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Spider Community Organization: Seasonal Variation and the Role of Vegetation Architecture¹

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ABSTRACT

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The relationships between vegetation architecture and spider community attributes were examined in a big sage (*Artemisia tridentata*) community. Spiders were separated into guilds using similarities of species' hunting behavior. Shrub architecture was experimentally manipulated in the field by either clipping 50% of a shrub's foliage to decrease foliage density or tying together a shrub's branches to increase foliage density.

Shrub perturbations resulted in changes in the number of spider species, spider guilds and guild importance values. The number on spider species and guilds in the tied shrubs were significantly higher than those in the clipped or control shrubs sampled. Spider species diversity and the number of species and guilds were positively correlated with indicators of shrub volume and shrub foliage diversity. This suggests that structurally more complex tied shrubs can support a higher number of spider species and species diversity.

Temporal patterns of the number of spider species, and species diversity (H') showed midsummer peaks in both 1974 and 1975. Evenness (J') remained relatively constant through both seasons.

The data suggest that architectural properties of habitat may be an important determinant of the distribution and species diversity of predatory invertebrates.

Introduction

Substrate spatial heterogeneity may be a major factor affecting animal species diversity in a community. Species diversity has been correlated to various measures of habitat physical complexity. MacArthur and MacArthur (1961) used measures of vertical habitat diversity (foliage height diversity) to explain and predict bird species diversity. Pianka (1966, 1967) included vertical and horizontal measures of habitat diversity (plant volume diversity) in studies that correlated shrub structure with lizard species diversity in flatland desert communities. The relationship between habitat diversity and species diversity has also been demonstrated for marine invertebrates (Abele 1973), spiders (Uetz 1975) and insects (Murdock et al. 1972, Southwood et al. 1979). Vegetation provides varying types of substrates or microhabitats which are differentially suitable for animal species. The type of substrate on which a species occurs may determine the food sources available to it and also dictate the method in which they are obtained.

Spiders are well suited for ecological studies. As a group they are cosmopolitan, and locally abundant in terms of individuals and taxa. Their small size permits definition of a community in a small area. Spiders, as predators, are not coupled to a particular plant species as a food source; vegetation structure may therefore be an important determinant of spider community attributes.

Spider distribution is affected by substrate structure (Lowrie 1948, Barnes and Barnes 1955, Duffey 1966, 1968, Uetz 1975). Coleburn (1974) found that the spatial nature of limestone fissures affected the patterns of *Araneus* web distribution. Bulan and Barrett (1971) found that arachnid density decreased in oak fields after mowing and remained lower in subsequently burned

fields than in unburned fields. The structure of spider communities has been found to change with plant succession through changes in spider species density and population density. In general the proportion of web-builders to hunting spiders increases during succession (Lowrie 1948, Dowdy 1950, Chew 1961).

Studies of vegetation structure with regard to spiders have included the vertical and horizontal aspects of foliage distribution but rarely the internal qualitative attributes of foliage density. The vertical stratification of spider populations has received the most study, especially in forest communities (Gibson 1947, Dowdy 1950). Enders (1974) found that orb web spiders chose different vegetation heights at different instars. Chew (1961) noted a correlation between the presence and abundance of spiders and the level of shrub development. He also found a horizontal separation of several shrub-dwelling species that preferred specific desert shrub species. Uetz (1975), studying the guild of wandering spiders, correlated spatial differences in species diversity with litter depth and a measure of habitat space.

A functional approach can be developed in community studies by examining the methods by which organisms exploit their environment. Functional analysis of community organization has been used in studies of plant-arthropod associations (Root 1973), wandering spider communities (Uetz 1975) and desert mammal communities (MacMahon 1976). Species guilds, defined by Root (1967) as "a group of species that exploit the same class of environmental resources in a similar way" can be used to identify functional roles present in a system. This approach considers sympatric organisms as a unit, involved in a competitive interaction, regardless of taxonomic relationships. Functional organization can then be considered independent of the individualistic response a single species may make to local conditions (Gleason 1939).

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Spiders can be arranged into guilds based on similarities in their methods of obtaining food, e.g., web builders, running and jumping spiders, and ambushing spiders.

