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TESTS FOR OLFACTORY COMMUNICATION IN FOUR SPECIES OF WOLF SPIDERS (ARANEAE, LYCOSIDAE)[1]

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ABSTRACT

Females of four species of wolf spiders were examined for the presence of an airborne pheromone(s): *Schizocosa saltatrix*, *S. ocreata*, *Lycosa rabida*, *L. punctulata*. Two types of olfactometers were employed: an open arena-type olfactometer and a Y-olfactometer. Data indicate that male *S. saltatrix* exhibit an orthokinetic response to distant conspecific females. Male *S. ocreata* may exhibit a taxis response to distant females. Neither *Lycosa* species exhibits a change in behavior in response to a hidden female.

INTRODUCTION

Contact and olfactory pheromones are important in intraspecific communication in arthropods (Shorey 1976). Among the Araneae, contact sex pheromones associated with the female integument and dragline elicit sexual behavior in conspecific males (Dijkstra 1976, Dondale and Hegdekar 1973, Hegdekar and Dondale 1969, Kaston 1936, Rovner 1968, Tietjen 1977). Airborne sex pheromones are known for two families of the Araneae. In salticids, distance chemoreception is a secondary releaser of courtship behavior, while vision is the primary releaser (Crane 1949). An airborne pheromone aids male orientation to female webs in some species of the Araneidae (Blanke 1973, 1975a, 1975b, Enders unpubl. data).

Hegdekar and Dondale (1969), working with four species of lycosids, found no evidence of an olfactory pheromone. Other researchers have suggested that some male lycosids may employ olfactory orientation to detect and locate conspecific females at a distance, but no experimental evidence was provided (Bristowe and Locket 1926, Dijkstra 1976, Vlijm et al. 1963).

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In the present study male lycosid spiders were used to assay for the possible presence of an airborne component of the female sex pheromone. *Schizocosa saltatrix* (Hentz) and *Schizocosa ocreata* (Hentz) exhibited evidence of chemical signaling at a distance while *Lycosa rabida* Walckenaer and *Lycosa punctulata* Hentz did not.

METHODS

Four species were examined: *Schizocosa saltatrix*, *S. ocreata*, *Lycosa rabida* and *L. punctulata*. *S. ocreata* has been reported previously as *S. crassipes* (Walckenaer) (Dondale and Redner 1978). Animals were collected near Athens, Ohio, USA, during the spring and summer of 1974 through 1976. General methods concerning maintenance and observation of lycosid spiders have been previously described (Tietjen 1977).

I constructed two types of olfactometers. An "arena olfactometer" was designed to determine the response of a test male in an open field to a concealed conspecific. A "Y-olfactometer" was designed to provide a test male with a choice among airstreams which had passed over a concealed conspecific or an empty cage. Both olfactometers were constructed with glass.

The arena olfactometer consisted of a 520 x 600 mm test field marked with 40 x 40 mm squares. An isolation chamber was randomly placed at one of the four corners of the arena. This chamber contained a wire cage which held the stimulus that was presented to the test male in the arena (Fig. 1). Three stimuli were used: a conspecific male or female, or an empty cage. The wire cage containing the stimulus was hung from a glass rod within the isolation chamber to minimize the transmission of vibrational cues from the stimulus animal to the test male. Visual isolation of the stimulus animal and test male was provided by an opaque glass cover with a fine mesh screen in front. A gentle stream of air issuing from a hair dryer was directed through the stimulus cage and into the test arena. The hair dryer was modified by removing all heating elements and baffling that could interfere with the flow of cool air. The air output hose was attached to a series of smaller

