MICROHABITAT SELECTION AND LOCOMOTOR ACTIVITY OF *SCHIZOCOSA OCREATA* (WALCKENAER) (ARANEAE: LYCOSIDAE)

Alan B. Cady[1]

Department of Zoology
Ohio University
Athens, Ohio 45701

ABSTRACT

Direct observations of the wolf spider *Schizocosa ocreata* (Walckenaer) in a deciduous woods during its breeding season indicated that soil moisture, deciduous leaf litter, and herbaceous vegetation influenced the patterns of their distribution and movement. Areas of high soil moisture, non-compressed litter, and a micro-canopy of herbaceous vegetation comprised the microhabitat with highest spider density. Spiders tended to travel greater distances in the drier patches, suggesting that the increased level of locomotion was related to increased searching for favorable environments. *S. ocreata* was found to aggregate at a litter patch size of 625 cm².

This lycosid appeared to employ a sit-and-wait foraging strategy based on the relationships of spider movement and microhabitat selection. A sex ratio of 1:1 differed from those previously obtained by pitfall trapping methods. Movement and distance information from direct observations of spiders provided support to the previous hypothesis of greater motility of male lycosids.

INTRODUCTION

Microhabitats and their associated microclimates play an important role in determining the local distribution patterns of small terrestrial animals (Odum 1971, Krebs 1972). Mainly due to their large surface area to volume ratio, arthropods are greatly influenced by even minor changes in temperature and humidity.

Leaf litter structure and associated herbaceous vegetation control the spatial distributions of litter dwelling spiders (Vlijm and Kessler-Geschiere 1967, Edgar 1971, Uetz 1975, Kronk and Riechert 1979), mainly through the amelioration of environmental extremes (Hagstrum 1970, Den Hollander and Lof 1972, Edgar and Loenen 1974, Riechert and Tracy 1975). Furthermore, the structure of leaf letter attracts potential prey, provides areas of reduced temperature fluctuations, retains moisture, and creates refugia for hunting spiders (Uetz 1975). Herbaceous vegetation of the woodland floor forms a "micro-canopy" over the litter layer, further modifying the microenvironment. Temperature and humidity were shown to be critical factors influencing microhabitat selection for a number of spider species (Nørgaard 1951, Williams 1962, Cherrett 1964, Duffey 1966,

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[1] Present address: Department of Biology, Lindenwood College, St. Charles, Mo. 63301.

Sevacherian and Lowrie 1972, Richert and Tracy 1975), and field studies provide evidence that lycosoid spiders select favorable thermal environments (Hallander 1970a, Riechert and Tracy 1975). Microhabitat selection has been shown to provide spatial separation and reduce cannibalism for closely related lycosid spiders (Hallander 1970b, Hagstrum 1970, Edgar 1971).

The ability of lycosids to move great distances (Richter et al. 1971) enables them to encounter many different microhabitats in their lifetime. It was formerly thought that wolf spider locomotor activity was related to their foraging behavior. However, Enders (1975) suggested that these predators may adopt a sit-and-wait strategy (Schoener 1971) to secure their food. This hypothesis predicts that movements of lycosids should be lowest within areas of favorable environmental conditions. Also, Ford (1977) found that the sit-and-wait strategy adopted by *Pardosa amentata* was more energetically efficient than actively hunting. Therefore, locomotor activity would reflect the spiders' search for suitable microhabitats or resting sites, and not necessarily their hunting tactics. Furthermore, predators may increase locomotor activity in areas where little prey is encountered, resulting in more movement within poorer habitats than in higher quality ones.

The present study describes influences of microhabitat structure on the local patterns of distribution and locomotor activity for the wolf spider *Schizocosa ocreata* (Walckenaer). My observations indicate that *S. ocreata* actively selects its microhabitat, and that its distribution and locomotor activity are related to available moisture and other physical features as leaf litter, spring seepage, the presence of saplings, and herba-- ceous vegetation.

