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TEMPORAL AND SPATIAL SEGREGATION OF WEB-BUILDING IN A COMMUNITY OF ORB-WEAVING SPIDERS

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ABSTRACT. The temporal pattern of activity and spatial distribution of six species of nocturnal orb-weaving spiders (Araneae: Araneidae and Tetragnathidae) were examined in coastal hedge vegetation in Israel. In Autumn, small spiders of all species built their webs early in the evening and progressively larger spiders put their webs up through the night. This activity pattern corresponded to the change in sizes of flying insects throughout the night. There was no interspecific segregation in time of activity. Spiders were highly clumped in space, but showed interspecific segregation only in web height. In Autumn, *Nuctenea suspicax* was the most abundant species, while in Spring *Singa lucina* predominated. During the latter season, spiders had two periods of activity: evening (at dusk) and morning (pre-dawn). Morning-active spiders had larger webs and larger clutches than evening-active spiders. As in Autumn, there was little interspecific segregation in time of activity or in spatial distribution. Spider removal experiments suggest that the timing of activity does not change following density reduction, but that individuals that were previously inactive may take advantage of the newly available spaces. The number of active spiders increased when sites for web attachments were added, supporting the hypothesis that space availability limits spider activity. The results are discussed in terms of the importance of niche partitioning in time and space.

The study of the factors influencing the distribution and abundance of animals has long been fundamental to ecology (Andrewartha & Birch 1954). The dispersion of animals in time and space has often been used to ascertain the influence of conspecifics and heterospecifics on the behavioral ecology of a variety of animals (Davies 1978). Web-building spiders are particularly suitable for such studies because: (1) they spend much of their time in a fixed position, facilitating measurement of dispersion, (2) they are easily manipulated, by removal or supplementation experiments, and (3) many species often coexist in large numbers and in relatively small areas (Robinson et al. 1974; Lubin 1978; Hoffmaster 1985).

Some studies of web-building spiders have shown that patterns of dispersion are related to aggressive interactions among individuals, which may influence website selection and web-building behaviour (Riechert 1981; Pasquet 1984; Leborgne & Pasquet 1987). Other studies, however, have indicated that individuals may aggregate in order to take advantage of clumped prey distributions or to reduce predation risk (e.g., Lubin 1974; Uetz et al. 1978, 1982; Schoener & Toft 1983a). In some communities of orb-weaving spiders, there is considerable separation of species according to the vegetation types selected (Enders 1973; Harwood 1974), heights at which webs are placed (Enders 1974; Taub 1977; Olive 1980; Brown 1981), and types of prey taken (Olive 1980). These differences have been used as indications of interspecific competition (Enders 1974; Brown 1981; Spiller 1984), although Spiller (1984) noted that seasonal reversals of competitive advantage may occur. These studies contrast with that of Hoffmaster (1985) who showed that, in multi-species orb-weaving spider communities in Panama, the spatial distributions of species were not significantly different from random. Hoffmaster (1985) suggested, like Wise (1984), that interspecific interactions are not important in orb-weaving spider communities.

In this study, we examine the temporal and spatial distribution of web-building behavior in a guild of six nocturnal orb-weaving spider species (Araneae, Araneidae and Tetragnathidae) in coastal hedge vegetation at Ma'agan Michael, near Haifa, Israel. The structural simplicity of the vegetation, combined with high densities of web-building spiders, suggested a potential for space limitation. Natural history observations indicat-

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ed that there was temporal segregation of web-building behavior in these nocturnal orb-weaving spiders. These changes in activity appeared size-correlated, with larger spiders building their webs later in the night than small spiders. We set out to determine if the different species segregated temporally and to assess the possible causes of this activity pattern. We then experimentally manipulated both spider densities and the space available for web building in a series of short-term experiments in order to examine the interaction between temporal and spatial scales of community organization.

METHODS

Study area and spider dispersion.—Six orb-weaving spider species (Table 1) occur in the almost homogeneous hedges of the perrenial composite *Inula viscosa* (L.) Ait. surrounding fish ponds at Ma'agan Michael on the Mediterranean coast of Israel. These hedges are about 1–2 m high and 1 m wide and are bounded on one side by sand roads and by ponds on the other. The vegetation is typical of coastal Mediterranean pond-edge communities. Other plant species occur patchily, notably a reed (*Phragmites* sp.), tamarisk trees (*Tamariskia* sp.) and a grass (*Bromus* sp.). The study was conducted in Autumn of 1986, 1988 and 1989 and in Spring 1989. We measured ambient temperature and relative humidity with a sling psychrometer (Bacharach, Inc.) at the study site before each census. Climatic conditions during the study periods were similar: nighttime ambient temperatures recorded in Autumn near the ponds were 22–13.5 °C and in Spring from 22–14 °C. The relative humidity at night increased from 70 to > 90% from early evening to about 2300 h and remained high until dawn.

Plots were established in *I. viscosa* hedges. We used three 15 m-long plots in our experiments in September–October 1986 and 1988, one 18 m plot in our experiments in April–May 1989 and three 3 m long plots (each separated by one meter) in October 1989. The plots were delineated by vertical poles connected by string at a height of 1 m above the ground, with the exception of the last mentioned experiments which involved string supplementation, and were subdivided into 1 m^3 sections.

Spiders with intact orb webs were denoted as active. Active spiders in the study plots were counted and identified to species at approximately 2 h intervals throughout the night. We estimated spider size to the nearest mm, and measured maximum web diameter and web height above the ground (measured from the hub). To determine the relationship between spider length and web diameter, we removed spiders and measured them in the laboratory with vernier calipers. All mean measurements are given ± SE. Eggsacs of *Singa lucina* (Audouin) were collected in May 1989 to determine whether there were changes in reproductive output associated with different temporal activity patterns in this species.

Activity of spiders was studied in conjunction with trapping of flying insects (potential spider prey) using a blacklight placed above a tray of preservative (70% ethyl alcohol) in nearby hedge vegetation. While the traps may not capture the different prey types in the same proportions as webs (Eberhard 1991), we believe that the temporal distribution of the numerically dominant insect groups in this structurally simple habitat is adequately represented in our lighttrap samples. Earlier observations showed that orb webs present in the hedges in early evening were choked with small midges that emerge from the ponds at dusk. Webs present later in the night were largely free of midges, but had large, scale-lined holes attributed to moth interceptions.

We used the standard Index of Dispersion, the variance divided by the mean ($I = s^2/\bar{x}$) to measure the randomness and clumping of webs: I = 1 denotes random dispersion and I> 1, clumped dispersion. This index has a χ^2 distribution and was tested against this for significance (Pielou 1977). We used the number of spiders in the 1 m^3 quadrats for the purpose of this analysis. The index of dispersion is affected by sample size, although this effect is considered to be minimal with the sample sizes we used (18 quadrats in April–May 1989 to 45 in September–October 1986 and 1988) (Pielou 1977). We calculated the index of dispersion separately for each census to minimize errors due to possible lack of independence of censuses (some spiders remained active over more than one census period).