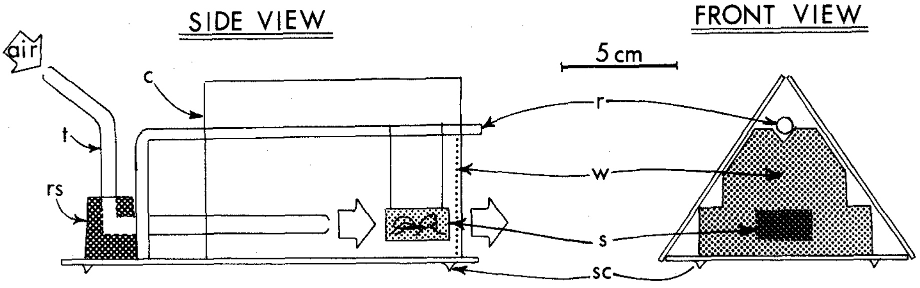

Fig. 1.—Arena olfactometer isolation chamber. Air flow through the metal tubing (t) and over the hidden stimulus (s) is indicated by the large arrows. A bored rubber stopper (rs) supported the metal tubing. Visual isolation between the test male and the stimulus was achieved through the use of an opaque glass construction, a closed back (c), and a fine meshed screen on the open front (w). A glass rod (r) provided support for the stimulus. Mechanical isolation between the test male and stimulus was augmented by silicone rubber supports (sc).

hoses (I.D.=3.0 mm) which provided a back pressure thus reducing the speed and volume of air flow over the stimulus. Each trial was 10 min in duration. At the conclusion of the trial the test male was placed in a cage containing conspecific female silk. If the test male did not show courtship behavior within 5 min, he was considered to be of low sexual tone (Crane 1949), and the trial was not used in the analysis of data. I washed the apparatus between runs with distilled water and attached a clean tissue paper substratum to the floor of the arena.

The Y-olfactometer permitted simultaneous presentation of three airborne stimuli to a test male located in a central area (Fig. 2). Empty stimulus cages, or cages containing a conspecific male or female were positioned at the end of each of the three arms. Vibrational cues from the stimulus animals were minimized by hanging the cages from a rod that had its support in a petri dish filled with sand. This was also shock-mounted by means of silicone rubber supports. Opaque baffles in the arms provided for visual isolation between the test males and the stimuli.

Air flow over the stimulus cages and into the central test arena was generated by heating air in a chimney located above the test arena with a rheostat-controlled (V=90VAC) 200 ohms, 3 watt, wire-wound resistor. Krafft (pers. comm.) used a similar method for generating air flow through a two-arm olfactometer. In preliminary tests, smoke released at the end of each arm indicated that air flow was similar among arms. Air from the three arms showed little mixing until a level of 80-100 mm above the substratum. The entire apparatus was rotated 120° between experimental runs to minimize possible directional bias.

Experimental runs began with a 2-min acclimation period for the test male. This period also allowed for equilibration of the olfactometer. Each trial was 15 min in duration, during which time the behavior of the test male was recorded at 15-sec intervals. The location of the male's right palp defined his position within the arena. If the male was in the third of the arena in front of the first arm, he was recorded as occupying Field 1, and so forth for the second and third fields. Males could also enter the first 45 mm of an arm and were then recorded as having a position within that arm. The direction the test male was facing, defined by an imaginary anteriorly directed midline vector, was recorded in degrees. This orientation was recorded to the nearest 30°. The measurement in degrees was referred to, and proceeded counterclockwise from Arm 1 of the olfactometer. Additional behaviors such as courtship, sound-production, threat display and body position were recorded (Kaston 1936, Rovner 1968, 1975, Tietjen unpubl. data).

Following a 15-min trial, the test male was transferred to a cage containing conspecific female silk, and the latency of chemoexploratory and courtship behavior were recorded. Chemoexploratory behavior has been characterized by the male examining the substratum and silk such that the dorsum of the palp contacts the explored surface as the palps move alternately in an anterior direction (Tietjen 1977). Males that did not court within 5 min were considered to be of low sexual tone and their trials were not used in the analyses of data.

Statistical analyses were performed according to the methods of Sokal and Rohlf (1969), Conover (1971) and Batschelet (1965). All means are accompanied by their standard errors unless otherwise indicated.

Male *L. rabida* were confined in an isolation cage containing silk deposited by female *L. rabida* to induce courtship behavior. Measurements were obtained with a General Radio sound level meter (Type 1551-C) and a high-sensitivity vibration pickup (Type