This study investigates the role of spatial heterogeneity in determining community organization as represented by species and guild attributes. This is implemented through experimental perturbation of shrub architecture in a field situation. The main objectives are:

1. To examine the interaction of vegetation architecture and spider species diversity;
2. to describe the functional organization of spiders in a shrub community using spider guilds;
3. to examine the role of vegetation architecture in determining functional organization of spiders in a shrub community;
4. to determine seasonal changes in spider community membership.

Study Area and Methods

The study area is located 3.2 km northeast of Logan on the Bonneville Lake terrace of the Bear River Range, 100 m south of the mouth of Green Canyon, Cache County, Utah. In this area mean annual precipitation varies from 38.1 to 43.2 cm, mean annual temperature varies between 7 and 9°C and frost-free days average between 100 and 120 (USDA-Soil Conservation Service and Forest Service 1974). The plot is at an elevation of 1477 m and faces southwest (28% slope). Land is used mainly for watershed and wildlife.

The area is dominated by big sage (*Artemisia tridentata* Nutt. ssp. *tridentata*). Other shrubs present include *Purshia tridentata* (Pursh) DC., *Gutierrezia sarothrae* (Pursh) Britton & Rusby, and *Chrysothamnus nauseosus* (Pall.) Britton. Major herbaceous species include *Balsamorhiza sagittata* (Pursh) Nutt., *Wyethia amplexicaulis* Nutt., *Bromus tectorum* L., and *Bromus brizaeformis* Fisch. & Mey.

A one hectare (100 × 100 m) plot was established on the study area. This was divided into twenty-five (20 × 20 m) subplots. A hygrothermograph (WeatherMeasure Corp.) was operated on the plot during the 1974 and 1975 field seasons.

Shrubs

An individual shrub in this study was operationally defined as a shrub mass discontinuous with the foliage of another shrub by 10 cm or more. Linear measurements of height and minimum and maximum width were recorded for each shrub sampled. These measurements were used to estimate shrub volume and cover. Volume was calculated using the formula for the volume of a prolate spheroid

$$V = 4/3\pi ab^2 \quad (1)$$

where a is the linear dimension on the major semi-axis and b is the linear dimension of the minor semi-axis. Cover was estimated using the area of an ellipse,

$$A = \pi ab \quad (2)$$

where a and b are defined above.

In April, 1975 shrubs (*Artemisia tridentata*) were experimentally manipulated to change their foliage density, in preparation for a second sampling season. The subplots were randomly divided into 3 groups. On each of eight subplots fifty shrubs, chosen randomly, were altered by clipping 50% of their foliage. On each of eight other subplots 50 shrubs, chosen randomly, were tied up to increase their foliage density. Nine additional subplots were used as controls. The Wilcoxon ranked sum statistic was used to compare spider parameters in the clipped, tied and control shrubs. Significance is at the 5% level.

Differences in foliage density of sampled shrubs were estimated with the use of Polaroid photographs. Photographs of the shrubs were taken against a contrasting background grid of 20 cm squares. The foliage was separated into three foliage types (dense foliage, open foliage, and canopy) and three height classes (0-40, 41-80, and 81-120 cm). Canopy was defined as those peripheral vertical branches of a shrub that produced the paniculate inflorescences of *Artemisia*. For each photograph, areas in each category were cut out and weighed on an electrobalance. Since Polaroid film is of constant weight, the percent composition of each foliage type and height class could be calculated. These values were used in the Shannon-Wiener function (Pielou 1966):

$$H' = -\sum_{i=1}^s p_i \ln p_i \quad (3)$$

to calculate an index of shrub foliage diversity (SFD), where s equals the total number of foliage types in the height classes (9 possible) and p_i equals the proportion of the shrub in the i^{th} foliage type of each height class.

Correlations were performed relating the shrub architectural parameters measured. Significance was at the 1% level.

The photographs were also used to separate the shrubs into three general groups on the basis on foliage density. Group I includes shrubs composed of greater than 50% open foliage, group II includes shrubs composed of less than 50% open foliage, less than 50% canopy and less than 50% dense foliage, and group III includes shrubs with greater than 50% dense foliage. Shrubs with greater than 58% canopy did not occur. Analysis of variance (ANOVA) and least significant difference (LSD) tests were used to compare spider parameters in the three shrub groups (treatments). Significance was at the 5% level.