STUDY SITE AND METHODS

Schizocosa ocreata primarily occupies deciduous leaf litter substrates in moist areas across the eastern United States (Kaston 1948), although it is also found in drier uplands (Uetz and Denterlein 1979). The data were collected from a deme located at Stroud's Run State Park, Athens County, Ohio, USA from 13 March thru 16 June, 1977.

Study Site.—The study site was within a second growth temperate deciduous forest (Odum 1971) composed mainly of broadleaf hardwoods, and was located in a small ravine formed by an intermittent stream. A spring seepage drained through the site down a 5-25% southwest slope towards the stream. At times the water flow was copious, inundating a 1 m wide (0.5-1.0 cm deep) swath down the slope. The soil was a heavy montmorillonite-type clay, with a shallow (0.0-2.0 cm) mull humus layer. Leaf litter covered the entire area. Its depth varied from 0.0-6.0 cm, and consisted of the previous autumn's leaves [mainly oaks (*Quercus* spp.), beech (*Fagus grandifolia*), and sycamore (*Platanus occidentalis*)]. The litter structure varied from Heatwole's (1961) Class I curled to Class II thick. Litter was deepest in depressions, around the bases of saplings or shrubs, and where herbaceous stems prevented it from being scattered by the wind. Litter was compressed and moist in the area of the spring seepage. Most of the herbaceous vegetation was associated with the drier litter; very little grew in the seepage. The following herbaceous plants occurred in the ground layer: Muhly (*Muhlenbergia* sp.), Peruvian Daisy (*Galinsoga* sp.), Virginia Creeper (*Parthenocissus quinquefolia*), Plantain (*Plantago* sp.), and Wood Sorrel (*Oxalis* sp.).

Two 2x2 m plots each enclosing distinctly different physical features were placed within the study site to assess spider locations and activities within different microhabitats. Plot I contained two areas of deep litter and herbaceous vegetation separated by the

spring seepage. Nine saplings (5-15 cm dia.) were present. Two crayfish (*Orconectes*) burrows on the plot's boundaries were indicative of the soil's wetness.

No surface water occurred at any time in Plot II; seepage affected a small part of one border only during rainy periods. Two saplings (7-8 cm dia.) were present while herbs covered most of the plot.

Methods.—The investigation was based upon direct field observations of free ranging wolf spiders, as this method yields more detailed data on the exact locations, activities, and duration of behaviors than pitfall trapping. The frequency, duration, direction, and location of locomotory activity were used as a bio-assay for microhabitat preference.

Galvanized wire outlined the plots' boundaries, and tags painted with light-reflective paint (to facilitate night observations) were placed at 10-cm intervals along the wire. The habitat structure (litter, saplings, spring seepage, rocks, wood, and herbaceous vegetation) of each plot was mapped on the basis of a 10-cm grid using the point intercept method. "Full litter" was recorded if litter at a point was not compressed and over 1 cm deep; bare ground, compressed litter, or litter under 1 cm deep was scored as "sparse litter." Soil moisture was determined gravimetrically after drying.

Observation sessions were four hours long during each day of the study. The entire diel period was sampled to ascertain any diurnal-nocturnal differences in spider activity. This resulted in approximately 100 hrs of observations on adults and 140 hrs on immature spiders. The plots were divided into 4 sections, and each section was closely scrutinized for 15 min. Thus, one plot was completely surveyed each hour. A headlamp was used at night. When a spider was sighted, its position and movements during a two minute observation period were mapped, and the spider's sex and time of sighting were noted. A relative measure of the distance a spider moved during the two minute observation period was obtained by measuring the mapped route of a spider to the nearest 0.5 cm. Spiders were placed into 3 groups (male, female, total [males + females]), and further division was made based upon their relative degree of activity (stationary, moving, total [stationary + moving]).