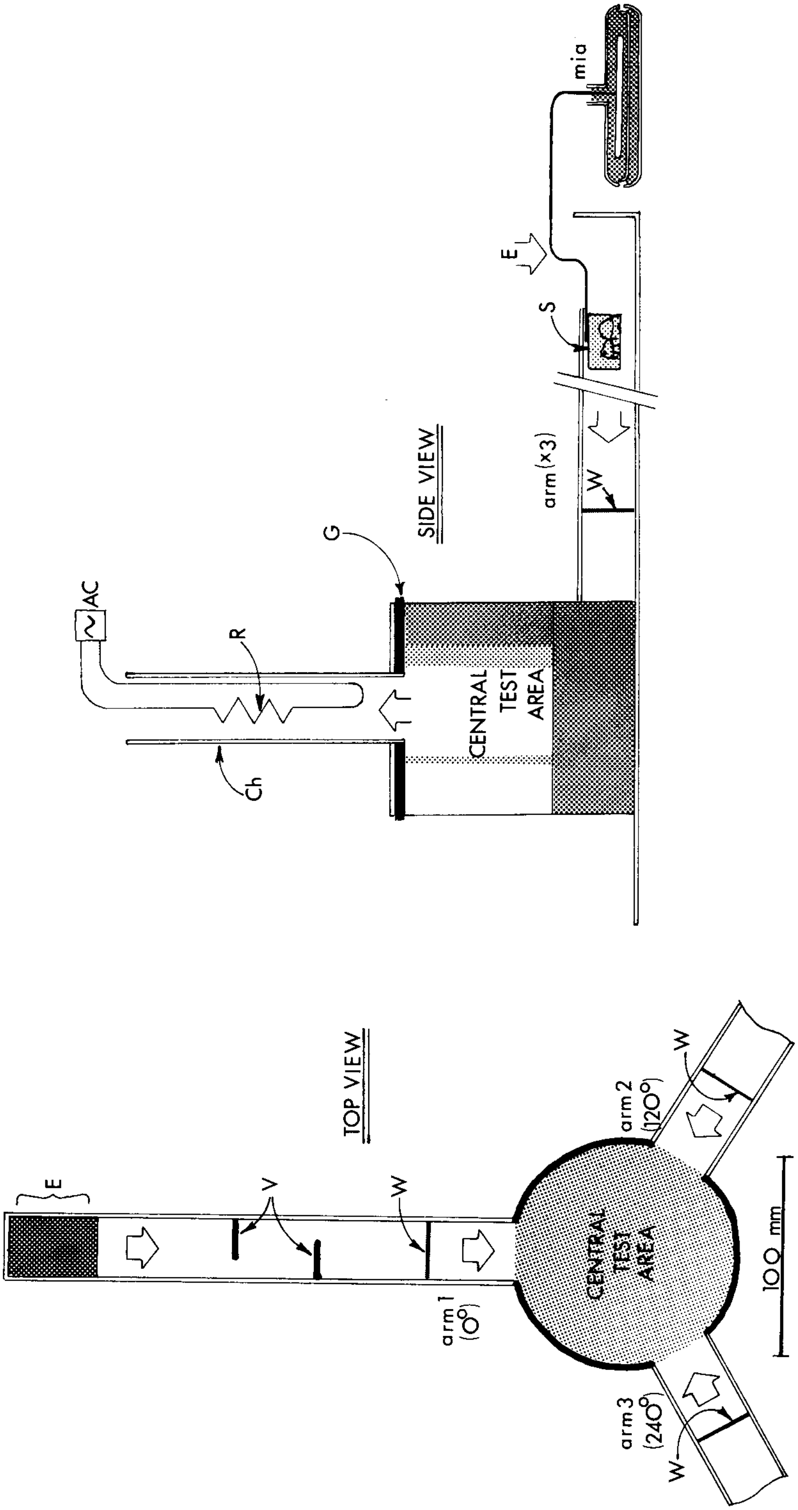
SIDE VIEW
AC
G
R
Ch
CENTRAL TEST AREA
arm (x3)
W
S
E
mia
TOP VIEW
E
V
W
arm 1 (0°)
CENTRAL TEST AREA
arm 2 (120°)
W
arm 3 (240°)
W
100 mm

Table 1.–Behavioral responses of male *Schizocosa saltatrix*, *S. ocreata*, *Lycosa rabida* and *L. punctulata* to concealed stimuli in the arena olfactometer. The distance covered was estimated as the number of 40 X 40 mm squares traverced by a test male during a 10 min trial. The center time data provides an estimate of the time a test male spent in the central area of the arena in min. The distance covered and center time data are shown as the $\bar{Y}$±SE. The frequencies of courtship (Court Freq.), males entering an isolation chamber (Enter Freq.), males exhibiting sound-production (Sound-prod. Freq), threat display (Threat Freq.) and directed exploratory behavior (DEB Freq.) are shown as the percent of test males exhibiting the indicated behavior. The sample size is shown in parentheses following the concealed stimuli for each species. A T-statistic indicates the value for a Kruskal-Wallis test while a χ^2 statistic indicates the value calculated for a Chi-square test. Significant test values are indicated as follows: *=P<0.05, **=P<0.01.

