HABITAT PARTITIONING BY THE WOLF SPIDER (ARANEAE, LYCOSIDAE) GUILD IN STREAMSIDE AND RIPARIAN VEGETATION ZONES OF THE CONEJOS RIVER, COLORADO

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ABSTRACT. Members of a guild of cursorial spiders (*Pardosa* spp. and *Alopecosa* spp.) spatially segregate among five discrete habitats, ranging from a streamside cobble habitat extending laterally along a successional gradient to the leaf litter zone of a transition or climax high elevation (2348 m) riparian coniferous forest in Colorado. Seasonal activity peaked in midsummer for all guild members. Spiders were diurnally active earlier in streamside habitats, and levels of activity were positively correlated with light intensity. Guild members *Pardosa tristis* and *P. uncata* were most different in habitat selection and periods of diurnal activity. Males and females of all guild species differed in their distribution among habitats and over months of collection. Measures of guild species diversity and evenness were variable between habitats, and were largely influenced by the relatively high abundance of one or two guild species, particularly in the streamside habitats.

Several workers have reported that vegetative diversity and structural complexity are important determinants of spider community structure (Luczak 1959, 1963; Duffey 1966, 1970; Hatley & MacMahon 1980; Bultman et al. 1982; Abraham 1983; Greenstone 1984; Rypstra 1986; Uetz 1991), yet little is known about species composition or diversity of spiders associated with individual forest stands, forest stand types, or forest communities in North America (Jennings et al. 1988).

The relatively open-canopied river ecosystems of western North America typically have an unvegetated streamside zone characterized by erosional or depositional materials, grading laterally into floodplain successional zones culminating in a transition or climax riparian forest. Because of the biological and physical differences of these zones and the probable species-specific differences in habitat, trophic, and reproduction requirements of spiders, we expected to find a partitioning of the available microhabitats in these zones.

In this study, we examined the seasonal and diurnal patterns of distribution and activity among members of a wolf spider guild (Lycosidae) in a streamside zone and four lateral successional plant zones along the Conejos River in south-central Colorado. Wolf spiders are one component of the wandering or cursorial spider "super-guild" consisting of the families Clubionidae, Gnaphosidae, Lycosidae, Pisauridae, Thomisidae, Hahniidae and some Agelenidae. The Lycosidae represent a guild of "sit-and-wait" predators that are generally stationary with only occasional movements between sites (Bultman et al. 1982). Uetz (1975) indicated that guilds provide an appropriate functional group for addressing species composition and community structure.

METHODS

Spiders were collected in five zones adjacent to the Conejos River in the San Juan Mountains of South-Central Colorado, 24.1 km west of Antonito, Colorado, Conejos County, at an elevation of 2348 m. The site was approximately 100 m south of the United States Forest Service River Springs Work Station. The seral and climax woody vegetation were generally characterized by a riparian mixed deciduous and coniferous forest, consisting of Douglas fir (*Pseudotsuga menzesii*), yellow pine (*Pinus ponderosa*), Englemann spruce (*Picea englemanni*), narrow leafed cottonwood (*Populus augustifolia*), and dense willow stands (*Salix* sp.) adjacent to the stream. Grasses and willow predominated within approximately 5 m of the stream, with a 2 to 5 cm deep litter layer on the ground under the canopy

of mixed conifers and cottonwoods more distant from the stream.

Five distinct habitats were selected based on substrate type (rock, sand, grass, or leaf litter), intensity of incident solar radiation, and variation in air and substrate temperatures (Table 1). The first habitat was approximately a 2 m wide rock-cobble zone (RC) along the north margin of the stream channel, subject to periodic inundation, particularly during peak stream flow of late spring and early summer. The second habitat (GW) was an area 3–5 m wide, approximately 3 m from the stream channel, characterized by a variety of grasses and dense stands of willow coppices resulting from recurrent cutting by beavers. Habitat three (SC) was an old stream channel located 20–30 m from the stream's edge with a sand and large cobble substrate and little or no vegetation. The fourth habitat (GL) was composed of leaf litter, interspersed with patches of grass and was approximately 50–60 m from the stream channel. The fifth habitat (LL), also 50–60 m from the stream, consisted of a litter layer 2–5 cm deep (primarily from the cottonwoods).