Vegetation density was measured by line transects at 1 m intervals along the hedge and at 40 cm increments above the ground to determine whether there were differences in vegetation structure among the quadrats. Vegetation density is expressed as the mean number of 5 cm sections of each transect line covered by vegetation (maximum = 20). In October 1988 and in May 1989, spiders were censused in three additional 6 m plots near the ponds to determine if the different orb-weaver species had separate habitat preferences. These plots, also in the hedges, were chosen to represent a variety of hedge habitats differing in vegetation structure.

Discriminant analysis was used to help elucidate the usage of different habitat and environmental selection features (vegetation density, distance from the front or exposed side of the plots, web height, distance along the plots) by the various species. Discriminant analysis distinguishes among groups (spider species) by weighting and linearly combining independent variables (habitat features) into a new variable, or discriminant function, which gives maximal statistical separation of the groups (species) (Green 1971). By extracting a second, orthogonal, discriminant function, overlap is viewed in a plane. As many discriminant functions are extracted as contribute to significant discrimination among groups. Plotting species centroids along all relevant discriminant function axes (those axes that are statistically significant in a Wilks λ test) gives a visual representation of overlap along a reduced set of axes. Standardized coefficients of the discriminant functions indicate the associations of the function with each of the original variables.

Experimental manipulations.—Experimental manipulations of spider density and of space available for web construction were performed over periods of 3–5 days each in Autumn 1988 and 1989 and in Spring 1989.

Removal experiments: We conducted removal experiments in order to test whether the temporal stratification of activity was due to space limitation acting on spiders building their webs at preferred times of the night. In September 1988, we removed all spiders as they became active each hour through the night in a 15 m plot. The temporal stratification of active spiders of the different size classes was compared with that of active spiders in an adjacent unmanipulated 15 m plot.

To determine if changes in spider numbers following removal could be explained by movement of spiders from adjacent areas, we conducted a second removal experiment in April 1989. We removed all active spiders in two central 3 m plots and compared spider activity in these plots with that in two adjacent 3 m plots on either side.

In May 1989, we removed all the predawn active spiders (henceforth "morning spiders") from two 3 m plots to determine whether spiders active in the post-dusk period (henceforth "evening spiders") would become "morning spiders". In another 3 m plot, all "evening spiders" were removed, to determine whether "morning spiders" would change their activity pattern to become "evening active". Activity in these experimental plots was compared with that in two neighboring control plots on either side. The retreats (curled leaves in which the spiders sat when not active on their webs) of "morning" and "evening" spiders were marked with different colors of paint to facilitate recognition.

Space-supplementation experiments: We conducted space-supplementation experiments by adding strings for web attachment to two 3 m plots in spring 1989. In one, string was tied around the perimeter of the plot at 50 cm intervals both vertically and horizontally. String was also tied in horizontal and vertical planes through the plot, with the effect that the plot was divided into 50 cm × 50 cm × 50 cm cubes with a total of 44 m of string. In the second experimental plot, string was tied in the same manner, but at 25 cm intervals. Thus, this plot was divided into 25 cm × 25 cm × 25 cm cubes and contained 116 m of string. Another 3 m plot (control) had only a single line of string demarcating the perimeter.

In these experiments, each plot was first censused for one night prior to string supplementation in order to determine the number of spiders active under pre-experimental conditions. The number of spiders active subsequent to supplementation was then compared with the initial density in each plot, and with the control plot on the same night.

RESULTS

Temporal dispersion patterns.—Activity patterns of spiders in Autumn 1986 and 1988 showed a peak of web-building at dusk, with additional webs appearing through the night. There was a significant increase in the size of new webs (ANOVA, $P < 0.05$ for each of 8 nights in 1986 and 1988) from early evening until morning (Fig. 1). Web diameter was highly positively correlated with spider body size (Spearman rank correlations, 1986: $R = 0.86$, $n = 62$; 1988: $R =$

Table 1.—The species of orb-weaving spiders in hedge vegetation surrounding the ponds at Ma'agan Michael. The two *Tetragnatha* species are as yet unidentified. They were distinguished by the presence of an unhumped (Sp. A) or humped (Sp. B) opisthosoma.

Species (family)	Orbweb	Retreat
Singa lucina (Araneidae)	vertical	curled-leaf
Nuctenea suspicax (Araneidae)	variable	curled-leaf
Larinia chloris (Araneidae)	vertical	underside of grass-blade
Neoscona subfusca (Araneidae)	generally vertical	underside of leaf
Tetragnatha sp. A (Tetragnathidae)	variable	twig
Tetragnatha sp. B (Tetragnathidae)	variable	twig

0.75, $n = 87$, $P < 0.0001$ in both years). The increase in web size throughout the night was not due to a shift in species activity. In a two-factor ANOVA (factors = species and time), there was no significant interaction effect ($P > 0.05$) over any of the census nights, indicating absence of interspecific segregation in activity patterns. Rather, a large proportion (>50%) of spiders building their webs in the early evening were immatures of all species.

Blacklighting of insects in Autumn showed that insects had the same size-based temporal activity patterns as the spiders. Many small insects were active early in the evening and progressively larger insects became active through the night (Fig. 2). At dusk, there was an emergence peak of midges (Nematocera, Chironomidae) from the ponds; by early morning, most active insects were large moths (Lepidoptera).

In Spring 1989, we attempted to examine the temporal segregation of web-building behaviour more rigorously. However, at this time of year few immature spiders occurred on the plots and web-building was less evenly spaced throughout the night than in Autumn. There were two main periods of web-building, at dusk and again before dawn (Fig. 4). Insect activity patterns (determined by blacklighting) followed the pattern described above for Autumn; i.e., many small insects appeared early in the night, and larger insects increased in numbers towards morning (Fig. 3).

We marked the retreats of *Singa lucina*, which was the predominant species present in Spring. As the retreat is connected to the orb web by a