Species	Distance covered	Center time	Court Freq.	Enter Freq.	Sound-prod. Freq.	Threat Freq.	DEB Freq.
S. saltatrix							
Female (20)	16.2±6.0	4.59±1.0	35.0	15.0	–	–	5.0
Male (20)	46.6±5.7	3.78±0.6	5.0	5.0	–	–	5.0
Empty cage (5)	25.8±9.0	7.04±1.7	0.0	0.0	–	–	20.0
Test	T=14.2*	T=2.6	X^2=7.4*	X^2=1.8	–	–	X^2=1.63
S. ocreata							
Female (20)	125.9±21.6	3.98±0.8	–	25.0	75.0	–	35.0
Male (20)	*129.1*±19.1	3.49±0.8	–	10.0	50.0	–	0.0
Empty cage (20)	143.8±19.3	2.06±0.5	–	0.0	60.0	–	5.0
Test	T=0.49	T=2.52	–	X^2=6.2*	X^2=2.7	–	X^2=12.4**
L. rabida							
Female(20)	76.0±20.6	5.24±0.7	10.0	0.0	60.0	40.0	60.0
Male (20)	90.5±30.8	5.53±0.9	5.0	0.0	35.0	15.0	10.0
Empty cage (20)	58.0±19.7	5.80±0.8	5.0	0.0	50.0	20.0	40.0
Test	T=0.08	T=0.21	X^2=0.5	X^2=0.0	X^2=2.5	X^2=3.7	X^2=10.9**
L. punctulata							
Female (20)	146.1±37.8	3.61±0.7	0.0	0.0	30.0	45.0	50.0
Male (20)	163.2±45.2	2.67±0.6	5.0	5.0	20.0	40.0	25.0
Empty cage (20)	106.6±19.5	3.36±0.5	0.0	0.0	15.0	50.0	25.0
Test	T=0.14	T=2.01	X^2=2.1	X^2=2.1	X^2=1.4	X^2=0.4	X^2=3.8

1560-P14) was placed within the area normally occupied by the test male. No increase in vibration levels during male stridulation was noted over the 35-40 decibel background noise. Similar results were obtained when the Y-olfactometer was tested. This indicated that mechanical isolation between the test male and isolated animals is adequate under the extreme condition of male stridulation.

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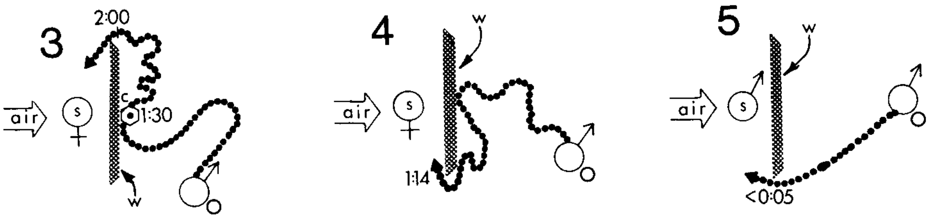
Fig. 2.–Y-olfactometer and mechanical isolation apparatus. A top and side view of the Y-olfactometer is shown. The mechanical isolation apparatus (mia) is shown in its normal position in the side view. Air entered the Y-olfactometer at the end of each arm (E) and flowed over the hidden stimuli (s), as indicated by the open arrows. A gentle air flow was provided by heating air in a chimney (Ch) with a 200 ohm, 3 watt resistor (R). An oil gasket (G) provided an air-tight seal. The male in the central test area was prevented from entering the entire length of the arm by means of wire screens (w). Opaque barriers (V) provided for visual isolation between the hidden stimuli and the test male.

RESULTS

Arena olfactometer.—The number of 40 x 40 mm squares traversed during a 10-min observation period was used to estimate the total distance traveled by a male. Unlike males of the other three species, the distance traveled by male *S. saltatrix* was affected by the concealed stimulus (Table 1). In the presence of a concealed female, male *S. saltatrix* traveled less distance than they did in the presence of a concealed male or clean cage (Mann-Whitney test, T=65.0, $p<0.001$; T=76.0, $p<0.05$). In the presence of a concealed male, conspecific male *S. saltatrix* covered the same distance as those in the presence of an empty cage (Mann-Whitney test, T=30.0, $p>0.05$). No differences were observed in the frequencies of other behaviors under various experimental conditions (Table 1).

