hereafter referred to as a block, was repeated. Group I spiders were run for 5 blocks (15 days of actual testing) and Group II spiders for 9 blocks (27 days of actual testing).

Table 1.—The frequencies of each behavior during the morning, afternoon and evening. Total number of observations is 862. *=Two spiders died before the final evening observations were recorded.

Response	Time of day			
	Morning	Afternoon	Evening	Total
Jumped from web	116	172	169	457
Moved to edge	26	11	13	50
Remained in position	70	38	39	147
Shook web	76	67	65	208
Total	288	288	286*	862

If a spider died or disappeared before half of the observations were completed, all the previous observations for that individual were eliminated from the data set. This ensured that each spider in Group I and in Group II contributed an approximately equal sequence of observations to the data set. Consequently, a spider from Group I had to survive through block 3 for its behaviors to be included in the analyses and one from Group II had to survive through block 5. Observations for 22 Group I and for 21 Group II spiders were used in the final analyses.

To supplement their diet of small insects that passed into the enclosure, we fed all spiders by blowing several fruit flies (*Drosophila* sp.) into their webs, either after testing in the evening of the three-day cycle or on the fourth (non-test) day. Group II spiders relied solely on this source of food.

To determine the validity of pooling the responses of all 43 spiders, we conducted a Replicated Goodness-of-Fit Test for heterogeneity (Sokal and Rohlf 1981), comparing the pooled responses of Group I spiders with the pooled responses of Group II spiders. To determine the effect of the variable Time on the responses of these spiders, we pooled the observations for each of the behavioral categories made during each of the three time periods across all 43 spiders for a total of 882 observations (Table 1). We conducted a log-linear analysis to determine if the variables Time and Response are associated and, if so, to establish the patterns of behavioral switching that occurred (Bishop et al. 1975; Fienberg 1987).

To assess the magnitude of the interactions between each of the three Time categories with each of the four Response categories, we calculated the ratios of the log-linear parameter estimates to the standard errors for the log-linear model with the two-way interaction term between Time and Response. These ratios are somewhat analogous to cell chi-square values. The greater the ratio term, the greater the effect of those categories on the association between Time and Response. As the parameter estimates are calculated according to the assumption of normality, ratio terms greater than /1.96/ correspond to a significance level less than 0.05 in a Z-table and indicate category interactions that contribute most to the association between Time and Response. Positive ratios indicate a positive interaction between the categories; negative ratios indicate a negative interaction (Kennedy 1983).

To determine the effect of Temperature on the behaviors, we conducted a discriminant analysis, defining Temperature as the independent continuous variable and Response as the classification variable.

Table 2. Ratio terms (Z-values) for the Time $\times$ Response association. * = $P < 0.05$.

Response	Time		
	Morning	Afternoon	Evening
Jumped from web	-5.541*	2.919*	2.333*
Moved to edge	2.233*	-1.290	-0.581
Remained in position	2.107*	-0.867	-0.972
Shook web	-1.023	0.800	0.139

RESULTS

Association between Time and Response.—The test for heterogeneity between Groups I and II indicated that they were homogeneous ($G^2 = 1.1078$, $P > 0.5$). Therefore, we pooled responses for all 43 spiders. Over the entire testing period, spiders jumped from the web 53% of the time, moved to the edge 6% of the time, remained in position 17% of the time, and shook the web 24% of the time (Table 1).

The two-way log-linear analysis comparing the interaction between the Time and Response variables indicated that spider response is influenced by the time of day ($G^2 = 34.947$, $P < 0.001$). The magnitudes of the interactions between each of the Time categories with each of the Response categories is presented in Table 2. In the morning, spiders did not tend to jump from the web in response to the disturbance but did tend to either move to the edge of the web or remain in position. Spiders tended to jump from the web in the afternoon and the evening. They showed no time-related preference for the shaking behavior although shaking the web was the second most frequent response (Table 1).

Effect of Temperature on the behaviors.—The mean temperature during the morning tests was 20.2°C (SD = 3.05); the mean during the afternoon tests was 28.2°C (SD = 3.01); and the mean during the evening tests was 26.8°C (SD = 3.07).

To calculate the discriminant function, the within-group covariance matrix rather than the pooled covariance matrix was used because the within-group covariance matrix for the Response variable was not homogeneous ($\chi^2 = 0.004$, $P < 0.05$, Kleinbaum and Kupper 1978). According to the discriminant analysis, temperature is not a good predictor of the disturbance behaviors (Table 3).