Spiders were sampled within each habitat with a set of ten pitfall traps, consisting of aluminum cans (diameter = 5.5 cm, volume = 354 ml) placed at 1.5 m intervals in two rows of five over a 23.1 m² area. The cans were buried so that the tops were level with the substrate surface, and each trap was half-filled with a 1:1 mixture of 100% ethylene glycol and 70% isopropyl alcohol. The ethylene glycol minimized the evaporative loss of preservative between collections. Pitfall traps are more effective in assessing what might be termed the "active density" (Uetz 1977) of cursorial spiders, and unlike quadrat sampling, allow for more continual sampling (Uetz & Unzicker 1976). The traps were emptied on a monthly basis, or approximately every 25–30 days from June through October in 1987, and May through October in 1988. Trap contents were separated from the preservative with a 420μm mesh sieve mesh, and the traps were recharged with preservative as needed.

Ambient air temperature (2 cm above the substrate), and substrate temperature (surface temperature) were taken with a Cole-Parmer (Model 8500-40) digital thermometer at two randomly selected (table of random numbers) sites in each habitat. Incident and reflective solar radiation were also measured at these sites with a Protomatic (Model 3171) photometer. These data were

recorded at approximately 0900 and 1400 h on each monthly sampling day, and only under clear conditions to control for variation (other than seasonal) that could be attributed to overcast skies.

Trapped spiders were sorted by habitat, species, age (juvenile, penultimate, or adult), and sex. Only sexually mature adults and penultimates were used for analysis. Prey abundance was determined monthly for each habitat by using what were defined as potential or available prey items from the pitfall traps. All adult Coleoptera, Hymenoptera, Hemiptera, and prey items exceeding the maximum length (1.6 cm) of the largest guild member (*Pardosa tristis*) were excluded as potential or available prey. Acarina (mites), Collembola (springtails), Diptera (true flies), Homoptera (plant and leafhoppers), Lepidoptera (noctuid moths), Opiliones (harvestmen), Orthoptera (crickets and grasshoppers), Plecoptera (adult stoneflies), and other miscellaneous soft-bodied insects were considered prey. Counts and total dry weight (samples oven dried for 24 hours at 60 °C) were determined for each identified prey category by month and habitat.

Microhabitat selection and patterns of diurnal activity were assessed during periods of peak adult activity (i.e., June through August) in the summers of 1988 and 1989. Areas within each of the five habitats were visually searched for 10, 15 minute-time periods for a total of 150 min of searching per habitat. The ten searches for each habitat were subdivided into five morning (0830 to 1200 h) and five afternoon searches (1300 to 1730 h). Spiders recognized as a guild members were collected with an aspirator, and the collection site marked. Each spider was placed on a small styrofoam block (highly reflective surface) and restrained. Body temperature was taken by inserting a 0.5 mm diameter probe, connected to the digital thermometer, into the dorsum of the spider's cephalothorax. Air temperature (2 cm above substrate), substrate temperature (substrate surface), incident radiation (foot candles converted to lux), time of day, and habitat type (sand, grass, leaf litter, or rock) were recorded for each marked collection site.

Adults and the majority of penultimate guild members were identified to species, with confirmation and some identification provided by C. D. Dondale of the Biosystematics Research Centre in Ottawa, Canada. Several species representing cursorial spiders of the families Clubionidae, Gnaphosidae, and Hahniidae were also

Table 1.—Physical characteristics and prey abundance (dry weight) of each of five discrete habitats in the riparian zone. Values are means and standard deviations based on data from May through October, 1987 and 1988.

| Habitat | Characteristics | | | |
	Air temp. (°C)	Substrate temp. (°C)	Incident radiation (foot-candles)	Prey abundance (G)
Rock-cobble	19.9 ± 8.85	20.4 ± 10.3	3380 ± 2158	0.575 ± 0.211
Grass-willow	22.1 ± 9.85	21.0 ± 9.21	3369 ± 2197	0.278 ± 0.136
Sand-cobble	22.7 ± 12.4	23.5 ± 13.6	3275 ± 2689	0.064 ± 0.067
Grass-litter	18.6 ± 9.59	16.7 ± 8.43	1567 ± 2156	0.265 ± 0.202
Leaf litter	18.8 ± 8.29	18.3 ± 8.00	1299 ± 1287	0.152 ± 0.093

collected, and identifications of these species are pending verification for use in future studies. Voucher specimens of all guild members have been deposited at the Biosystematics Research Centre.