Directed exploratory behavior (=DEB) is characterized by males initiating chemoexploratory behavior while touching the front screen of the isolation chamber. Unlike males of the other three species, male *S. ocreata* exhibited a higher frequency of DEB when in the presence of a concealed female than when in the presence of a concealed male or empty cage ($\chi^2=8.48$, df=1, $p<0.001$; $\chi^2=5.63$, df=1, $p<0.025$). The frequency of DEB exhibited by males in the presence of hidden males or empty cages did not differ ($\chi^2=1.03$, df=1, $p>0.50$). The experimental stimulus affected the proportion of test males entering the isolation chamber (Table 1). Male *S. ocreata* entered more often when females were concealed than when an empty cage was used ($\chi^2=5.71$, df=1, $p<0.025$). The number of males entering isolation chambers with concealed females versus concealed males, or an empty cage versus a concealed male, however, did not differ ($\chi^2=1.56$, df=1, $p>0.50$; $\chi^2=2.11$, df=1, $p>0.50$). The increase in DEB in response to a hidden female suggests that male *S. ocreata* detect hidden female *S. ocreata* at close range via an airborne pheromone. The analyses of the number of male *S. ocreata* entering isolation chambers showed conflicted results. However, it is likely that males entering an isolation chamber holding a concealed female are responding the different cues than males that enter an isolation chamber holding a concealed male, since their approach to a hidden female involved long, sinuous paths; often stopping to initiate chemoexploratory behavior, while males approaching a hidden male took short, straight paths (Figs. 3, 4, 5).



Figs. 3-5.—Sample trails of male *Schizocosa ocreata* in response to a hidden stimulus (s). The test male's trails began at the origin (O) at time 0:00 min. The origin was 10.0 cm or less from the wire screen (w) that covered the front of the isolation chamber (See Fig. 1). 3, chemoexploratory behavior (c) in response to a hidden female; 4, sinuous path traveled by a test male in response to a hidden female; 5, path of a test male in response to a hidden male.

Table 2.–Number of 15-sec intervals male *Schizocosa saltatrix*, *Lycosa rabida* and *L. punctulata* occupied each field or arm of the Y-olfactometer. The tests run for each species are described in the text. The sample size is indicated in parentheses. Those tests with a sample size less than 20 were analyzed with a Chi-square test; those with a sample size equal to or greater than 20 were analyzed with a Kruskal-Wallis test. A significant test is indicated as $*=P<0.05$.

Species	Test	Field 1	Field 2	Field 3	Arm 1	Arm 2	Arm 3
S. saltatrix							
	FME (20)	19.9± 7.0	23.3± 6.4	27.8±5.6	10.5±3.5	19.2±8.6	22.4±6.5
L. rabida							
	FME (20)	21.7± 7.6	28.4± 6.7	28.9±6.3	10.4±3.6	22.8±4.0	23.7±6.2
	EEE (7)	56.0± 2.2	10.7± 5.4	12.0±9.4	0.0	0.0	0.0*
	FFE (6)	47.5±12.5	36.0	24.0	60.0	0.0	0.0
	MME (5)	45.0±11.2	37.7±17.2	3.5±2.5	3.0±1.0	3.0	0.0
L. punctulata							
	FME (35)	20.2± 2.4	22.0± 4.5	24.9±4.3	16.4±5.4	9.3±3.7	13.5±4.6
	EEE (35)	14.1± 3.6	25.6± 0.1	19.7±4.3	16.2±3.7	9.0±1.8	14.9±3.6
	FFE (15)	20.0± 7.5	30.6± 5.9	26.6±7.4	2.0	6.0	1.0
	MME (35)	24.4± 4.9	22.7± 5.2	16.8±4.0	28.9±5.8	9.2±2.4	14.9±4.6

The frequency of DEB exhibited by male *L. rabida* was affected by the experimental stimulus while other behaviors were not (Table 1). A decrease in the incidence of DEB was observed in response to a concealed male versus a hidden female or clean cage ($\chi^2=10.99$, df=1, $p<0.001$; $\chi^2=4.80$, df=1, $p<0.05$). No difference was observed in the incidence of DEB in response to a hidden female versus a clean cage ($\chi^2=1.60$, df=1, $p>0.80$). This suggests that male *L. rabida* may be repelled by hidden males.