Spiders in shrubs were sampled in the field with the use of several beating sheets. The shrubs were measured, surrounded with sheets and struck vigorously with a heavy club. Spiders that fell from the shrubs were collected and preserved in the field. In 1974, during a ten week period, 108 shrubs (chosen randomly) were sampled. To validate the sampling method shrubs were quickly bagged in the field, cut, and removed to the laboratory. The shrubs were then cut into pieces and all spiders present were collected. The number of spider species collected and their relative abundance approximated that found in the beaten shrubs.

In 1975, during a 15 week period, 225 shrubs, including 75 each of clipped, tied, and control shrubs were photographed and sampled. During each week three subplots, one of each perturbation type, were chosen randomly, and five randomly chosen shrubs were sampled on each plot.

Spiders

The spiders present in each shrub sample were identified and counted in the laboratory. Body length (not including spinnerets) was measured and sex determined for each individual. The number of species, species diversity, and evenness were calculated for each sample week in 1974 and 1975. Species diversity (Equation 3) was determined where s equals the total number of species and p_i equals the proportion of individuals in the i^{th} species. Evenness (Pielou 1966) expresses the apportionment of individuals among the species and is calculated:

$$J' = \frac{H'}{\ln s} \quad (4)$$

where J' equals evenness, H' equals the calculated species diversity and s equals the number of species.

Spiders in early juvenile stages usually disperse from the area of emergence from the egg sac. Dispersion reduces crowding and potential cannibalism among siblings (Turnbull 1973). For this reason spider species size distributions were plotted and used to estimate the number of resident spiders in a shrub by elimination of those individuals in early juvenile stages. The number of resident species, resident species diversity and evenness were then calculated for each sample.

Spider guilds (sensu Root 1967) were defined using similarity of predation strategy (Kaston 1948, personal observation). Guild 1 (nocturnal hunters) includes the families Gnaphosidae, Anyphaenidae, and Clubionidae. These spiders usually build retreats in foliage and under bark where they remain during the day, coming out at night to hunt. Guild 2 (runners) includes the Philodrominae, a subfamily of the Thomisidae. These spiders are active runners and move quickly through a shrub, running down and pouncing on prey. Guild 3 (ambushers) includes the Misumeminae, a second subfamily of the Thomisidae, spiders which sit and wait, ambushing their prey. Guild 4 (agile hunters) includes the Salticidae and the Oxyopidae, spiders that have good eyesight and are active hunters. Guild 5 (web-builders) is composed of the families Theridiidae, Linyphiidae, Dictynidae and the Araneidae. The Araneidae, orb-web building spiders, composed only 11% of the individuals in this guild and were therefore not separated into another guild. The number of guilds, guild diversity and evenness were calculated for each sample.

Guild importance values (IV) for shrub samples were calculated as in Curtis and McIntosh (1951) ($IV = \text{relative frequency} + \text{relative density} + \text{relative dominance}$). Guild frequency was calculated by the number of shrubs in which a spider guild occurred out of a sample group.

Relative frequency was determined by the formula:

$$RN_i = \frac{N_i}{CN} \quad (5)$$

where RN_i equals relative frequency of the i^{th} guild, N_i equals the frequency of the i^{th} guild, and CN equals the combined frequency of all guilds. Guild density was the number of individuals in each guild in a sample group (perturbation type or week). Relative density was determined (Equation 5) where RN_i equals relative density of the i^{th} guild, N_i equals the density of the i^{th} guild and CN equals the combined density of all guilds. Spider volume was estimated using spider body length in the formula for the volume of a sphere,

$$V = 4/3r^3 \quad (6)$$

where r equals 1/2 the body length of an individual. Volume was then used to calculate relative dominance. Relative dominance was similarly determined (Equation 5) where RN_i equals relative dominance of the i^{th} guild, N_i equals the volume of the i^{th} guild, and CN equals the combined volume of all guilds.

In 1974 spider IV's were calculated weekly for all shrubs combined. In 1975 spider IV's were similarly calculated weekly for clipped, tied, and control shrubs and for all shrubs combined.

Correlation coefficients (r) were calculated relating spider species, resident species and guild parameters to seasonal factors and shrub architectural parameters. Significance was at the 5% level.