Differences in total abundance, abundance of guild members, and relative abundance of males and females between months and among habitats were each compared with log-likelihood goodness of fit tests (G statistic) for contingency tables (Zar 1984). Species richness (MAX S for each habitat) was measured as the maximum number of guild members represented in collections from each habitat. A Shannon index of species diversity was calculated for each habitat (Brower & Zar 1984). This species diversity index is appropriate when collections are thought to represent subsamples of a larger, unsampled community (Pielou 1966). The Shannon index takes the form of:

$$H = (log\ n! - \Sigma\ log\ ni!)/n$$

Species evenness (J) among the habitats was determined as $J = H/H_{max}$, where H_{max} is the maximum possible diversity with a given n (total sample size) and S (number of species). A community index of proportional similarity (PS) was derived for each habitat (Wolda 1981). Unlike the majority of community similarity indices, the index of proportional similarity accounts for the relative abundance of each species. Species rank abundance curves for each habitat were tested for fit to a theoretical log-normal distribution (Ludwig & Reynolds 1988). Pearson coefficients of correlation (r) were determined to assess the relationship between mean abundance (species pooled) and various abiotic variables for each habitat (SPSS-X 1985). Komolgorov-Smirnov one-sample goodness of fit tests (Brower & Zar

1984) were used to compare habitat samples from the visual search technique for five of the eight guild members. Species were pooled, and frequencies of males and females were tested for independence of distribution among the habitats in relation to sex with a log-likelihood test for goodness of fit. A Kruskal-Wallis nonparametric analysis of variance and multiple range test were used to compare temperature differentials (i.e., body temperature - air temperature) between the habitats (Brower & Zar 1984). Pooled-within-group coefficients of correlation between discriminating variables and the first two discriminant functions derived from a step-wise discriminant function analysis were determined, and mean discriminant function scores for five of the eight guild members were also calculated (SPSS-X 1985). Discriminant function analysis is a commonly-used multivariate technique in ecology and systematics to allow for the discrimination among individuals or groups such as species based on a linear combination of several predictor variables to form one or more new discriminating variable or functions (Sokal & Rohlf 1981).

RESULTS

Physical parameters varied among the five discrete habitats (Table 1). Both mean daily substrate and air temperatures increased from the rock-cobble and grass-willow habitats to the sand-cobble habitat, and decreased in the more closed-canopied grass-litter and leaf litter habitats. Incident solar radiation was highest in the rock-cobble adjacent to the stream, and decreased on average by 61.6% from the rock-cobble to the leaf litter habitats. Prey abundance was highest in the open-canopied rock-cobble, and lowest, as expected, in the more microclimatically extreme sand-cobble.

Table 2.—Guild members with total and relative abundance. Samples pooled for all habitats and months from 1987 and 1988 field seasons.

Species (n = 1121)	Total	Percent
Alopecosa aculeata (Clerck)	115	10.3
Alopecosa kochi (Keyserling)	80	7.1
Pardosa distincta (Blackwall)	338	30.1
Pardosa steva Lowrie & Gertsch	4	0.4
Pardosa tesquorum (Odenwall)	239	21.3
Pardosa tristis (Thorell)	72	6.4
Pardosa uncata (Thorell)	207	18.5
Pardosa yavapa Chamberlin	66	5.9

A total of 1121 adult and penultimate wolf spiders, representing two genera (*Pardosa* and *Alopecosa*) and eight species was collected in the pitfall traps over the two field seasons (Table 2). *Pardosa distincta* (Blackwall) was the most abundant guild member in pitfall collections, with *P. tesquorum* (Odenwall) and *P. uncata* (Thorell) second and third in number, respectively. Only four *P. steva* Lowrie & Gertsch were taken in pitfall traps across all five habitats. Spiders of the genus *Pardosa* spp. constituted 82.6% of individuals collected. Spiders (species pooled) were unevenly distributed between habitats and over the months of collection ($G = 65.38$, $df = 4$, $P < 0.001$). The largest number collected for any month (546) was taken during July (Fig. 1); and with the exception of *P. yavapa*, each species was most frequently taken in pitfall traps during July (Fig. 2). The distribution of guild members among the habitats was highly variable ($G = 677.3$, $df = 4$, $P < 0.001$). *Pardosa tesquorum* and *P. tristis* were most frequent in the rock-cobble habitat, and *P. distincta* was most abundant in the grass-willow habitat (Fig. 2). The sand-cobble habitat was characterized by the highest frequency of *P. yavapa*, and *P. uncata* was largely restricted to the two litter habitats.