Block size analysis of variance was employed to investigate the distribution patterns of spiders and litter types within each plot. Greig-Smith (1952, 1961, 1964) and Kershaw (1960, 1964) described and developed this method which involves partitioning the total variance of a grid or line of quadrats. A peak in mean square (variance) above the mean indicates maximum heterogeneity is found among the quadrats at that block size. Therefore, peaks in mean square at a particular block size indicate aggregation or clumping of spiders at that block size.

A rectangle and square system (Greig-Smith 1952) was used for analysis of pattern, where block sizes 1, 4, and 16 were square, and block sizes 2, 8, and 32 were rectangular. The basic quadrat (block size 1) was 156.25 cm^2. Associations between spider and litter distributions in each plot were measured by block size analysis of covariance (Kershaw 1961).

Other statistical procedures were from Sokal and Rohlf (1969) and Conover (1971).

RESULTS AND DISCUSSION

The results will be presented and discussed in three sections. The first deals with associations between the microhabitat and distribution of *Schizocosa ocreata* (microhabitat selection), the second pertains to locomotor activity of the spiders in relation to
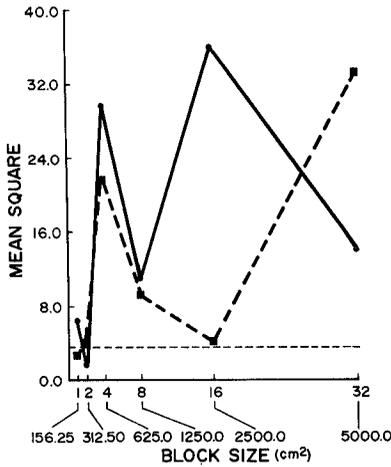
Fig. 1—Variance plotted against block size for Grouped + Stationary *Schizocosa ocreata* (dashed line) and full litter (solid line) in Plot I. Horizontal dashed line indicates mean. A peak in mean square above the mean indicates clumping at that block size. Peaks occur at block sizes 4 and 32 for spiders and block sizes 4 and 16 for full litter.
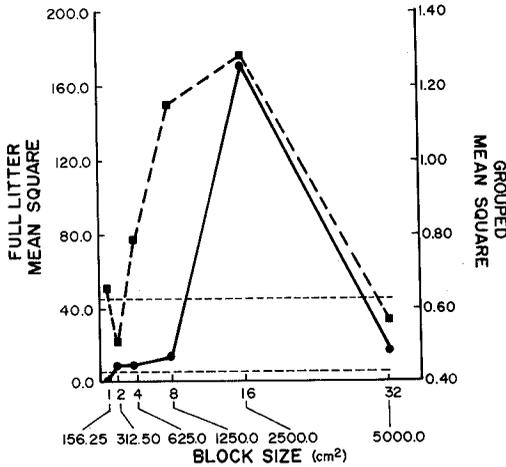

Fig. 2.—Variance plotted against block size for Grouped *Schizocosa ocreata* (dashed line) and full litter (solid line) in Plot II. Horizontal dashed lines indicate means. A peak in mean square above the mean indicates clumping at that block size. Peaks occur at block size 16 for spiders and full litter.
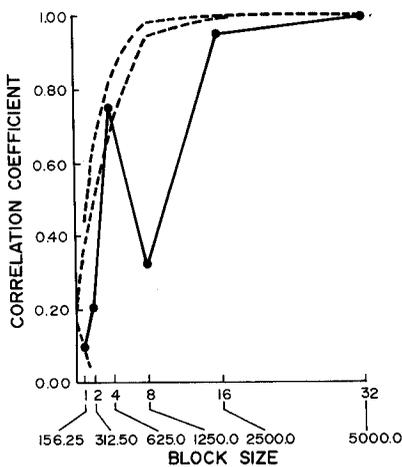

Fig. 3.—Results of correlation coefficients computed on covariances between stationary *Schizocosa ocreata* and full litter in Plot I. Dotted lines represent upper and lower confidence limits (P < 0.05 and P < 0.01). A peak outside a confidence limit indicates correlation at that block size (block size 4 in this case). The converse of this figure is identical in the negative (for sparse litter and stationary spiders).