Results and Discussion

Seasonal Variation

A total of 4613 spiders representing 40 species in 11 families were collected from the shrubs sampled. Indices of spider diversity reached maximum values during midsummer. The maximum number of species encountered was 24 and 25 in August of 1974 and 1975, respectively (Fig. 1). This pattern was also found in other studies of temperate arthropod communities (Murdock et al. 1972, Root 1973, Uetz 1975). Since the equitability component of diversity (J') remained relatively

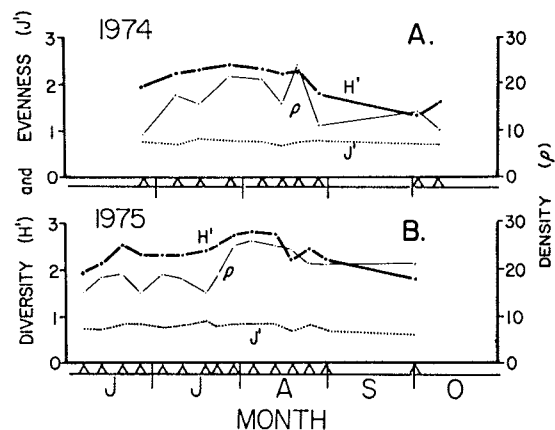


FIG. 1.—Seasonal patterns of spider species diversity (H'), evenness (J') and species density (ρ) in big sagebrush (*Artemisia tridentata*) in 1974 (A) and 1975 (B).

constant through both seasons, the seasonal pattern of species diversity was attributed to changes in the number of species.

Species diversity (H') in both 1974 ($r = 0.857$) and 1975 ($r = 0.547$) and the number of species in 1974 ($r = 0.758$) were positively correlated with mean weekly temperature. The number of species in 1974 ($r = -0.673$) was negatively correlated with relative humidity (RH). Guild diversity ($r = 0.674$) and evenness ($r = 0.758$) in 1975 and the number of guilds in 1974 ($r = 0.758$) were also positively correlated with mean weekly temperature. The seasonal pattern of spider species and guild parameters accounts for their significant correlations with temperature. This is probably the result of factors not included in this study, particularly the seasonal abundance and availability of spider prey. Temperature did not significantly correlated with RH in either 1974 or 1975.

It has been suggested that communities may be organized by a characteristic set of functions which determine community structure. The fulfillment of functions can affect community species composition, species diversity and the prominent species present. A function may be fulfilled by more than one species, creating a redundancy which buffers the effects of perturbations on the community and maintains community structure (MacMahon 1976). Since functions may potentially be fulfilled by many different species, within any community the species present may be the result of many successful species additions, subsequent population growths, and extinctions (Fager 1968, Whittaker and Woodwell 1972).

One manner of examining the functional organization of a community is to group those species using the same resource into guilds. If communities are organized by functional roles, individual changes of a guild member species might be balanced by complementary changes of another species within that guild (Root 1973). Guild values (e.g. IV and density) would therefore remain relatively constant within a community. However, we believe that community functions will not remain static over the course of a season or from year to year, and guild values, which reflect community functions, should not be expected to remain constant.

Temporal changes in the importance values of spider guilds are shown for 1974 (Fig. 2A) and 1975 (Fig. 2B). The nocturnal hunters (Guild 1) were collected in low numbers during both sampling seasons; density peaked in July of 1974 and August of 1975. Maximum IV's occurred in August of both years. Nocturnal hunters showed no significant correlation with temperature or RH. The runners (Guild 2) and the ambushers (Guild 3) showed offset peaks in density and IV in 1975. Runners had highest IV's and densities during midsummer of both seasons. Their density positively correlated with temperature in 1975 ($r = 0.747$). Ambushers peaked earlier, reaching greatest IV's and densities during July of both years. Their density was also positively correlated with temperature in 1975 ($r = 0.576$). The agile hunters (Guild 4) had high IV's throughout both seasons and densities peaked during late summer. Their densities were negatively correlated with RH in both 1974 ($r = -0.713$) and 1975 ($r = -0.747$). The web builders

(Guild 5) showed density peaks both early and late in the season. IV's were greatest in June of 1975 and relatively constant in July and August. Their density was negatively correlated with temperature ($r = -0.634$) and positively correlated with RH ($r = 0.695$) in 1975.