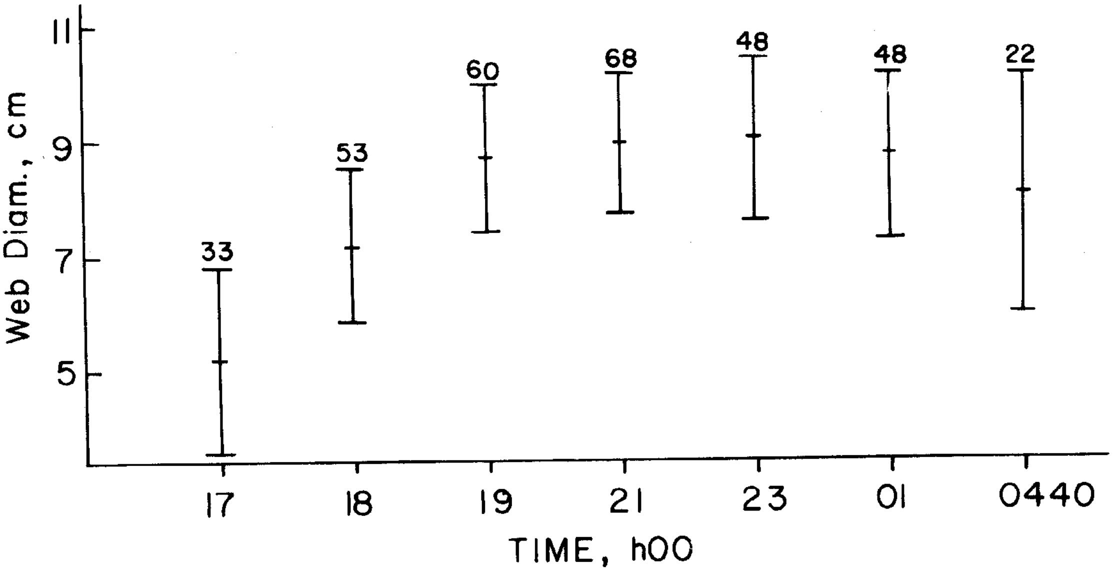
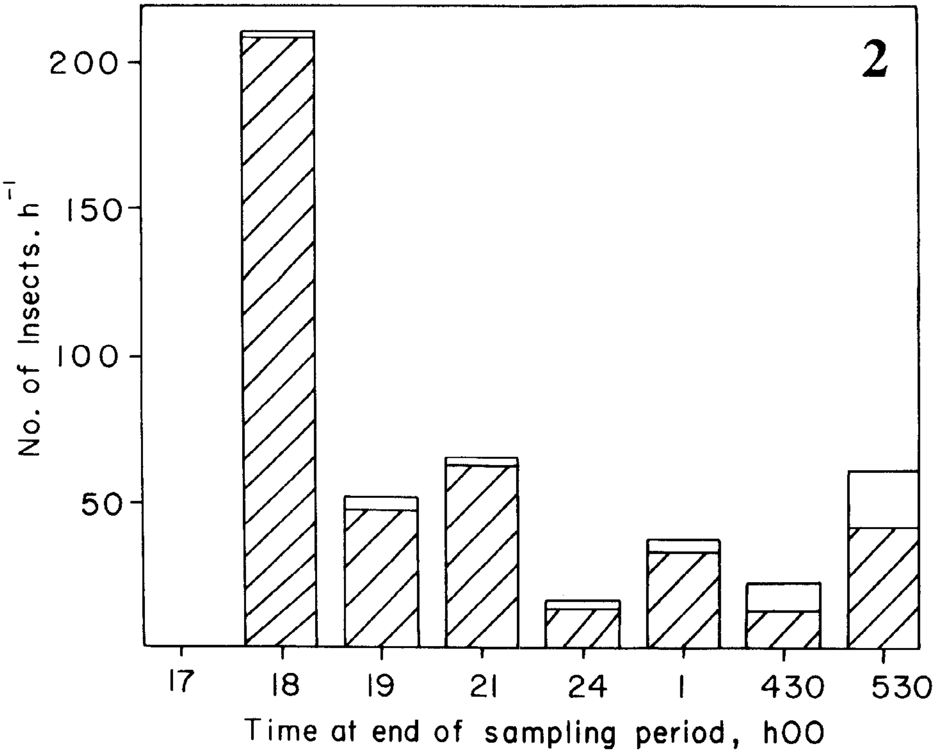
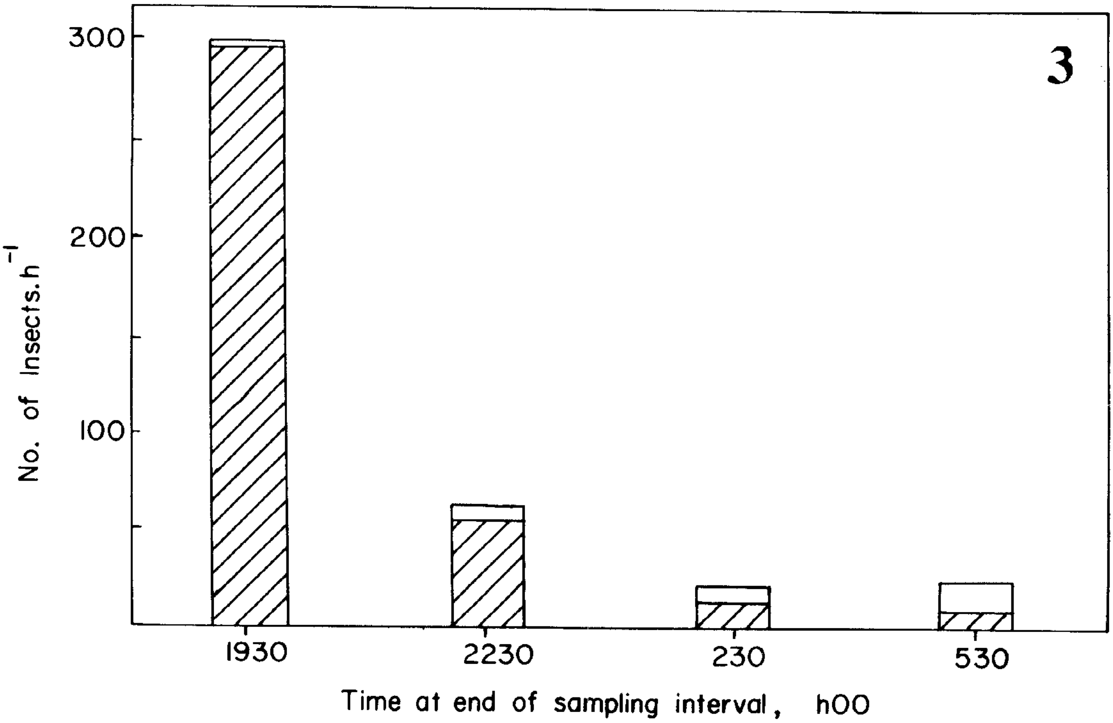


Fig. 1.—Changes in the diameter of new webs (means and 95% C. I. for all species combined) constructed throughout the night in Autumn 1988. Numbers of spiders are above each time period. Data for a single representative night are shown.





Figs. 2, 3.—Numbers of insects of different size classes appearing throughout the night. Size classes are: hatched = <10 mm total body length, clear = >10 mm total body length; 2. Autumn 1988; 3. Spring 1989.