Of the spiders collected in pitfall traps, 64.9% were adult males. The distribution of spiders among the five habitats was not independent of sex ($G = 30.20$, $df = 4$, $P < 0.001$). The highest ratio of males to females (316:99) was from the rock-cobble. Males and females were not distributed over time (months of collection) independent of sex ($G = 171.8$, $df = 5$, $P < 0.001$). The abundance of males was more than twice that of females during July, and the frequency of males decreased to numbers below that of females during September and October.

All eight guild members were trapped in the rock-cobble bordering the stream channel (Table 3). Both the grass-willow and grass-litter habitats
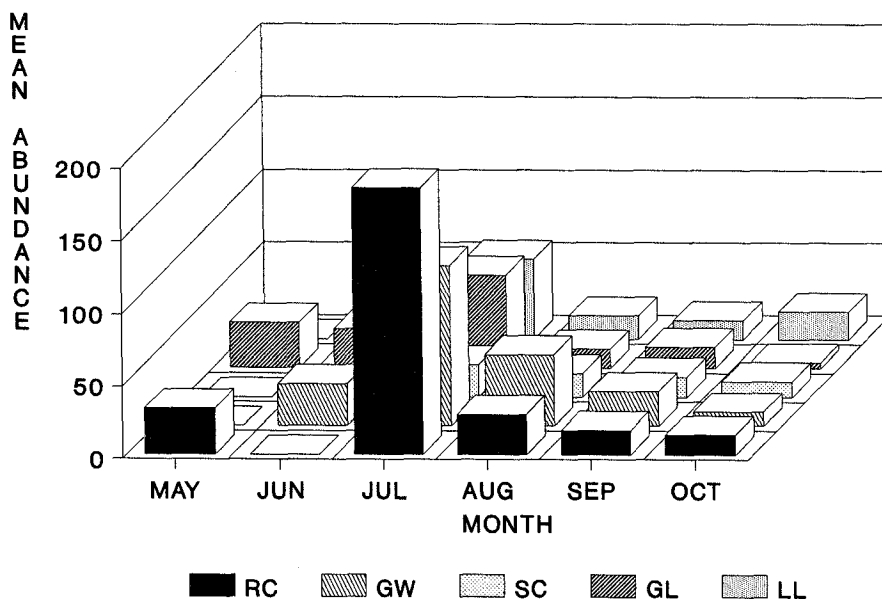