Spider guild densities and IV's observed in this study do not demonstrate consistent values, rather they fluctuate during the season and between years. The data, however, do not allow complete examination of the functional roles present in this shrub community. The duration of the study was too short to closely examine seasonal and yearly trends, and the guilds established include only the spider predators of this community.

The trends of guild IV and density observed reflect the temporal abundance of usually a single member species or genus. In the nocturnal hunter guild, *Chiracanthium inclusum* (Hentz) comprised 60.5% of the individuals. The runner guild is represented by *Philodromus histrio* (Latreille) (57.5%), and the ambusher guild by *Xysticus cuncator* Thorell. (77.3%). *Sassacus papenhoei* (Peckham and Peckham) (53.8%) represented the agile hunter guild and *Theridion* spp. (52.8%), represented the web builder guild. Weekly IV's of these species significantly correlated with their respective guild IV's. The variance of guild IV's accounted for by the prominent species is as follows: *C. inclusum*, 77%; *P. histrio*, 29%; *X. cuncator*, 89%; *S. papenhoei*, 30%; and *Theridion* spp., 53%. As seen above, most of the

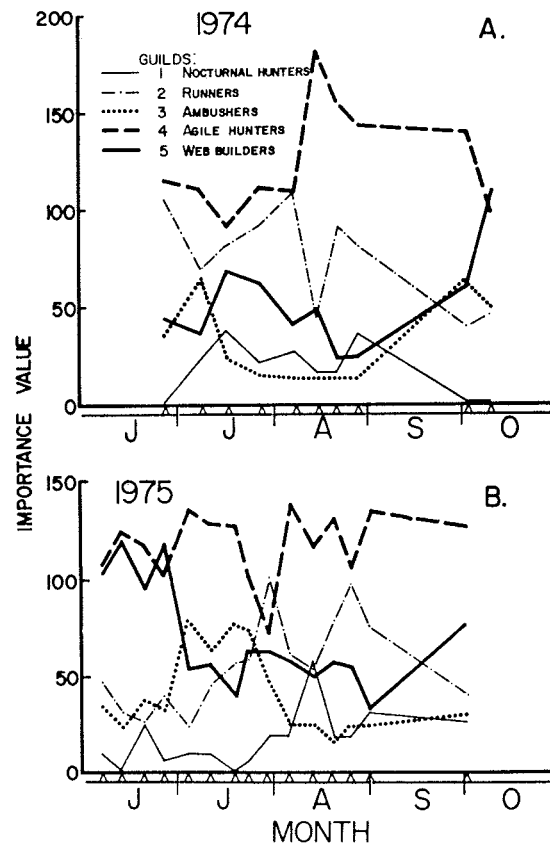


FIG. 2.—Seasonal variation in the importance value of each of five spider guilds, for 1974 (A) and 1975 (B).

seasonal variances in the nocturnal hunter and ambusher guilds are accounted for by one species in each.

Abundant spider species appeared to play a major role in the spider guilds studied. Spider guild densities and IV's fluctuated seasonally, reflecting in part reproductive patterns and response to annual weather patterns. The particular species most abundant in any guild varied throughout the year.

Shrubs

The proportion of foliage types in a shrub indicates the quality of substrate available to spiders. However, it is difficult to quantitatively assess vegetation structure in a manner that is biologically meaningful. The shrub attributes measured in this study were chosen in an attempt to do this by using experimental manipulation of shrub architecture in a field setting.

To assess the effect of the field perturbations on shrub architecture, the 1975 shrubs were objectively separated into three groups using foliage density data obtained from the shrub photographs. These shrub groups corresponded to the perturbation types in terms of foliage density (Table 1). Fifty-seven percent of the clipped shrubs had greater than 50% open foliage and 71% of the tied shrubs had greater than 50% dense foliage. The control shrubs were almost evenly distributed with 43% having greater than 50% dense foliage and 44% having greater than 50% open foliage. From the above it is clear that our perturbation regimes did significantly alter the architectural features we were measuring.

Shrub values of height, cover, volume, mass 0-40 cm, mass 40-80 cm, and mass 80-120 cm indicate spa-

tial characters of shrub structure. Correlation coefficients calculated for these factors demonstrated that in general shrub height, cover, volume and mass 80-120 cm are significantly correlated to each other and indicate shrub volume. Shrub mass 0-40 cm is negatively correlated to the above indicators of shrub volume.