Table 1.–Densities, means (number/16 quadrats in each plot), variance, and Coefficients of Dispersion (CD = variance/mean) for litter types and *Schizocosa ocreata* within Plots I and II. A significant CD indicates a clumped distribution (as tested with the Poisson distribution). * = $P < 0.05$, ** = $P < 0.01$, *** = $P < 0.001$.

CATEGORY	NUMBER	MEAN ± SE	VARIANCE	CD
		PLOT I		
FULL LITTER	165.75	10.36 ± 1.7	45.06	4.35***
SPARSE LITTER	214.25	13.39 ± 1.7	44.86	3.35***
STAT. SPIDERS	109	6.81 ± 1.7	47.81	7.02***
MOVING SPIDERS	44	2.75 ± .51	4.09	1.52
MALE SPIDERS	86	5.36 ± 1.1	19.99	3.73***
FEMALE SPIDERS	67	4.19 ± 1.1	20.53	4.90***
TOTAL	153	9.56 ± 2.1	68.16	7.13***
		PLOT II		
FULL LITTER	218.75	13.67 ± 2.0	63.98	4.68***
SPARSE LITTER	174.25	10.89 ± 2.0	65.67	6.03***
STAT. SPIDERS	25	1.56 ± 2.0	2.39	1.53
MOVING SPIDERS	15	.94 ± .30	1.69	1.79
MALE SPIDERS	21	1.31 ± .30	1.50	1.14
FEMALE SPIDERS	19	1.19 ± .30	1.29	1.09
TOTAL	40	2.50 ± .50	3.60	1.44

microhabitat, and the third considers differences between male and female spiders relative to their activity and microhabitat selection.

Microhabitat and Spider Distribution.–The overall density (over the entire study) of *S. ocreata* was higher in Plot I than Plot II (Table 1, $\chi^2 = 66.16$, $P < 0.001$, df = 1). More spiders were found in full litter than in sparse litter (Table 2). Spiders in Plot I aggregated at block sizes 4 and 32 (Fig. 1), whereas those in Plot II aggregated only at block size 16 (Fig. 2). However, only the spiders in Plot I were significantly clumped (Table 1, Coefficient of Dispersion). The overall distribution of full litter and spiders were positively correlated in both plots (Table 3), and the spatial patterns of spiders were positively correlated with full litter and negatively correlated with sparse litter in Plot I at block size 4 (Fig. 3). The significant clumping of spiders and their correlation with full litter in Plot I not found in Plot II, suggests the presence of some factor(s) which influenced aggregation within Plot I which was not found in Plot II. The soil and litter layer in Plot I was moister than that of Plot II (Mann-Whitney U Test, T = 0.00, $P < 0.001$, N = 4), and full litter was more strongly associated with herbaceous vegetation in Plot I (Fig. 4). Therefore, it appears that areas of high soil moisture, full litter, and herbaceous vegetation provided the preferred microhabitat for *S. ocreata* (i.e. Plot I). Because spiders were correlated with full litter at block size 4, the habitat patch size in this particular area was approximately 625 cm^2.

Hagstrum (1970) found a direct correlation between the depth of litter and the density of the lycosid spider *Tarentula kochi*, and Uetz (1976) showed that the number of wandering spider species was positively correlated with litter depth and negatively correlated with the percent reduction of litter due to flooding.

In the present study, flooding from the spring seepage similarly reduced the amount and depth of litter, and spider density was lower in the seepage area than in other areas of Plot I ($X^2 = 65.88$, $P < 0.001$, df = 1). Herbaceous growth shades and anchors litter, and

Table 2.—Chi-square test for goodness-of-fit comparing frequencies of stationary, moving, and total *Schizocosa ocreata* in full vs. sparse litter. One decree of freedom for all tests. All chi-squares adjusted for proportional amounts of full and sparse litter. * = P < 0.05, ** = P < 0.01, *** = P < 0.001.