Figure 1.—Mean abundance (species pooled) of wolf spiders by habitat and month based on pitfall trap collections over the 1987 and 1988 field seasons. Habitat designation in all figures: RC = rock-cobble, GW = grass-willow, SC = sand-cobble, GL == grass-litter, LL = leaf litter.
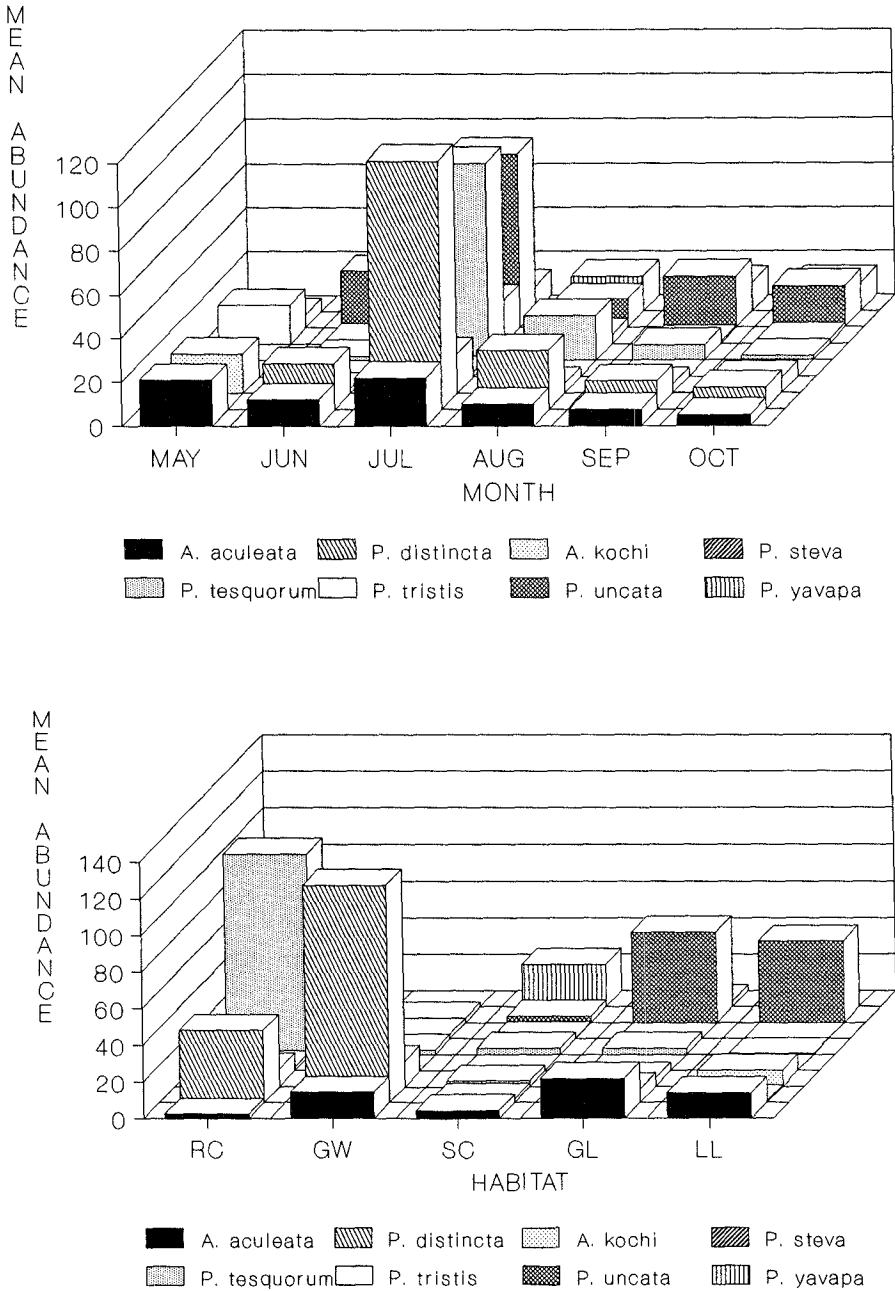
Figure 2.—Mean abundance of guild members by month and habitat based on pitfall collections over the 1987 and 1988 field seasons. Top – abundance by month; Bottom – abundance by habitat.

had a guild species richness of six, with no *P. steva* collected in either habitat. *Pardosa tristis* was absent from the grass-litter. Despite the low number of spiders collected (80) in the sand-cobble, seven of the eight guild members were represented, with only *P. steva* absent. *Pardosa*

distincta, *P. tristis*, and *P. steva* were not trapped in the leaf litter habitat over two field seasons.

Guild diversity *(H)* was highest for the rock-cobble habitat and lowest for the grass-willow habitat (Table 3). Higher guild evenness *(J)* values were derived for the three habitats (sand-

Table 3.—Total number of spiders (n), Guild species richness (S), Diversity (H), and Evenness (J) by habitat. Calculations based on data from 1987 and 1988.

Index	Rock-cobble	Grass-willow	Sand-cobble	Grass-litter	Leaf litter
			Habitat		
n	413	310	80	180	138
S	8	6	7	6	5
H	0.60	0.38	0.63	0.56	0.38
J	0.58	0.48	0.73	0.70	0.61

Table 5.—Pearson Coefficients of Correlation between mean abundance for months May through October (1987 and 1988) with physical variables and prey dry weight for each of five habitats. Ta = mean ambient air temperature, Ts = mean substrate temperature, Li = incident solar radiation, Prey = mean dry weight of pooled prey categories. Asterisks indicate $P < 0.05$.

Habitat	Ta (°C)	Ts (°C)	Li (lux)	Prey (G)
		Variables		
Rock-cobble	0.74	0.24	0.87	0.39
Grass-willow	0.41	0.40	0.69	0.77
Sand-cobble	0.91	0.89	0.96	−0.82
Grass-litter	0.48	0.64	0.94*	0.75
Leaf litter	0.52	0.47	0.71	0.01

cobble, grass-litter, and leaf litter) more distant from the stream than either the rock-cobble or grass-willow habitats (Table 3). The habitat with the lowest index of guild diversity (grass-willow) also exhibited the lowest evenness index. Community (guild) index values of proportional similarity (PS) were determined for each combination of habitats (Table 4). The grass-litter and leaf litter combination had the highest index of similarity. The lowest index values were for the two rock-cobble and leaf litter habitats that were most different in their physical characteristics (Table 1). The rock-cobble habitat had the least overall similarity with the other habitats (mean similarity = 22.1). Species rank abundance curves for each habitat were not significantly different from expected log normal distributions (Fig. 3). Correlations between physical parameters and mean spider abundance were highest for the more open habitats (Table 5).