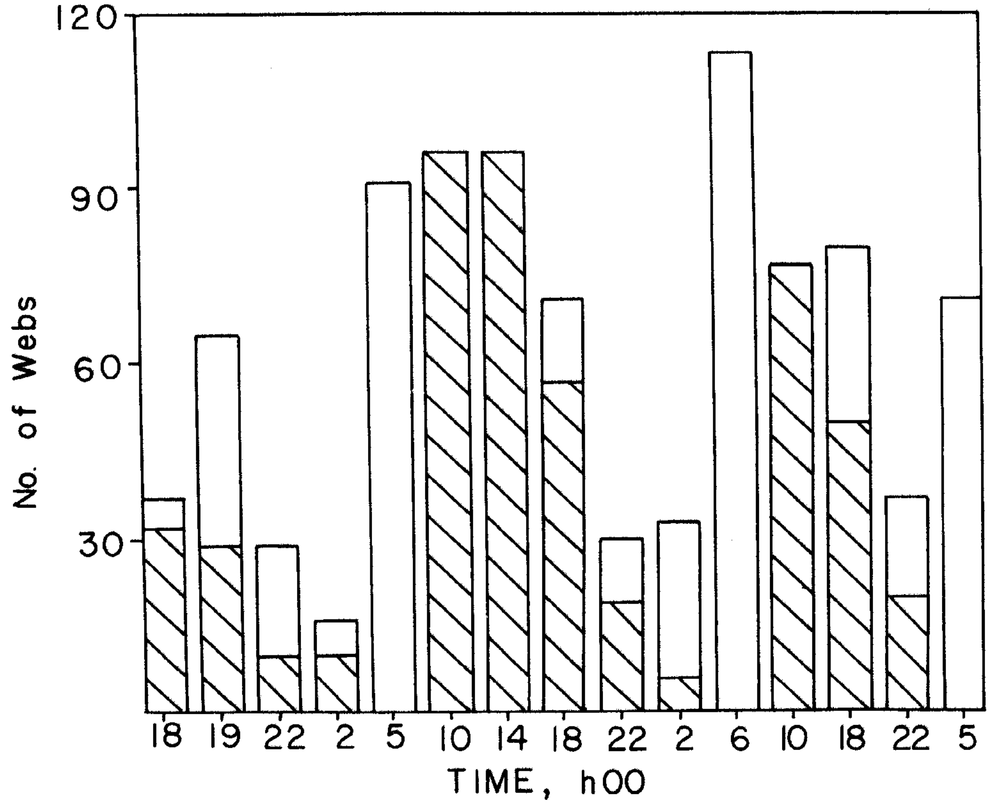


Fig. 4.—Numbers of spiders (all species) on new webs (clear) and on old webs (hatched) throughout a 36 h period in April 1989.

signal line, the activity of individual spiders could be tracked. Over two census days in May 1989, 19.5% of the individuals were active on newly-constructed webs in the evening only, 51.2% in the morning only, and 29.3% were active both morning and evening (n = 41 spiders total). "Morning only" spiders had significantly larger webs than "evening only" spiders (ANOVA, $P < 0.05$; Table 2). There were also differences in web geometry between spiders active at different times. New webs constructed in the morning had significantly more spirals per cm length of radius (3.1 ±0.17, $n = 33$) than webs constructed in the evening (2.3 ±0.15, $n = 31$, ANOVA, $P < 0.01$).

We counted the number of eggs laid by "morning only", "evening only" and "morning and evening" *S. lucina* to determine possible fitness consequences of the different activity patterns. "Morning only" spiders laid significantly more eggs (57.1 ±3.8 eggs per spider, $n = 52$) than "evening only" spiders (49.8 ±5.9 eggs per spider, $n = 11$) (Mann-Whitney U-test, $P = 0.04$). "Morning and evening" spiders also produced significantly more eggs (70.3 ±9.0 eggs per spider, $n = 9$) than "evening only" spiders ($P < 0.05$). The difference in number of eggs between "morning and evening" and "morning only" spiders was not statistically significant (Mann-Whitney U-tests, $P > 0.05$). However, 2 of the 9 "morning and evening" clutches were parasitized by an unidentified dipteran, significantly increasing the variance in clutch size in this group. There was no significant correlation ($P > 0.05$) between spider size and egg number.

Table 2.—Web diameters of "evening only", "morning only" and "morning and evening" (both) individuals of *S. lucina* in April 1989. Web diameters of "morning only" and "evening only" spiders differed significantly (ANOVA, $P < 0.05$).

	Web diameter		
Activity	mean	SE	n
Morning	16.6 cm	0.7	44
Evening	11.0 cm	1.04	96
Both	14.2 cm	0.68	12

Table 3.—Seasonal distribution of orb-weaving spiders on *I. viscosa* hedges at Ma'agan Michael: Percentages of different species found in the study plots on selected evening (E) or predawn (M) censuses. n = Total number of spiders.

Species	Nov 1988		Oct 1989		April 1989		May 1989	
	E	M	E	M	E	M	E	M
n	82	39	45	57	65	91	107	160
S. lucina	12.2	20.5	4.4	5.3	76.9	100	67.3	88.8
L. chloris	25.6	15.4	4.4	0	0	0	1.9	0
N. suspicax	4.9	23.1	37.8	35.0	16.9	0	24.3	10.6
N. subfusca	1.2	0	0	0	6.2	0	0.1	0
Tetragnatha A	1.2	0	2.2	0	0	0	4.7	0.1
Tetragnatha B	1.2	0	0	0	0	0	0.1	0
Immatures	53.7	41.0	59.7	59.7	0	0	0	0

Seasonal abundance and dispersion patterns.—All orb-weaving species were present in both Autumn and Spring sampling periods. However, the relative abundances of the different species and their age distribution varied seasonally (Table 3). *Singa lucina, Nuctenea suspicax* (O.P.-Cambridge) and *Larinia chloris* (Audouin) together comprised about 50% of the spiders in Autumn. In Spring, however, *S. lucina* alone comprised over 70% of the total number of spiders. *N. suspicax* was the second-most abundant species in Spring (10–17% of individuals) and *L. chloris* was rare. In Autumn, many small immatures of all species (≤ 2 mm body length) were present ($>50\%$ of spiders in the evening censuses), whereas in Spring, most spiders were larger juveniles or adults and only very few ($<0.01\%$) were small immatures.

In an attempt to elucidate the patterns of interspecific distribution, discriminant function analyses of both Autumn and Spring data were conducted, using 3-dimensional location in the quadrats and vegetation density in (1) the experimental plots before manipulation in Autumn (November 1988) and, (2) the experimental plots in Spring (May 1989) and the three additional hedge vegetation plots in May 1989. We first ran discriminant function analyses comparing 5 mm size classes of spiders, but derived no significant discriminant function (Wilks λ, $P > 0.05$) for any of the censuses.

The discriminant analyses among species derived two significant discriminant functions (Wilks λ, $P < 0.05$) for the Autumn data (Fig. 5). The first discriminant function explained 75% of the variation in distribution, and was most closely related to web height (standardized discriminant coefficient, SDC = 0.60) and vegetation density (SDC = -0.54). The second discriminant function, explaining an additional 17% of the variation among species, was most closely related to distribution along the length of the hedge (SDC = 0.96). The Spring spider distributions produced only one significant discriminant function which explained 87% of the variation in the data. This function was most closely related to web height (SDC = 0.92).

To examine these patterns in greater detail, we tested for (1) overall clumping of individuals within the hedges and (2) differences among species in their distribution within the plots. In Autumn, the dispersion pattern of all spiders combined was significantly clumped at most times of night. The index of dispersion (I) was > 1 (i.e., non-random) for 9 of 14 censuses over 3 nights (χ^2 tests, $P < 0.001$, $n = 45$ 1 m^3 quadrats). However, all species were found in all quadrats (though not always at the same census), and the individual species were randomly dispersed along the hedges both in evening and in early morning censuses (χ^2 tests for *S. lucina, L. chloris, N. suspicax* and unidentified immatures on four census dates, $P > 0.05$, $n = 45$ quadrats).