Male *L. punctulata* exhibited no difference in the frequency or latency of any behavior when compared among stimuli (Table 1).

Y-olfactometer.–All species except *S. ocreata* were run in the Y-olfactometer with a female in Arm 1, a male in Arm 2 and an empty cage in Arm 3 (=FME run). Male *S. ocreata* were found to be continously active and their behavior could not be recorded accurately. Male *L. rabida* and *L. punctulata* were also run with an empty cage in all three arms (=EEE run), females in two arms with empty cage in arm three (=FFE run), and males in two arms with an empty cage in arm three (=MME run).

The number of 15-sec intervals a test male was observed within a field or arm provided an estimate of the time spent within that field or arm. Males of all three species did not spend more time in one field or arm over another for most experimental runs (Table 2). In view of the arena olfactometer data on *S. saltatrix* and *L. rabida* the above results suggest that the pheromone has only a weak behavioral effect and males do not discriminate among airflows in a choice situation. Male *L. rabida*, however, did not enter the arms during EEE runs. No difference was observed in the time spent within each field during *L. rabida* EEE runs ($\chi^2=0.50$, df=2, $p>0.90$). Male *L. rabida* therefore may receive airborne information indicating that a conspecific is nearby.

Circular analyses of data were performed by two methods. As described below, time analysis was dependent on the frequency an orientation was observed, while incidence analysis depended on orientation events. If a test male had an orientation of 120° for 1 min, calculation of the mean vector for time analysis would depend on a frequency of four 15-sec orientations. Incidence analysis would be performed on a frequency of one

Table 3.—Time and incidence analyses of orientation by male *Schizocosa saltatrix*, *Lycosa rabida* and *L. punctulata* in the Y-olfactometer. The tests run for each species are explained in the text. Sample size for each case is indicated as n_i. The polar angle of the mean vector, ρ; the standard deviation of ρ corrected for a group interval of 30°,s_c; and the length of ρ on a unit circle, r are indicated for each case. The Smirnov's test statistic, U^2, is calculated assuming a circular uniform distribution. Significance levels are indicated as *=P<0.05, ***=P<0.001.

	S. saltatrix	*L. rabida*				*L. punctulata*			
	FME	FME	EEE	FFE	MME	FME	EEE	FFE	MME
					Time analysis				
n_i	1200	1200	420	360	300	2100	2100	900	2100
ρ	215.9	216.7	350.7	37.4	148.5	15.2	252.9	202.8	341.7
s_c	±71.9	±71.5	±69.9	±68.7	±69.9	±74.1	±76.9	±76.0	±71.4
r	0.21	0.22	0.26	0.28	0.42	0.17	0.10	0.12	0.22
U^2	4.9***	5.7***	2.8***	2.8***	3.7***	6.4***	5.5***	2.4***	10.0***
					Incidence analysis				
n_i	59	56	20	13	22	147	148	48	159
ρ	202.9	194.0	313.1	334.1	103.9	39.4	302.2	5.6	332.2
s_c	±78.7	±78.0	±71.5	±62.9	±74.0	±79.0	±79.7	±78.7	±77.1
r	0.06	0.07	0.22	0.40	0.17	0.05	0.03	0.06	0.09
U^2	0.09	0.11	0.09	0.12	0.06	0.14	0.16	0.06	0.19*

120° orientation event in the above example. Time analysis resulted in a significant deviation from a circular uniform distribution for all runs (Table 3). Statistical analysis and visual examination of the circular graphs indicated a multimodal distribution consonant with the arms of the olfactometer. Since the distribution of EEE runs was also multimodal, this suggests that test males exhibit a positive anemotaxis which is unaffected by the stimulus over which the air had passed. Incidence analysis "factored out" the anemotactic responses and indicated a circular uniform distribution for all tests but *L. punctulata* MME runs (Table 3). Examination of the *L. punctulata* MME circular graph did not indicate an apparent modality, however, and a Smirnow test indicated that the data did not fit a circular normal distribution (χ^2=0.364, n_i=159, p<0.001). A Raleigh test indicated that the data fit a circular uniform distribution (z=1.405, k=0.0, p>0.05). The absence of an apparent modality and the results of the above tests suggest that the *L. punctulata* MME runs do fit a circular uniform distribution.