Visual searches of the five habitats produced 162 wolf spiders, representing seven of the eight guild species (Table 6). The largest number of wolf spiders was collected in the rock-cobble habitat. The distributions of the five dominant (i. e., frequency greater than five) guild members (A. aculeata, P. distincta, P. tesquorum, P. tristis, and P. uncata) among the habitats were all sig-

Table 4.—Proportional similarity (PS) matrix between habitats. RC = rock-cobble, GW = grass-willow, SC = sand-cobble, GL = grass-litter, LL = leaf litter.

	RC	GW	SC	GL	LL
RC	—	29.8	25.9	23.0	9.67
GW	—	—	26.3	25.9	22.2
SC	—	—	—	37.2	29.2
GL	—	—	—	—	82.4
LL	—	—	—	—	—

nificantly different from expected distributions (Table 6). Pardosa distincta (dmax = 10.2, df = 4, $P < 0.01$) and P. tesquorum (dmax = 8.2, df = 4, $P < 0.01$) were more evenly distributed between habitats than either P. tristis (dmax = 27.4, df = 4, $P < 0.001$) or P. uncata (dmax = 16.0, df = 4, $P < 0.001$), that were restricted to the open-canopied (rock-cobble, grass-willow, and sand-cobble) habitats and closed-canopied (grass-willow and leaf litter) habitats, respectively. Despite pitfall collections of A. aculeata in all habitats, this guild member was only observed during searches of the grass-litter and leaf litter. A total of 16 juvenile spiders that could not be identified to species was collected during visual searches.

Unlike the overall ratio of males to females from pitfall collections, a higher ratio of females to males (121:31) was observed during visual searches of the five habitats. The distribution of these spiders among the habitats was not independent of sex ($G = 192.9$, $df = 3$, $P < 0.001$). Females observed with egg cases attached to their spinnerets were distributed unevenly among four (i. e., none observed in sand-cobble) of the five habitats (dmax = 12.6, $df = 3$, $P < 0.001$). Of the females with egg cases, 88.5% were observed in the rock-cobble and grass-willow habitats.

Patterns of diurnal activity were highly variable ($G = 89.30$, $df = 4$, $P < 0.001$) among guild members (Fig. 4). Wolf spider activity in the rock-cobble peaked at 1000 h, with a marked drop in activity after 1200 h that continued through the afternoon (Fig. 5). Incident solar radiation was significantly negatively correlated ($r = -0.631$, $P < 0.05$) with frequency of activity
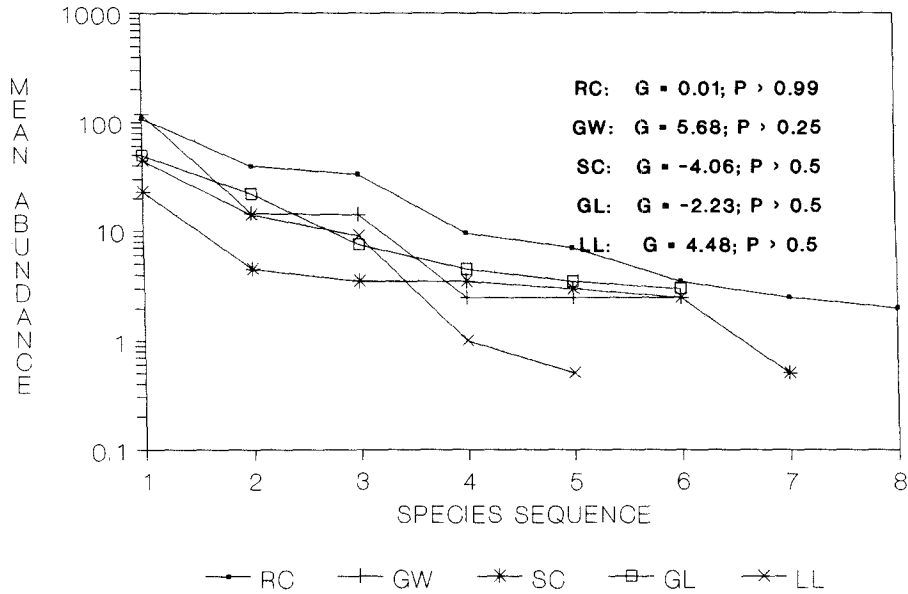
Figure 3.—Rank abundance plots of guild species by habitat. Plots for each habitat were tested for fit to a log normal distribution with log-likelihood goodness of fit test (G statistic).