We tested whether *N. suspicax* and *L. chloris* (the second- and third-most abundant species) were significantly clumped away from the most abundant species *S. lucina*. The null hypothesis was that the likelihood of the nearest neighbour being a conspecific or *S. lucina* was no different to that predicted by random association of individuals, i.e., that there was no interspecific separation. The null hypothesis could not be rejected (χ^2 tests, $P > 0.05$, $n = 45$ quadrats). Thus, *N. suspicax* and *L. chloris* were not clumped away from *S. lucina*.

We examined the three-dimensional distri-

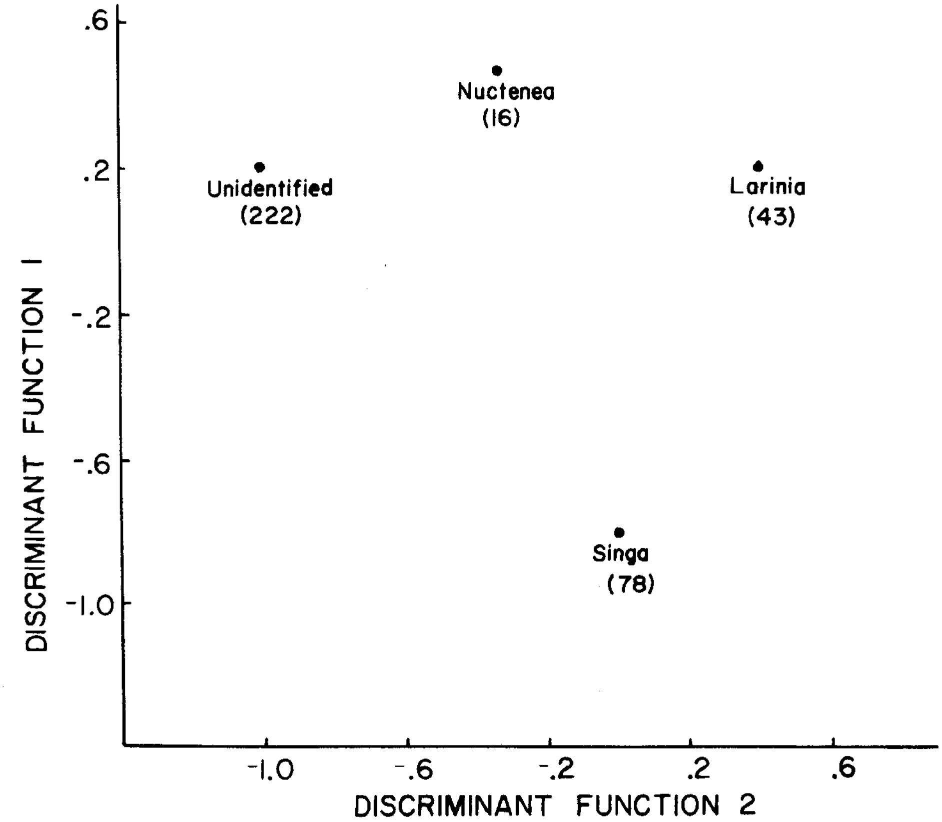


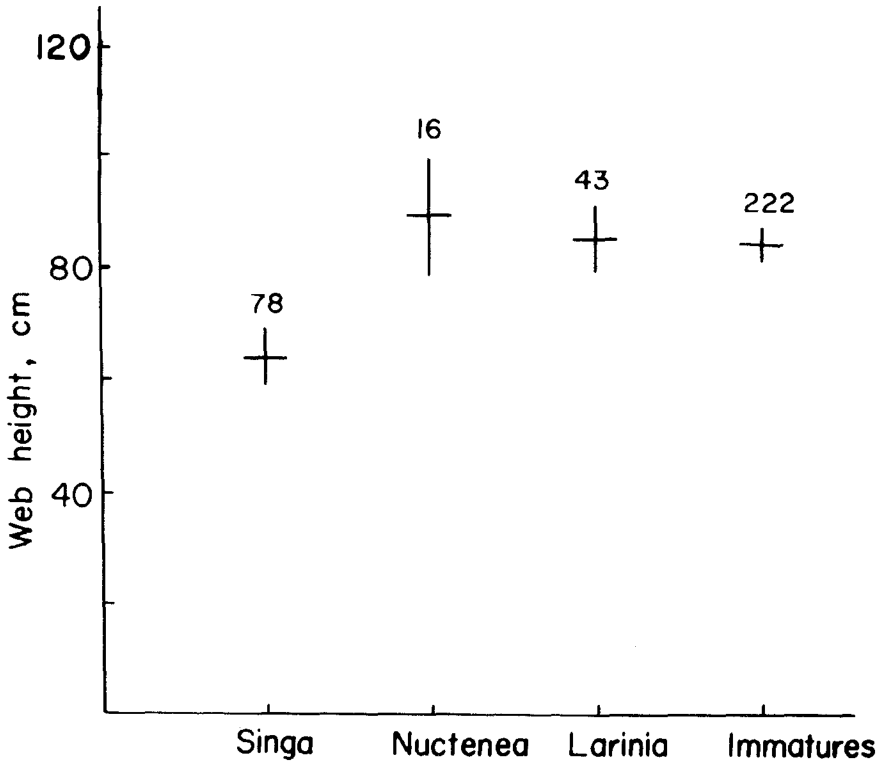
Fig. 5.—Spatial separation of species on experimental plots in Autumn 1988. Separation of the species' centroids in a two-dimensional space determined by discriminant function analysis. *Nuctenea subfusca* and *Tetragnatha* spp. were excluded because of small sample sizes (<10). Sample sizes in parentheses.

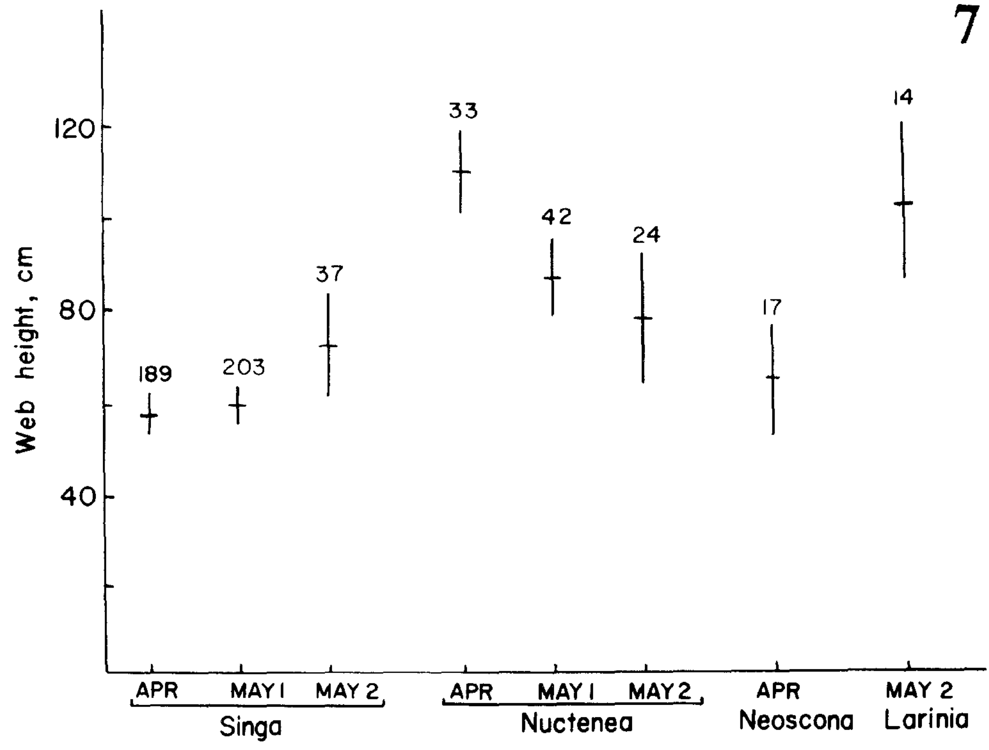
bution patterns of webs within the 1 m^3 quadrats. The only difference among the species was along the height axis: webs of *S. lucina* were significantly lower in the vegetation than were those of other species (ANOVA, $P < 0.001$; Fig. 6). This difference was not due to differences in body size among the species (ANOVA, $P > 0.05$). There was no correlation within any species between spider size and web height ($P > 0.05$).