DISCUSSION

Shorey (1976) describes two behavioral responses to an airborne pheromone that could bring individuals together: a change in the rate of locomotion (orthokinesis), or a change in orientation (taxis). An orthokinetic response occurs when an animal decreases its rate of locomotion when in the presence of a pheromone. A chemotactic response may be effected through orientation within a concentration gradient of pheromone or by a response to the flow of the medium (i.e., anemotaxis).

Male *S. saltatrix* in the arena olfactometer exhibited a decrease in the rate of locomotion when in the presence of a concealed female. In the Y-olfactometer, however, male *S. saltatrix* did not exhibit a stimulus dependent orientation. Similarly, the stimulus did not overcome the propensity of males toward a positive thigmotaxis since the time spent in the center of the arena was similar in all arena olfactometer runs. In the Y-olfactometer male *S. saltatrix* did not spend more time in one field than another. The above results suggest that the airborne pheromone acts as a secondary releaser of a component of male sexual behavior or has only a relatively weak behavioral effect and does not direct the male to the female. Female lycosid spiders exhibit low motility during the breeding season while the active males seek them out (Hallander 1967, Hollander 1972, Richter et al. 1971). *S. saltatrix* are found in a leaf-litter habitat (Fitch 1963). Female *S. saltatrix* are found in the refugia formed by the leaves (Cady, pers. comm.) where a pheromone cloud may be expected to build up. Males passing through the cloud would exhibit a decrease in locomotion thus increasing the chance that the male finds the female (or she finds him) through another sensory modality.

Male *S. ocreata* exhibited a qualitative difference in their approach to hidden stimuli (Figs. 3, 4, 5). It is unlikely that a male pheromone could have directed the test male since they ran directly to the isolation chamber in less than 5 sec and no chemo-exploratory behavior was observed. The test male's behavior towards hidden females suggested a taxis response while the response to hidden males suggested visual orientation to the only conspicuous object in the environment (i.e., the isolation chamber). The design of the apparatus made it unlikely that a pheromone concentration gradient could be produced. An airborne pheromone may have increased the rate of turning by the male or may have initiated an anemotaxis response. However, the relatively long time taken during the approach and the periods of no locomotion suggested that the male was searching for the female through vibrational, visual, or contact chemoreceptive cues. The increase in Directed Exploratory Behavior indicated that males were alerted to the presence of the female. As in *S. saltatrix*, male *S. ocreata* were not observed to change the frequency of positive thigmotaxis in response to various stimuli. *S. ocreata* is found in a habitat similar to that of *S. saltatrix* (Fitch 1963). The males are active while the females are inactive and found in refugia formed by the litter (Cady, in prep.). Unlike *S. saltatrix*, male *S. ocreata* would not be expected to slow their rate of locomotion. *S. ocreata* are expected to increase their rate of turning or actively search for the female using other sensory modalities.

Male *L. rabida* and *L. punctulata* exhibited no differential behavioral responses in either olfactometer that could be attributed to the presence of an airborne female pheromone. Male *L. rabida*, however, exhibited a decrease in DEB in the arena olfactometer with a concealed male. This suggests that a male interference strategy which depends on pheromone cues may exist in this species, but further experimentation is necessary.

The difference between genera could have resulted from the different habitat preferences of the *Schizocosa* and *Lycosa* species. Dragline-following behavior has been observed in the *Lycosa* species, while neither *Schizocosa* species has exhibited dragline-following (Tietjen 1977). Both Lycosa species are found in grassy fields where they spend much of their time in the foliage (Fitch 1963). An airborne pheromone would be easily dispersed by air currents in such a habitat. Both *Schizocosa* species are found in leaf litter (Fitch 1963). Females hiding beneath the leaves could produce a pheromone cloud that would not be easily dispersed by wind. On the other hand, the moist leaf habitat of the *Schizocosa* species would quickly inactivate the contact pheromone on the female dragline, as suggested by the laboratory studies of Hegdekar (1973), Hegdekar and

Dondale (1969) and Tietjen (1977). The inactivation of contact female pheromone could explain why dragline-following does not occur in the *Schizocosa* species.

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