

Tietjen, W. J. 1979. Is the sex pheromone of *Lycosa rabida* (Araneae, Lycosidae) deposited on a substratum? *J. Arachnol.*, 6:207-212.

IS THE SEX PHEROMONE OF *LYCOSA RABIDA* (ARANEAE: LYCOSIDAE) DEPOSITED ON A SUBSTRATUM?¹

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ABSTRACT

Male *L. rabida* were used to bioassay seven experimental substrata. Latency and frequency of five behaviors were recorded: courtship, chemoexploration, sound-production, puppet-walking and jolting. Some experimental substrata were covered with conspecific male or female silk. Other substrata were those from cages of females that had their spinnerets occluded before living on a substratum. Lepidopteran silk and clean substrata were used as controls. Data indicate that males exhibit a change in behavior only in response to experimental substrata covered with female silk. These results agree with findings based on species studied by Kaston (1936) and Dondale and Hegdekar (1973), but are opposite from results obtained on other species of wolf spiders by Bristowe and Locket (1926) and Richter et al. (1971).

INTRODUCTION

Bioassay experiments have indicated that a sex pheromone is associated with the dragline of female lycosid spiders (Dondale and Hegdekar 1973, Kaston 1936, Rovner 1968). There has been, however, conflicting evidence concerning a sex pheromone deposited by females through their body surface. Dondale and Hegdekar (1973) and Kaston (1936), by sealing the spinnerets of certain lycosids, showed that a pheromone was not released from the integument of the female and deposited on a substratum. On the other hand, Bristowe and Locket (1926), utilizing a similar experimental design, found that male *Tarentula barbipes* Walkenaer were stimulated by substrata over which a female with sealed spinnerets had walked. Richter et al. (1971) incorporated a larger sample size than the other researchers and indicated that, although male *Pardosa amentata* (Clerck) were not induced to court in the absence of female silk, substrata over which females with sealed spinnerets had walked induced searching behavior in conspecific males.

¹ This study was supported by National Science Foundation Grant BNS 76-15009 to J. S. Rovner.

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Table 1.—Behavioral responses of male *Lycosa rabida* to experimental substrata. Refer to the text for an explanation of the experimental substrata. The sample size for each experimental substrate is indicated in parentheses. The frequencies behaviors were observed are shown in percent of males exhibiting the indicated behavior. The latencies for each behavior are indicated in min \pm SE.

| Experimental substrata | | Behaviors | | | | |
|------------------------|-----------|----------------|------------------|------------------|----------------|----------------|
| | | Courtship | Chemoexploratory | Sound-production | Puppet-walk | Jolting |
| SS (40) | frequency | 25.0 | 27.5 | 47.5 | 2.5 | 2.5 |
| | latency | 4.04 \pm 0.6 | 2.47 \pm 0.7 | 4.68 \pm 0.6 | 0.00 | 0.87 |
| CS (40) | frequency | 25.0 | 35.0 | 52.5 | 5.0 | 5.0 |
| | latency | 5.52 \pm 0.8 | 3.49 \pm 0.7 | 4.93 \pm 0.6 | 1.04 \pm 0.8 | 4.74 \pm 0.6 |
| CR (40) | frequency | 50.0 | 75.0 | 55.0 | 12.5 | 0.0 |
| | latency | 278 \pm 0.4 | 1.96 \pm 0.3 | 4.53 \pm 0.6 | 3.47 \pm 1.5 | --- |
| clean (20) | frequency | 15.0 | 30.0 | 35.0 | 5.0 | 10.0 |
| | latency | 4.98 \pm 1.9 | 3.66 \pm 1.3 | 5.21 \pm 1.0 | 6.37 | 7.35 \pm 0.4 |
| lep (20) | frequency | 5.0 | 35.0 | 40.0 | 15.0 | 5.0 |
| | latency | 6.07 | 4.62 \pm 1.4 | 6.23 \pm 0.9 | 6.59 \pm 1.7 | 9.87 |
| male (20) | frequency | 0.0 | 60.0 | 50.0 | 20.0 | 0.0 |
| | latency | --- | 2.02 \pm 0.6 | 4.21 \pm 0.7 | 2.24 \pm 1.0 | --- |
| female (20) | frequency | 72.5 | 57.5 | 25.0 | 2.5 | 2.5 |
| | latency | 4.06 \pm 0.6 | 0.66 \pm 0.3 | 3.62 \pm 0.7 | 2.27 | 5.00 |

The present study includes a statistical analysis of the behavior of male *Lycosa rabida* Walkenaer in response to experimental substrata including those of "sealed-spinneret" females. A variety of male responses to experimental substrata were recorded in an attempt to increase the sensitivity of the bioassay. The results indicate that this species is similar to those studied by Kaston (1936) and Dondale and Hegdekar (1973), in which the female sex pheromone is not released from the integument but is associated with the dragline.