DISCUSSION

This study supports Cushing and Opell's (in press) finding that *Uloborus glomosus* responds differently to disturbance at different times of the day. It also indicates that ambient temperature may not be the principal factor explaining these differences. Temperature correctly predicted whether a spider moved, shook, or remained in position less than 42% of the time; the jumping response was correctly predicted 66% of the time. The jumping response appears to be an energetically expensive behavior (Cushing and Opell in press) and, therefore, may be enhanced by higher temperatures.

Jumping from the web is effective against aerial hunters such as spider-hunting wasps and hummingbirds (Eberhard 1970; Coville 1976; Hoffmaster 1982;

Table 3.—Observations (Total 862) correctly and incorrectly assigned by a discriminant analysis to each of the Response categories using Temperature as a predictor.

Response	Freq.	% Correctly assigned	% Incorrectly assigned to:			
			Jumped	Moved	Remained	Shook
Jumped from web	457	66.1	—	1.8	19.9	12.3
Moved to edge	50	12.0	40.0	—	42.0	6.1
Remained in position	147	41.5	28.6	13.6	—	16.3
Shook web	208	17.3	45.7	1.9	35.1	—

Cushing and Opell in press). Wasps are not very successful at stinging spiders hanging on threads beneath orb-webs and rarely pursue spiders after they have jumped unless they have landed on a solid substrate (Eberhard 1970). The same is probably true for hummingbirds, one of the more important avian predators of spiders. These birds supplement their nectar diet with protein from spiders (including orb-weavers) and insects (Pyke 1980; Johnsgard 1983).

Jumping behavior does not appear to be effective against ambulatory predators such as salticid spiders. Robinson and Valerio (1977) noted that araneids that jumped from their webs after being attacked by salticids could not displace the jumping spider. When a spider jumps from its web, it also risks losing a productive web site if its dragline breaks or becomes entangled in surrounding vegetation, falling into the web of a neighboring spider, or becoming prey of an ambulatory predator on the substrate to which it falls. Therefore, if the stimulus is not immediately threatening an alternate avoidance strategy such as shaking the web may be advantageous. This behavior may dislodge an ambulatory predator (i.e., a salticid spider) from both the orb-spider and the web plane (Robinson and Valerio 1977; Hoffmaster 1982).

If it is true that jumping from the web is most effective against aerial predators and shaking the web against ambulatory predators, then the expression of these behaviors at particular times of day may have been selected by differences in the activity patterns of these predators. Hummingbirds are primarily nectar feeders. Nectar flows most abundantly from one to two hours before hummingbirds become active (about 0430 hours) until around 1830 hours when hummingbirds cease activity (Cruden et al. 1983). Hummingbirds tend to hunt insects and spiders only casually in the morning, spending most of their time feeding on nectar. They more actively hunt arthropods as the day progresses (after nectar production has dropped off) (Stiles and Wolf 1979; Gill pers. comm.).

Adult spider-hunting wasps of the families Sphecidae and Pompilidae are also primarily nectar feeders only occasionally eating the spiders they hunt (Evans and Eberhard 1970). Coville (1987) states that these wasps are active from one to three hours after sunrise to one to three hours before sunset. Although their daily activity cycles have not been described, it is probable that they also spend the early morning hours foraging for nectar. They seem to build their nests and hunt for spiders most actively between 1100 hours and 1830 hours (Bristowe 1948; Cushing 1988).

The activity patterns of these aerial predators may explain the tendency of *U. glomosus* to jump in the afternoon (1200-1400 hours) and the evening (1600-1800

hours) but not in the morning (0800-1000 hours). If this explanation is correct, the jumping response should be as infrequent late in the day (i.e., from 1800-2000 hours) as in the morning. Spiders that jump in the afternoon and the evening but not in the morning must switch to some other behavior in the early hours. This study suggests that these spiders move to the edge of the web or remain in position when disturbed. Both of these behaviors are energetically and strategically inexpensive, but probably not very effective if the stimulus is an actual ambulatory (or aerial) predator.

Shaking behavior is the second most frequent behavior and occurs at equal frequency regardless of time of day or temperature. This may also be related to the activity pattern of the main predator group to which it is directed, namely ambulatory predators. Salticid spiders are an important ambulatory predator of orb-weaving spiders, especially in the tropics (Bristowe 1941; Enders 1974, 1975; Robinson and Valerio 1977; Edwards pers. comm.). Their activity patterns have been described as beginning as early as 0700 hours and ending as late as 1900 hours (Anderson 1970; Abraham 1983), although Gardner (1965) and Edwards (pers. comm.) have observed salticids hunting most actively between 1000 hours and 1600 hours. Because these ambulatory predators are active throughout the day, the shaking behavior should also be shown throughout the day, as this study shows it to be.

ACKNOWLEDGMENTS

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