in the rock-cobble. Activity in the grass-willow was highest at 1200 h with a corresponding increase in light intensity, and activity was continual through the afternoon (Fig. 5). No active wolf spiders were observed in the grass-litter habitat until 1100 h, and incident solar radiation and frequency of activity were significantly correlated ($r = 0.894$, $P < 0.05$) in this habitat (Fig. 5). Spider activity (only one individual) was first observed in the leaf litter at 0900 h, with activity peaking at 1100 h, followed by a sharp drop in activity after 1200 h. Activity in the leaf litter was relatively constant through the afternoon even with a corresponding drop in light intensity

(Fig. 5). Spider body temperature to air temperature ratios were not significantly different between habitats ($F = 0.0526$, $df = 3, 80$; $P > 0.75$). For all habitats, with the exception of the grass-litter, mean spider body temperature exceeded an air temperature-body temperature line of equivalence.

Habitat type ($F = 14.83$, $df = 4,60$; $P < 0.0001$) and time of activity ($F = 10.17$, $df = 4,60$; $P < 0.0001$) were the variables selected by the stepwise discriminant function analysis as the best discriminators between the five dominant guild members. The first discriminant function accounted for 93.7% of among group (species) vari-

Table 6.—Frequencies of each guild member by habitat ($n = 162$) from visual diurnal searches. RC = rock-cobble, GW = grass-willow, SC = sand-cobble, GL = grass-litter, LL = leaf litter.

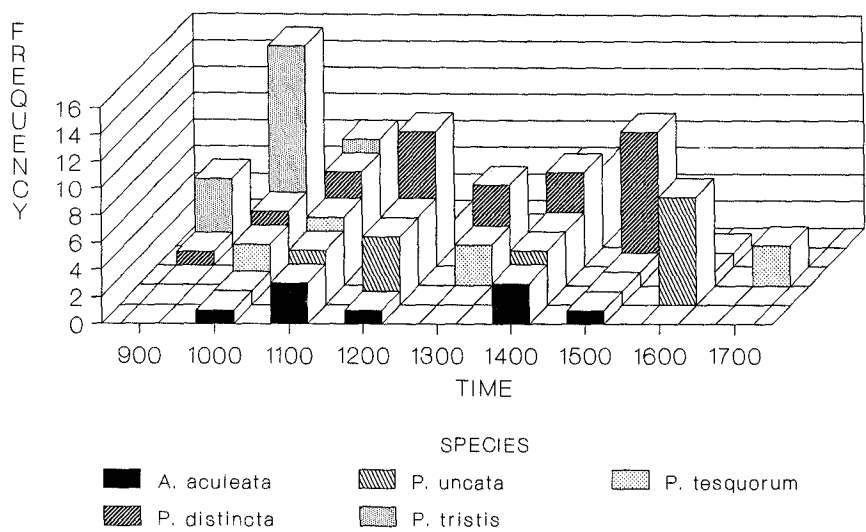| Species	Habitat					Totals	$P <$
	RC	GW	SC	GL	LL		
Alopecosa aculeata	0	0	0	4	5	9	0.01
Pardosa distincta	2	27	1	13	4	47	0.01
Pardosa tesquorum	13	2	0	3	6	24	0.01
Pardosa tristis	35	2	1	0	0	38	0.001
Pardosa uncata	2	0	0	2	21	25	0.001
Pardosa yavapa	0	0	0	0	1	1	—
Pardosa steva	0	0	0	0	1	1	—
Pardosa spp.	3	4	2	3	5	16	—
Totals	55	35	4	25	43	162	—