	FULL LITTER	SPARSE LITTER	χ^2
STATIONARY			
MALES	53	14	23.99***
FEMALES	44	23	7.12**
BOTH	97	37	20.84***
MOVING			
MALES	19	21	.130
FEMALES	11	8	.545
BOTH	30	29	.099
TOTALS			
MALES	72	35	13.77***
FEMALES	55	31	7.29**
BOTH	127	66	20.84***

saplings allow litter to collect around their bases. Thus, where these two vegetational features occur, a deep, stable litter layer is created, providing a favorable area where *S. ocreata* and their prey may live. It is evident that the physiognomy of the woodland floor exerts an important effect upon the patterns of local distributions of *S. ocreata*.

Locomotor Activity and Microhabitat Selection.—If this spider was actively selecting the most suitable microhabitat, less locomotor activity should be observed within preferred areas. The data suggests that full litter is a preferred habitat. There were more stationary than moving spiders within full litter (data in Table 2, χ^2 = 16.05, p < 0.001), and the distance which spiders travelled was positively correlated with sparse litter (Table 3). The percentage of spiders found moving in sparse litter was higher than that found in full litter, and the percentage of stationary spiders was higher in full litter than within sparse litter (Table 4). Stationary spiders were positively correlated with full litter and negatively correlated with sparse litter (Fig. 3). These results show that spiders moved farther and more often in sparse litter than full litter, and suggests that microhabitat selection is cued by the environmental and biological conditions which exist within full litter.

Spiders tended to move across areas of sparse litter and stop upon contact with a patch of full litter (Table 5). If a spider began movement in sparse litter it tended to continue moving, whereas ones initiating movement in full litter did not move very far, terminating the bout of activity within full litter (Table 5). Hallander (1967) suggested that substrate type influences the level of activity of *Pardosa chelata* and *P. pullata*, since there was less locomotion in a preferred substrate (leaves) compared to non-preferred substrates. In the present study, moving spiders were found more often in the less preferred microhabitat, and stationary spiders occupied the areas with more cover. Therefore, stimulation of activity or non-activity by the substratum probably was a major factor underlying *S. ocreata*'s microhabitat selection. Spiders in non-preferred (unfavorable) areas may be stimulated to move, increasing the chance of encountering a preferred (favorable) microhabitat. Once there, stimulation to move would be less, and the spider would be more likely to remain in a favorable spot.

Table 3.–Phi coefficient (nonparametric meaure of association, Conover 1971) showing correlation of stationary, moving, and distance moved by *Schizocosa ocreata* with litter types. N = 426. * = P < 0.05, ** = P < 0.01, *** = P < 0.001.

	MALES	FEMALES	TOTAL
FULL LITTER			
Stationary	0.2267***	0.1526***	0.2865***
SPARSE LITTER			
Moving	0.0284	0.0065	0.0287
Distance moved	0.1103*	0.0080	0.1088*