The calculation of shrub foliage diversity (SFD) incorporating the distribution of foliage types among the height classes, was an attempt to describe the overall architectural properties of a shrub. SFD correlated positively with indicators of shrub volume (height, cover, volume, mass 81-120 cm) and negatively with mass 0-40 cm (data available upon request). A greater diversity of shrub structure (SFD) is realized in a larger shrub volume since vertical and horizontal attributes of shrub structure can be better developed.

Spiders

The mean weekly number of spider species, resident species, and guilds were each used in the Wilcoxon ranked sum statistic to compare clipped, tied and control shrubs. Tied shrubs had significantly more resident species and guilds than either control or clipped shrubs. No significant differences were found between clipped and control shrubs. Correlations between shrub, species and guild parameters are given in Table 2. In general spider species diversity, evenness and the number of species for all spiders and resident spiders, show positive significant correlations with shrub height, cover, volume, mass 81-120 cm, percent dense foliage, and SFD. Significant negative correlations are found with shrub mass 0-40 cm, and percent open foliage. The number of spider guilds shows significant positive correlations with height, percent dense foliage and shrub foliage diversity (SFD), and negative correlations with mass 0-40 cm, and percent open foliage.

Shrub groups, as described in Table 1, were examined for differences in spider species and guild parameters. ANOVA and LSD tests were run on the three shrub groups (treatments) using the number of species, resident species and guilds (Table 3). F ratios among shrub groups were significant for all variables. LSD calculations show that group I differs significantly from groups II and III for all three ANOVA's. Shrub groups II and III have greater numbers of species, resident species and guilds (Table 3).

Table 1.—Separation of shrubs into groups using shrub photographs. Group I includes shrubs with greater than 50% open foliage, Group II includes shrubs composed of less than 50% open foliage, less than 50% canopy and less than 50% dense foliage, and Group III includes shrubs with greater than 50% dense foliage.

	Number of Shrubs		
	Group I	Group II	Group III
Clipped	43 (57%)	23 (31%)	9 (12%)
Tied	8 (11%)	15 (20%)	52 (71%)
Control	32 (43%)	10 (13%)	33 (44%)

Table 2.—Correlation coefficients (r) for indices of spider species and guild diversity and shrub architectural parameters.

	All Species			Resident Species			Guilds		
	H'	J'	No.	H'	J'	No.	H'	J'	No.
Height	.301**	.155*	.321**	.276**	.230**	.253**	.140*	.074	.199**
Cover	.178*	.064	.206**	.260**	.211**	.259**	.023	-.027	.118
Volume	.106	.044	.164*	.269**	.217**	.291**	.016	-.038	.122
Mass 0-40 cm	-.171*	-.163*	-.221**	-.172*	-.180*	-.181**	-.084	-.105	-.138*
Mass 41-80 cm	.054	.078	.035	.050	.045	.058	.081	.107	.077
Mass 81-120 cm	.163*	.136	.237**	.167*	.181**	.171*	.039	.043	.106
Percent dense foliage	.157*	.074	.096	.139**	.151*	.202**	.105	.044	.164*
Percent open foliage	-.180*	-.089	-.124	-.181**	-.155*	-.193**	-.134	-.064	-.185**
Percent crown	.075	.045	.076	.000	.030	.008	.078	.051	.071
SFD	.230**	.173*	.270*	.214**	.236**	.212**	.122	.115	.181**

* .05 > P > .01.
** P < .01.

Table 3.—Results of ANOVA and LSD calculations comparing the number of spider species, the number of resident species, and the number of guilds in the three shrub groups. Shrub groups are as in Table 1.

Shrub Group	No. Shrubs	Mean No. Species	Mean No. Resident Species	Mean No. Guilds
I	83	3.75 ± 1.99a ¹	2.22 ± 1.49a	2.54 ± 1.17a
II	48	5.12 ± 2.51b	3.18 ± 1.77b	3.06 ± 1.26b
III	94	5.08 ± 2.6 b	3.07 ± 1.92b	3.10 ± 1.10b
F		8.36*	7.34*	5.90*

*F .05 [2,222] = 3.03.