Although we did not find any clear spatial segregation among the different species in Autumn, there could still occur density-dependent influences on the overall abundance of one species on another. In such a situation, the slopes of the regression of the abundance of one species on another is a direct estimate of the competition coefficient for that species pair (Hallet & Pimm 1979). We tested for such effects among the three most common species (*S. lucina, N. suspicax* and *L. chloris*) using pairwise linear regressions of spider densities per quadrat. There were no significant correlations between any pairs of species ($P > 0.05$).

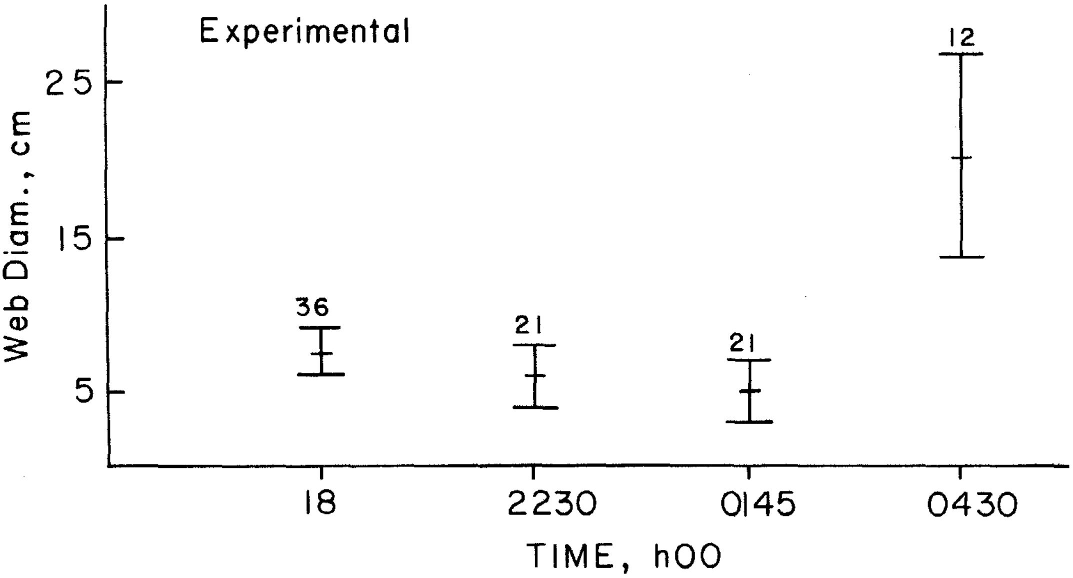
In Spring, the dispersion of all spiders combined was highly clumped at all times ($I \gg 1$, $P < 0.001$ for 8 census dates, $n = 18$ quadrats per census). *S. lucina* and *N. suspicax* were tested for departures from randomness among the quadrats. *N. suspicax* was randomly distributed among the quadrats ($n = 18$ quadrats, 3 census dates), as was *S. lucina* in the evening censuses ($n = 18$ quadrats, 2 census dates). However, in the morning samples, the distribution of *S. lucina* was significantly clumped (χ^2 tests, $P < 0.001$, $n = 18$ quadrats, 3 census dates). Clumping was associated with the high densities of webs of *S. lucina* in the morning samples (14–24 spiders/m^3): there was a significant correlation between the χ^2 value and spider density for the 8 dates tested ($R = 0.77$, $P = 0.01$).

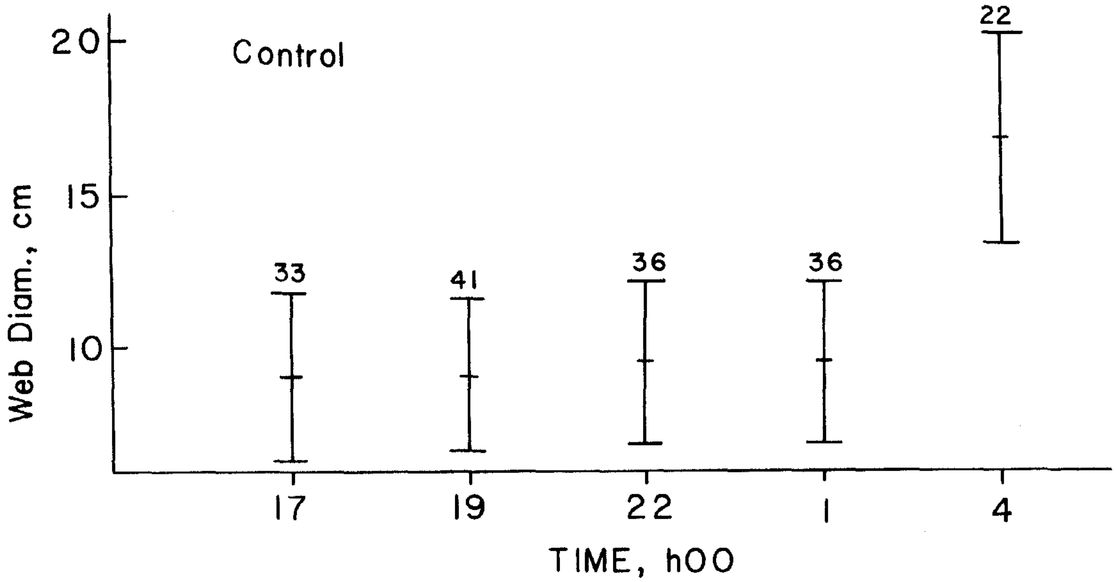
We tested for differences in species distribution in plots differing markedly in vegetation





Figs. 6, 7.—6. Web heights (cm) of dominant species in Autumn. Means and 95% C. I. are shown for *S. lucina*, *N. suspicax*, *L. chloris* and unidentified immatures (< 2 mm body length). Numbers of spiders are above each census; 7. Web heights (cm) of dominant species in Spring, as in Fig. 6. Shown are web heights on the experimental plot (April and May #1) and on three additional 3 m vegetation plots in May (May #2).