Males vs. Females.–During the time of this study, it is likely that female spiders were searching for prey while male spiders were searching for females (Vlijm and Richter 1966). This was reflected in the differential microhabitat selection and levels of loco- motor activity found between the sexes. Female *S. ocreata* tended to remain within full litter whenever possible, as they were found most often in full litter (Table 2). The distribution of stationary females was positively correlated with that of full litter (Table 3). Laboratory observations have shown that female *S. ocreata* tended to stay under the paper "cage cards" and inside of water vials, whereas males were mostly on top of the cards and not in the vials (Table 6). These results indicate that females in the field may be responding to cover and higher humidity provided by full litter.
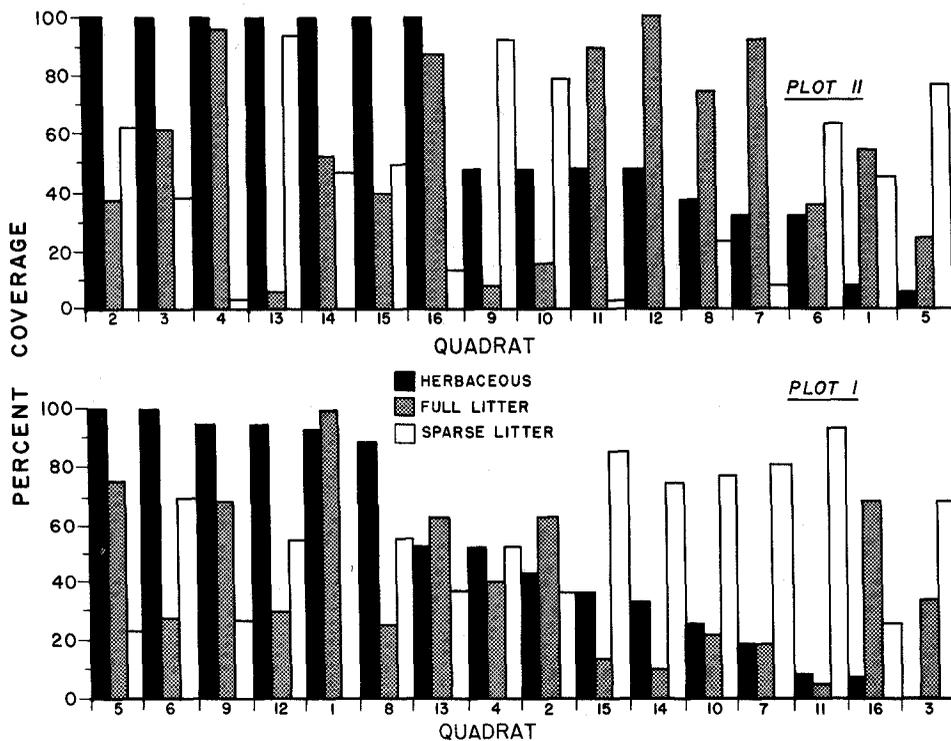

Fig. 4.–Percent coverage comparisons of herbaceous vegetation, full litter, and sparse litter for each quadrat in Plots I and II.

Table 4.–Percentages of stationary and moving male and female *Schizocosa ocreata* within full and sparse litter. T = the test statistic for equality of two percentages; Sokal and Rohlf (1969). * = P < 0.05, ** = P < 0.01, *** = P < 0.001.

	PERCENT WITHIN FULL LITTER	PERCENT WITHIN SPARSE LITTER	T
STATIONARY			
MALES	42.70	21.20	3.08***
FEMALES	34.6	34.8	0.03
BOTH	76.0	56.1	2.80***
MOVING			
MALES	14.9	31.8	2.67***
FEMALES	8.6	12.1	0.76
BOTH	24.0	43.9	2.80***
SAMPLE SIZES			
MALES	72	35	
FEMALES	55	31	
TOTAL	127	66	

Reproductive success could be enhanced by utilizing a microhabitat which supplied numerous prey. Uetz (1976) found that potential prey species richness was positively correlated with deciduous leaf litter depth. Therefore, females which occupy deeper litter would have a higher probability of encountering prey. Spaces under the litter offered a warm, moist area where time of activity would be extended (Uetz 1979), and which also provided a favorable site for egg incubation. Thus, by selecting the proper microhabitat, female *S. ocreata* are able to exploit the enhanced environmental and energy-supplying characteristics of full litter.