METHODS

General methods concerning collection, maintenance and observation of lycosid spiders have been previously described (Tietjen 1977). One hundred and eighty five *L. rabida* were collected during 1975 near Athens, Ohio, USA; 80 of these were males. Female spiders were divided into three groups. Two groups were experimentally altered. "Sealed-spinneret" females (=SS females, N=10) had their spinnerets sealed and immobilized with paraffin (Dondale and Hegdekar 1973). "Covered-spinneret" females (=CS females, N=10) had their spinnerets and anal tubercle covered with a small patch of nylon cloth which was fixed to the abdomen with paraffin. Care was taken to insure that the anal tubercle was not occluded by paraffin for both SS and CS females. The nylon patch was later removed from the CS females as a control to determine the effect of occluding the spinnerets (=CR females, N=10). Experimentally altered females were transferred to clean plastic cages (130 x 70 x 65 mm) and were provided with a filter paper substratum and a cotton-stoppered water vial. Females were not fed during a two-day holding period and, for the SS and CS conditions, cages were examined to insure the absence of silk. Four additional experimental substrata were employed. Clean substrata (=clean) had not been previously occupied by experimental animals. Lepidopteran substrata (=lep) had lepidopteran silk obtained from the cocoon of

Table 2.—Chi-square analysis of male *Lycosa rabida* courtship frequency in response to experimental substrata. Refer to the text for an explanation of the experimental substrata. Significance levels are indicated as follows: * $P < 0.05$; *** $P < 0.001$; ns=not significant. Row frequencies that are less than column frequencies are indicated as "a"; row frequencies greater than column frequencies are indicated as "b".

| | Experimental substrata | | | | | | |
|--------|------------------------|------|------|--------|------|-----|-------|
| | CR | SS | CS | female | male | lep | clean |
| CR | — | | | | | | |
| SS | *a | — | | | | | |
| CS | *a | ns | — | | | | |
| female | *b | ***b | ***b | — | | | |
| male | ***a | *a | *a | ***a | — | | |
| lep | ***a | ns | ns | ***a | ns | — | |
| clean | ***a | ns | ns | ***a | ns | ns | — |

Platysamia cecropia Linnaeus on a paper card. Male and female occupied substrata (=male and female) were cage substrata previously occupied by male or female conspecifics respectively for a period of one-two weeks.

Experimental males were selected randomly with the provision that they not be used more than once during a 24-hour period. The latencies (in min) and frequencies of five behaviors exhibited by males in response to the above substrata were recorded during a 10-min trial. Courtship, chemoexploratory behavior and sound-production have been previously described (Rovner 1967, 1968, Tietjen 1977). Puppet-walking (Vlijm et al. 1963) was similar to the threat display described by Rovner (1968), except that the body was often held higher off the substratum such that the palps either did not extend to the substratum or were curled posteriorly. Sound-production usually occurred when the palps touched the substratum. Such instances were recorded only as "Puppet-walking". "Jolting" is characterized by the body being held high above the substratum with the palps in contact with the substratum. The body is then moved posteriorly with a sudden jerky motion. The first legs may be lifted from the substratum; and jolting is always accompanied by sound-production. Sound-production occurring during jolting was not recorded separately as "sound-production".

Statistical analyses of data were performed according to the methods of Conover (1971) and Sokal and Rohlf (1969). Means are accompanied by their standard errors.

RESULTS

The frequency and latency of sound-production, puppet-walking and jolting did not differ among experimental substrata (Chi square test, Kruskal-Wallis test, $df=6$, $0.50 < P < 0.80$; Table 1). This indicates that male *L. rabida* perform these behaviors at a level that is unaffected by the chemical and tactile stimuli provided by conspecific silk.

The frequency of courtship behavior differed among substrata (Chi square test, $df=6$, $P < 0.001$; Table 1). Courtship frequency was analyzed by a Chi square analysis for each pair of substrata (Table 2). Data indicated that female substrata induced a higher level of courtship than all other substrata and CR induced a higher level than all but female substrata. The frequency of courtship was lower on male substrata when compared to lep

Table 3.—Frequency and latency of chemoexploratory behavior by male *Lycosa rabida* in response to experimental substrata. Refer to the text for an explanation of the experimental substrata. The frequency of chemoexploratory behavior was compared among substrata with a Chi-square test (df=1). The latency of chemoexploratory behavior was tested among substrata with a Mann-Whitney test (df=1). Significance levels are indicated as follows: * P<0.05; ** P<0.01; *** P<0.001; ns=not significant. Row frequencies (or latencies) that are less than column frequencies (or latencies) are indicated as "a"; row frequencies (or latencies) greater than column frequencies (or latencies) are indicated as "b".