Figs. 8, 9.—8. Changes in web diameter (means and 95% C. I. of all species combined) throughout the night on the (top graph) experimental plot (spiders removed through the night) in November, 1988. Numbers of spiders are above each time period; 9. Changes in web diameter (means and 95% C. I.) on the (bottom graph) control plot (unmanipulated), as in Fig. 8.

density (mean ± SE vegetation densities in three plots: 6.0 ±1.52, 9.4 ±1.65, 10.4 ±1.5). We found no significant differences in species distribution among the plots (Kruskal-Wallis, $P > 0.05$).

In Spring, species composition (Table 3) changed from April to May 1989. *Singa lucina* and *N. suspicax* were dominant in both censuses. In April, however, *L. chloris* was absent and *Neoscona subfusca* (C. L. Koch) was the third

Table 4.—Second removal experiment: Total numbers of spiders on control and removal quadrats on days 1 and 2. Numbers of *S. lucina* removed are shown in parentheses. E1, E2 = evening censuses of days 1 and 2, respectively; M1, M2 = morning censuses of days 1 and 2, respectively.

	Day 1		Day 2	
Quadrats	E1	M1	E2	M2
Control	38	61	55	53
Removal	34 (26)	52 (50)	34	21

most abundant species. This was reversed in May, when *N. subfusca* was rare (one spider) and *L. chloris* was third in abundance.

The spatial distribution of webs also changed from April to May (Fig. 7). In April, webs of *N. suspicax* were significantly higher in the hedge than one month later (ANOVA, $P < 0.001$) due to an influx of small individuals in the later censuses. In May, webs of *L. chloris* were significantly higher in the hedge than either *S. lucina* or *N. suspicax* (ANOVA, $P < 0.05$), and *N. suspicax* was significantly closer to the exposed edge of the vegetation (facing away from the ponds) than the other species (ANOVA, $P < 0.05$).

Removal experiments.—*First removal:* In the Autumn of 1988, we removed spiders as they initiated web-building, expecting that if space was the factor preventing simultaneous activity of spiders, the larger spiders that are usually active later in the night should initiate web-building earlier. However, there was no significant difference in the web diameter of spiders at each time period censused in the control and experimental plots (Figs. 8, 9), indicating that larger spiders did not take advantage of the space available to put up webs earlier in the night.

Second removal: If space for web building is limiting, we expected that the removal of active spiders would open up new spaces and that new individuals would move in to occupy them. To test this, in Spring 1989, we divided an 18 m section of hedge into six contiguous 3 m^3 quadrats and removed all the active *S. lucina* (the dominant species) from the two central quadrats during one evening census and the following morning.

New spiders became active in the removal quadrats on both the evening and morning following the removals (Table 4). The increase in the number of evening-active spiders in the removal quadrats was not significantly different from that in the control quadrats. In the morning, however, the control quadrats exhibited a decline in numbers (from 61 to 53), whereas 21 new spiders became active in the removal quadrats ($\chi^2 = 7.44$, $P < 0.01$). Thus, the increase in the number of morning-active spiders on the removal quadrats may be only partly explained by movement of spiders from the control quadrats.

Table 5.—Third removal experiment: Numbers of spiders observed on quadrat 2 from which all *S. lucina* were removed on the second evening (E2); quadrats 3 and 4 combined, from which spiders were removed on the first morning (M1); and quadrats 1 and 6 combined, which were unmanipulated (C). Shown are the numbers of *S. lucina* only, as other species occurred only in small numbers. The numbers of spiders removed are underlined.

Quadrat	Day 1		Day 2		Day 3	
	E1	M1	E2	M2	E3	M3
E	23	25	$\underline{27}$	20	24	22
M	41	$\underline{76}$	22	21	—	—
C	33	46	25	42	32	37

Third removal: There were more spiders active in the morning than in the evening in Spring, and morning-active spiders had significantly larger webs and more eggs than evening-active ones (see above). Therefore, we hypothesized that morning was the preferred period of activity, but that space limitation for web-building forced some spiders to be active in the evening. Using spiders whose activity period had been determined during the previous two days of observation, we tested this possibility by removing all "morning only" spiders from two 3 m quadrats, expecting that "evening only" spiders would become active in the morning. We also removed "evening only" spiders from another 3 m quadrat, expecting no change in the time of activity of "morning only" spiders.

As in the second removal experiment, removing evening spiders had little effect on the activity of spiders either the following morning or the following evening (Table 5). On the third evening, new spiders replaced those that had been removed on the second evening.

Removing morning-active spiders caused a significant decrease in activity on the following morning in comparison with the control plots (χ^2 test, $P < 0.05$). Activity was reduced also on the evening following removal of morning-active

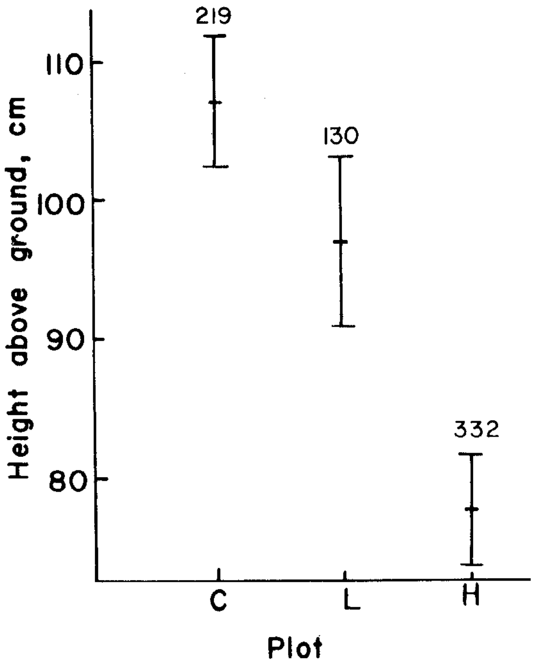


Fig. 10.—Changes in web height of spiders following space supplementation in October 1989. Shown are means and 95% C. I. of web height in control (C), low-string availability (L) and high-string availability (H) plots. Numbers of spiders (all census days combined) are shown above each plot.

spiders. There were no significant changes in the numbers of spiders active in the morning and evening on the control plots over the three days of the experiment (χ^2 tests, $P > 0.05$). Thus, the appearance of 21 new webs on the morning following the removal of morning-active spiders cannot be explained by movement of spiders from the control plots into the removal plots.

In all three of the removal experiments, there was no change in the web characters measured (web diameter and the number of spiral threads per cm^{-1}) with reduced population density (ANOVA, $P > 0.05$), suggesting that web geometry is not sensitive to short-term changes in spider density.

Space supplementation experiments.—In Autumn 1988, we found a significant positive correlation ($R^2 = 0.94$, $P < 0.05$) between the number of active spiders and the number of spiders attaching their webs to the string delineating the plots. This suggested that space for building webs was limited. To test this idea, we provided additional web supports, using string to subdivide two plots into squares of 50 cm^2 (=low string availability) and 25 cm^2 (=high string availability) respectively.