Male spiders moved more than females. The mean relative distance travelled by males was greater than that for females (male mean = 22.03 cm, female mean = 14.36 cm; Mann-Whitney Text T = 807.5, P < 0.01, N = 80), and a higher percentage of males were moving than were females within sparse litter (males = 72.41%, females = 27.59%, test statistic = 2.237, P < 0.01). These direct observations of *S. ocreata* support earlier hypotheses (based on studies utilizing pitfall trapping) of elevated male lycosid motility during the breeding season. The higher motility of male lycosids is attributed to the

Table 5.–Frequencies of continuation or termination of a bout of locomotor activity by *Schizocosa ocreata*. A. The direction of movement (i.e. from one litter type to the other) and the frequency of either stopping or continuation of movement upon crossing that boundary. B. Frequencies of locomotory bouts occurring entirely within one litter type during a 2 min. observation period. Stopping indicates the spider halted before the end of the observation period, no stop shows the spider was still moving after 2 min. * = P < 0.05, ** = P < 0.01, *** = P < 0.001.

	STOP	NO STOP	χ^2
A. Full to Sparse	3	7	1.6
Sparse to Full	12	2	7.14**
B. Within Full	17	4	8.05**
Within Sparse	2	19	13.76***

Table 6.–Frequencies of male and female *Schizocosa ocreata* on top or under paper cage cards (on bottom of cages) or inside water vials. (Data courtesy of Gail Stratton, Univ. of Cincinnati.)

	ON TOP	UNDER
MALES	79	18
FEMALES	46	69

$$\chi^2 = 37.35 \quad df = 1 \quad P < 0.005$$

male's search for females during the reproductive period (Vlijm and Richter 1966, Hallander 1967, Richter et al. 1971). Typical sex ratios resulting from pitfall trap studies usually show a higher proportion of males than females. The sex ratio obtained from these direct observations was approximately 1:1 (males = 107, females = 86, χ^2 = 2.28 ns, df = 1; ratio = 1:1.2). Therefore, results obtained from direct observations give a truer representation of the actual sex ratio than studies using pitfall trapping, which typically indicate more males.

The sit-and-wait foraging strategy (Enders 1975) would predict the optimal location for foraging by *S. ocreata* would be in full litter. The above results support this hypothesis. This wandering spider preferred the favorable environmental conditions found in full litter over those found in sparse litter for their resting (and hunting) spots. Spiders under full litter were protected from environmental extremes and easy predation (birds and spider wasps [Pompilidae]), and were in an area of high prey density. Sparse litter did not provide avenues for quick escape from predators or adverse physical conditions, so spiders would not have been expected to remain on sparse litter for prolonged periods of time. Most moving spiders seen in or on sparse litter continued moving (Table 5).

Proper microhabitat selection by *S. ocreata* is probably important to courtship and subsequent meeting of the sexes. Stridulation is part of the acoustic display performed in the courtship of many lycosid spiders (Rovner 1975). A stridulating male *S. ocreata* may be heard over 2 m away when he is on full litter. The large leaves found there supply a good "sounding board" for amplification and conductance of acoustical signaling. It has been shown for other lycosids that the female spider orients to and approaches hidden stridulating males (*Lycosa rabida*, Rovner 1967; *Schizocosa rovneri*, Stratton and Uetz 1981). *S. ocreata* is closely related to *S. rovneri*, and probably responds in a similar fashion. Therefore, a male spider courting on full litter would have a higher probability of attracting a female than a male on sparse litter. A higher density of females occurs within full litter, and the substratum is well suited for acoustical displays. This, along with possible chemical attraction (Tietjen 1979) and the physical characteristics of full litter may explain the aggregations of *S. ocreata* found in and on full litter.

Schizocosa ocreata utilizes a heterogeneous habitat by actively selecting the microhabitat most favorable for their reproductive and environmental requirements. We now need information on what takes place under the litter, for these animals live in three dimensions. Mating was observed on the surface only twice, so it probably occurred under the litter most of the time. This is only one example of the many different activities which are not easily seen by surface observations, and indicates a direction for future investigations.

ACKNOWLEDGMENTS

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