¹ Numbers in columns followed by the same letter are not significantly different at the 5% level according to LSD calculations.

Increased environmental complexity may allow larger numbers of predatory species to coexist within a given habitat. More types of substrate, kinds and numbers of prey, and varieties of microhabitat are available to species within more complex environments. The data presented indicate that more structurally complex habitats, here generally represented by tied shrubs, support greater spider species densities and species diversity. The data also demonstrate that changes in shrub structure can cause changes in the distribution of spiders in shrubs. We believe that spatial and architectural properties of habitat structure can be a very important determinant of species diversity, density and distribution of small predatory invertebrates in a community.

Nature of Guilds

The guilds examined in this study were broadly defined on the basis of observations of spider hunting methods. The resulting spider guilds corresponded with general taxonomic groupings. It was assumed that differences in spider hunting behavior indicated differences in potential prey used, since prey are differentially susceptible to predator capture methods (Turnbull 1973). It was also assumed that each hunting behavior is best suited to a certain type of habitat structure. For example, web building spiders require substrate suitable for web attachment and ambushing spiders require a place for concealment. This study attempted to elucidate the relationship between species hunting behaviors and spatial requirements, by analyzing the effects of change of spatial properties of the habitat on spider guilds in a shrub community.

The clipped, tied and control shrubs (perturbation types) were compared using mean weekly guild IV's in the Wilcoxon Ranked Sum statistic. ANOVA and LSD tests were performed for each guild on the three shrub

groups (Table 1) using the number of guilds. Many of the guild values for individual shrubs were zeros, therefore 0.5 was added to the values to alleviate this problem (Sokal and Rohlf 1969). The square root data transformation was performed to make the variances independent of the means, as a Poisson distribution was expected. A correlation matrix relating the number of spider guilds and shrub architectural parameters was also performed.

No significant differences were found between shrub perturbation types for the nocturnal hunter guild (Guild 1). Shrub group III (greater than 50% dense foliage) had a significantly higher number of spiders in this guild than shrub group I (greater than 50% open foliage) (Table 4). The greater densities of this guild found in density foliated shrubs may reflect the location of retreats of these spiders in dense foliage. For example, the retreats of *C. inclusum* are constructed between the leaves of densely foliated branches in *Artemisia*. Nocturnal hunters captured were probably knocked from diurnal retreats.

No significant difference was found between perturbation types for the runners. Significantly greater densities were found in shrub group II (less than 50% open foliage, dense foliage and crown) (Table 4). Runner densities also correlate positively with shrub height, and SFD, and negatively with percent open foliage (Table 5). (Values of shrub height correlated positively with SFD). *Philodromus histrio*, the most abundant species in this guild (57.5%), is grey-green in color, blending well with the color of *Artemisia* leaves. *Philodromus histrio* was frequently observed in all foliated areas on the shrubs. This may explain the lack of difference between shrub perturbation types observed for this guild. It appears that shrubs with a diversity of foliage types may be more attractive to these spiders and this condition can occur in all of the perturbation types.

Table 4.—Results of ANOVA and LSD calculations comparing the number of spiders in each guild, in the three shrub groups. Shrub groups are as in Table 1. Data transformation was $\sqrt{Y + 0.5}$; original means are reported.

Shrub Group	No. Shrubs	Mean Number of Spiders				
		Guild 1	Guild 2	Guild 3	Guild 4	Guild 5
I	83	0.24 ± 0.13a	0.79 ± 0.16a	0.58 ± 0.13a	3.07 ± 0.49a	1.91 ± 0.38a
II	48	0.62 ± 0.18ab	1.62 ± 0.21b	0.77 ± 0.17ab	4.31 ± 0.64a	2.68 ± 0.50a
III	94	0.70 ± 0.13b	1.25 ± 0.15ab	1.11 ± 0.13b	3.65 ± 0.46a	3.98 ± 0.36b
F		3.42*	4.55*	3.50*	1.58 ^{ns}	8.86*

*F .05 [2,222] = 3.03.

¹ Numbers in columns followed by the same letter are not significantly different at the 5% level according to LSD calculations.