The number of spiders active did not increase significantly in the high string-availability plot on the night immediately after supplementation, but increased four-fold on the second night (from 28–119 spiders; $\chi^2 = 30.90$, $P < 0.001$). Web height decreased significantly as more supports for web-building became available closer to the ground (ANOVA, $P < 0.05$; Fig. 10). There was no significant change in the number of spiders active in the low-string availability plot after supplementation (χ^2 tests, $P > 0.05$), nor in the control plot. Had these changes in activity in the high-string availability plot been due to increased disturbance, we would expect a reduction rather than an increase in activity. Thus, we ascribe this change to extra supports provided for web-building.

DISCUSSION

Temporal segregation of activity.—We have shown that the spiders use stratified activity periods in Autumn to partition a homogeneous habitat. In a review of resource partitioning in animal communities, Schoener (1986) observed that resource partitioning most commonly occurs by division of habitat use, then of food and only rarely, time. He suggests that theoretically there is no advantage to temporal specialization because no energetic gain can be derived from not feeding during most time periods (for empirical evidence, see Jaksic 1982). Temporal specialization should occur only if the risk of predation is large relative to the need for energy, and then all species may specialize on the same time period (Schoener 1986).

For the Ma'agan Michael orb-weavers, small spiders that are active early in the evening can prey on the large numbers of small Nematocera emerging from ponds at dusk, while spiders foraging later in the evening have small numbers of large prey available. Why are large spiders not active earlier? Three possible explanations are: (1) Large webs are inefficient for trapping small prey; (2) Webs are damaged or clogged by many small insects, producing low rewards per unit effort of silk production; (3) There is a greater predation risk early in the evening than later on.

We favor the last explanation because early activity would at least yield some food and a damaged web may be renewed. For example, at least some individuals of *S. lucina* in Spring renewed their webs for both morning and evening activity. Thus, prey arguments (1 and 2) do not apply. However, to take advantage of dusk insect emergences, webs must be built in the light. Large spiders in large webs are more vulnerable than smaller ones because they tend to be higher in the vegetation and, in the case of *N. suspicax*, closer to the exposed edge of the vegetation.

In Spring, temporal stratification was not correlated with either spider size or web size, although we observed the same pattern of insect activity as in Autumn, i.e., small insects active early and larger insects active later in the night. However, for *S. lucina*, spiral density was greater in "morning spiders", whose activity coincided with that of larger flying insects, than in "evening spiders". This supports Eberhard's (1986) hypothesis that webs designed to intercept large prey should have greater spiral density (and therefore greater resilience) than orbs designed for small prey. Further investigation is required to establish whether this difference in spiral density is a behavioral response to prey size availability.

In Spring, "morning only" and "morning and evening" individuals of *S. lucina* produced more eggs than did "evening only" individuals. As these differences were uncorrelated with body size, it is not clear what prevented some spiders from becoming active in the early morning. Our second and third removal experiments indicate that there was no major shift of activity from evening to morning following removal of spiders from plots. Active spiders did not take advantage of the extra space provided in either evening or morning periods, although spiders that were hitherto inactive became active. Given the advantage to morning activity, it is puzzling that some spiders retain their low-reward (evening) activity periods. We suggest the following explanations that bear further investigation: First, evening-active spiders may have a more reliable, albeit lower quality, food resource (Nematocera) than morning-active spiders. Second, short-term experiments may allow insufficient time for spiders to adjust their activity pattern to a new situation.

Spatial distribution.—Clumped distribution, especially of small or subordinate individuals in the presence of dominant individuals, may indicate aggression (Pielou 1977). In spite of considerable evidence of clumped distribution of spiders in this study, we were unable to detect strong interspecific interactions. There was little interspecific separation of the species on any axis examined, although *L. chloris* was on occasion significantly higher in the vegetation than the other species, and *S. lucina* significantly lower in the vegetation in Autumn than the other species. Divergence in web height selection has been found in other studies of orb-weavers (Enders 1974, 1975; Tolbert 1975; Olive 1980; Brown 1981) although species populations often switch vertical positions in different studies (Brown 1981). In our study, switches in web height selection were also found, notably in *N. suspicax* (Fig. 7), perhaps as an effect of a seasonal change in the mean size of spiders.

Our study indicates that the slight interspecific differences that occurred were not due to interspecific interaction, because there was no change in the pattern of activity or in species composition with removal of potential competitors. Only a single case of overt interspecific aggression was observed in 24 nights (a *N. suspicax* removed the web of a *L. chloris*). A lack of movement in response to short-term changes in conditions may be typical of species with rolled-leaf retreats (e.g., *S. lucina* and *N. suspicax*, see Table 1) which have relatively fixed websites.

There is little other evidence that interspecific competition occurs in orb-weavers (Brown 1981; Wise 1984). Manipulative studies indicate that yearly differences in weather patterns may affect population densities and foraging patterns as much as, if not more than, competition (Wise 1981; Horton & Wise 1983). Thus, only Spiller (1984) has shown that interspecific competition occurs between orb-weavers. There too seasonal reversal of competitive advantage occurred, so the long-term effects of competition on the two species studied may be minimal. Other studies (Spiller & Schoener 1988, 1989; Schoener & Toft 1983b) have shown that predators (lizards) may have more important effects on spider densities than competition.

Although interspecific competition for living space does not appear to play an overt role in the community of orb-weavers at Ma'agan Michael, intraspecific competition (e.g., "scramble competition", see MacArthur 1972) may have an important effect on activity. Space limitation restricts the web-building activity of some spiders, although the results of the string supplementation experiments indicate that the spiders may only react, over short periods, to a large increase in space availability. Other field experiments have revealed significant intraspecific competition between spiders (Colebourn 1974; Wise 1975; Schaefer 1978; Riechert 1981), although certainly not in all species studied (Wise 1981, 1983; Horton & Wise 1983).

An interesting possibility is that a "lottery for living space" (Sale 1977) exists in this spider community. Spiller (1984) has also suggested that a lottery model best explained the seasonal reversal of competitive advantage between two species of orb-weaving spiders. Chesson & Warner (1981) modelled the lottery system based on competition for space. When the environment varies such that each species has times when it can have strong recruitments, the net effect is to favor positive growth rates at low density for all species (Chesson 1986).

On the hedges at Ma'agan Michael, *S. lucina* and *N. suspicax* fluctuate in abundance and exhibit a seasonal reversal in dominance. These fluctuations are apparently associated with different reproductive periods of the species (May for *S. lucina*, September–October for *N. suspicax*). Natural history observations at Ma'agan Michael indicate that there is considerable predation on spiders by leaf-gleaning warblers (mostly *Phylloscopus* spp., Sylviidae), particularly during the Spring and Autumn bird migrations. We suggest that predation may influence orb-weaver community structure in these hedges as follows: The first spiders, regardless of species, to become active after recruitment may establish control over empty sites. By being the first spiders to establish, they may grow quicker and reach large sizes earlier. As observed intraspecifically in *S. lucina*, those spiders using the preferred activity periods have the largest clutches. However, predators will encounter more spiders of the common species (especially because spider species are mostly distributed at random within the hedges) and this should result in greater predation on the dominant species. Vacant areas in the hedge may be taken over by new recruits or by previously inactive spiders. Therefore, differences in the time of recruitment will cause different species of spider to be dominant at different times of year, while predation and/or other environmental effects (e.g., storms) will facilitate coexistence.

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