| | | Experimental substrata | | | | | | | Chemoexploratory latency |
|-------------------------------|--------|------------------------|-----|----|--------|------|-----|-------|-----------------------------|
| | | CR | SS | CS | female | male | lep | clean | |
| Chemoexploratory frequency | CR | — | ns | ns | ***b | ns | *a | ns | |
| | SS | ***a | — | ns | **b | ns | ns | ns | |
| | CS | ***a | ns | — | ***b | ns | ns | ns | |
| | female | ns | **b | *b | — | **a | **a | *a | |
| | male | ns | *b | ns | ns | — | ns | ns | |
| | lep | ***a | ns | ns | ns | ns | — | ns | |
| | clean | ***a | ns | ns | *a | ns | ns | — | |

and clean. Courtship latency did not differ among experimental substrata (Kruskal-Wallis test, df=5, $0.50 < P < 0.90$).

The frequency and latency of chemoexploratory behavior differed among substrata (Chi square test, Kruskal-Wallis test, df=6, $P < 0.001$; Table 1). The frequency of chemoexploratory behavior exhibited on SS and CS substrata did not differ from lep and clean (Table 3). In addition, the frequency of chemoexploratory behavior in response to SS and CS substrata was lower than on female and CR substrata. The differences found between female and CR substrata can be attributed to the greater amount of silk found on female substrata. The supernormal stimulus provided by the female substrata also explains the observed decrease in the latency of chemoexploratory behavior (Table 3).

DISCUSSION

These data suggest that female *L. rabida* do not deposit a pheromone from their integument onto a substratum. These results indicate that *L. rabida* is similar to the species studied by Kaston (1936) and Dondale and Hegdekar (1973), but are opposite from the results of Bristowe and Locket (1926) and Richter et al. (1971).

Excreta were deposited on all substrata except CS, lep, and clean. SS substrata with excreta did not induce a higher frequency of courtship or chemoexploratory behavior when compared to CS, lep, or clean. This indicates that a pheromone is not associated with the excreta of female *L. rabida*. These results are in agreement with those of Kaston (1936).

The frequency of chemoexploratory behavior did not differ among substrata having silk. Male substrata, however, induced less courtship behavior than either CR or female substrata. This suggests that, although male silk provides cues that induce chemoexploratory behavior, these cues alone are insufficient to induce courtship. Mechanical

cues provided by female draglines have been shown to direct dragline-following behavior in male *L. rabida* (Tietjen 1977). Such tactile cues may also induce chemoexploratory behavior. In addition, silk from male *L. rabida* may have an associated male pheromone that has an inhibiting effect on male courtship, however additional research is necessary.

In a related study (Tietjen, unpubl. data) male *Lycosa punctulata* Hentz exhibited responses to experimental substrata similar to those of *L. rabida* indicating the female sex pheromone is associated with the dragline and not deposited on a substratum from the integument. *L. rabida* and *L. punctulata* are found in field-type vegetation (Kaston 1948) and are expected to produce relatively large quantities of dragline compared to lycosids found in open-ground type vegetation (Richter 1970). If females lay down relatively large quantities of silk with the associated pheromone, the additional deposition of pheromone from the integument on a substratum may be superfluous and energetically expensive.

Pardosa amentata (Clerck) is found in open-ground type vegetation (Vlijm et al. 1963), as is *Tarentula barbipes* (Bristowe and Locket 1926). If the open-ground species lay down relatively less dragline than those found in field-type vegetation (Richter 1970), then the cost of deposition of pheromone from the integument to a substratum may be justified due to the resulting increase in information flow. Both *T. barbipes* and *P. amentata* have been shown to deposit a pheromone from the integument (Bristowe and Locket 1926, Richter et al. 1971). However, *Pardosa lapidicina* (Emerton), *P. milvina* (Hentz), *P. saxatilis* (Hentz), and *Schizocosa crassipes* (Walckenaer) are found in open-ground type vegetation (Fitch 1963, Kaston 1948), but do not exhibit evidence of an integument-deposited pheromone (Dondale and Hegdekar 1973, Kaston 1936).

The optimum habitats of *P. lapidicina* and *P. milvina* are moist areas surrounding a pond or lake (Fitch 1963). *S. crassipes* has been found to exhibit temperature and moisture preferences (Cady, unpubl. data). The pheromone found on the female dragline has been found to be inactivated by water in a variety of lycosids (Dondale and Hegdekar 1973, Tietjen 1977). An integument-deposited pheromone may be precluded in the above species due to similar constraints imposed by microhabitat preferences. The absence of an integument-deposited pheromone in *L. rabida* also may be related to microhabitat preferences.

ACKNOWLEDGMENTS

The author wishes to express his gratitude to Dr. J. S. Rovner for his suggestions and discussions. Anne Tietjen assisted in the typing of the manuscript.

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