In 9 of 15 weeks ambushing spiders had higher IV's in tied shrubs than in either clipped or control shrubs. Tied shrubs were found to be significantly different than clipped and control shrubs ($P < .05$). ANOVA of shrub groups revealed significantly greater ambusher densities in shrub group III (greater than 50% dense foliage) than in shrub group I (greater than 50% open foliage) (Table 4). Ambusher densities also correlate positively with percent dense foliage and negatively with percent open foliage and SFD, suggesting that shrubs with dense foliage support higher densities (Table 5).

Parameters for agile hunters relate positively with indicators of shrub architectural diversity and shrub volume. In 11 of 15 weeks agile hunter IV's were higher in both clipped and control shrubs than in the tied shrubs. Clipped and control shrubs were found to be significantly differently from tied shrubs ($P < .05$). Agile hunter densities correlated positively with shrub height, cover, volume, mass 81-120 cm and SFD. They correlate negatively with mass 0-40 cm (Table 5). Since these spiders are quick active hunters with excellent vision, dense foliage may obstruct their vision and impair the rapid jumping movements used to capture prey. No difference for this guild was found among the shrub groups. However, these groups are based on foliage density alone and segregate shrubs in a manner which eliminates recognition of shrubs with other structurally diverse foliage characters e.g., foliage height distribution and SFD.

A small proportion of web builders were in the family Araneidae (11%), the orb-weaving spiders, which use a more open substrate for web attachment. Most of the web builders collected in this study construct irregular snare webs which require complex structural support, available in shrubs with dense branching. The majority of these spiders were also relatively small and built small webs. In 9 of 15 weeks web builder IV's were higher in both tied and control shrubs than in clipped shrubs. Tied and control shrubs were found to be significantly different than tied shrubs ($P < .05$). These spider densities correlated positively with percent dense foliage and negatively with percent open foliage (Table 5). In ANOVA of shrub groups, web builder densities were highest in group III shrubs (greater than 50% dense foliage) (Table 4). As demonstrated by the data, the density of web-building spiders in a shrub is related to shrub fo-

liage density. If larger species of web builders were present we would expect them to be found in shrubs with a more open architecture.

Spider guild densities and importance values were significantly altered by shrub architectural changes. The observed guild distributions were in accord with known behavior and life histories of the member species. The data demonstrate a correlation between hunting behavior and habitat structure for small invertebrate predators. The data also suggest that guild analysis may be useful in examining niche dimensions in community studies.

Problems and Areas for Future Study

No data were collected on prey abundance, availability, or utilization by spiders in this study. Experimental changes of shrub architecture may have caused a subsequent change in prey distribution and abundance. These factors may then have affected the distribution of spider guilds. A similar study examining the effect of vegetation architectural changes on available prey as well as on predator guilds would yield information clarifying this relationship.

The relationship between animal and plant species diversity is a confounding issue in many investigations. This study did not examine the influence of substrate architecture, independent of plant species, on spider species diversity, distribution and abundance since the shrub perturbations were performed on only one shrub species, *Artemisia tridentata*. The natural variation of architecture and associated insect faunas of different plant species could determine predator guild distributions. Studies which examine similar changes of vegetation architecture using several plant species would be helpful in understanding this relationship. Also comparative guild studies between communities with different species compositions should be conducted. This study and that of Robinson (1980) suggest that the architecture of a community is an important variable determining spider community organization.

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Table 5.—Correlation coefficients giving r values for relative guild density and shrub architectural parameters. Guild 1 = Nocturnal hunters; 2 = Runners; 3 = Ambushers; 4 = Agile Hunters; 5 = Web Builders.

	Guild 1	Guild 2	Guild 3	Guild 4	Guild 5
Height	.083	.162*	.065	.315**	.042
Cover	.007	.007	.096	.299**	.092
Volume	.033	.022	.078	.346**	.123
Mass 0-40 cm	-.022	-.092	-.051	-.240**	-.059
Mass 41-80 cm	.000	.052	.011	-.028	.075
Mass 81-120 cm	.025	.070	.053	.309**	.014
Percent dense foliage	.098	.091	.250**	.010	.283**
Percent open foliage	-.136	-.145*	-.189**	-.046	-.243**
Canopy	.099	.133	-.103	.083	-.051
Shrub Foliage Diversity	.086	.157*	.096	.343**	.042

* .05 > P > .01.

** $P < .01$.

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