Figure 4.—Diurnal activity of the five most abundant guild members based on visual searches of five discrete habitats.
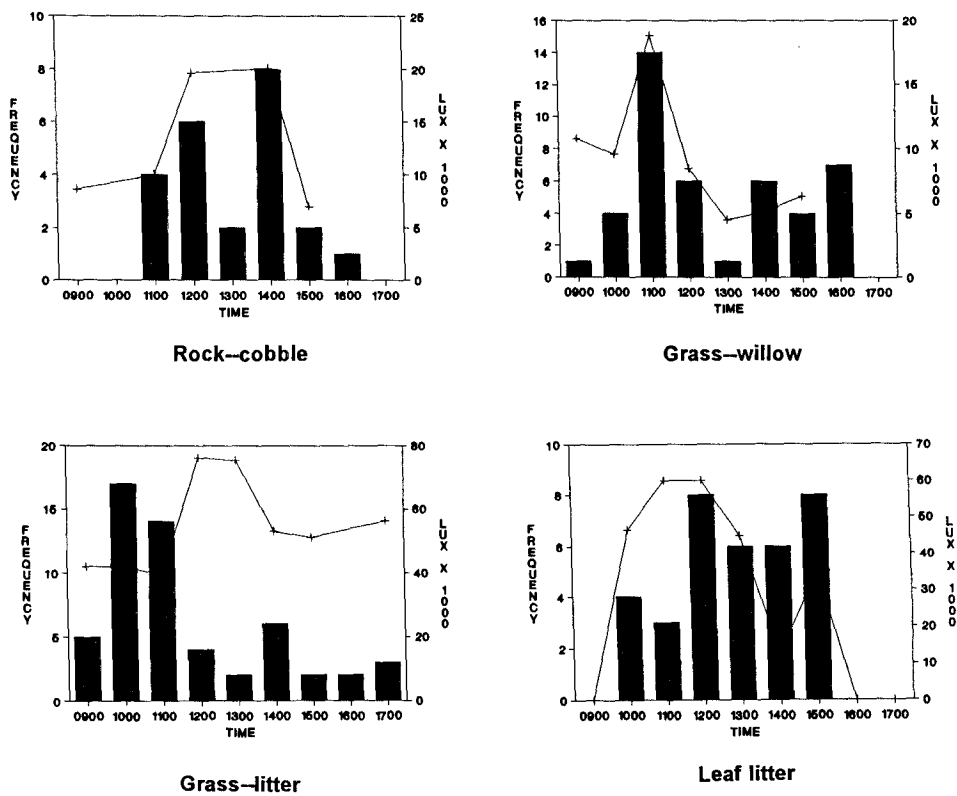

Figure 5.—Diurnal activity of wolf spiders (species pooled) in four of five discrete habitats (Rock-cobble; Grass-willow; Grass-litter; and Leaf litter) in relation to incident solar radiation.

ation (Table 7). Habitat type selected was significantly correlated with the first discriminant function ($r = 0.705$, $P < 0.05$), and physical parameters such as body temperature, substrate temperature, air temperature, and incident solar radiation were all significantly correlated with the second discriminant function. The correlation of these physical variables with the second function can be explained in part by the probable high intercorrelation between these parameters. The second function explained only 4.90% of the between-species variation. A plot of mean function scores for each guild member for the first two discriminant functions (Fig. 6) graphically illustrates the differences between species based on the predictor variables. *Pardosa tristis* and *P. uncata* had the highest negative and positive loadings on the first discriminant function, respectively; an indication of their broad differences in habitat selection and diurnal activity. The low loadings on both discriminant functions for *P. tesquorum* and *P. distincta* indicate the greater range of distribution among the habitats and thus variation in time of activity for these species. *Alopecosa aculeata* was similar in habitat preference and time of activity to *P. uncata* as indicated in Fig. 6.

DISCUSSION

The concept of resource partitioning among closely related species, one facet of which is spatial segregation, is a central concept in community ecology (Pianka 1969; Schoener 1971; MacArthur 1972). Rivas (1964) found that several congeners of the *distincta* group of wandering spiders are typically allopatric, but often overlap in syntopic or sympatric associations. In this study, guild members *P. distincta*, *P. tristis*, and *P. uncata* showed a high degree of habitat selectivity (Fig. 2 and Table 6). *Pardosa distincta* was most abundant in the drier and more open rock-cobble and grass-willow habitats. This is consistent with Lowrie's (1973) observations that members of the *distincta* group commonly occur in open, nonforested habitats. *Pardosa tristis*, the largest species in the genus, is widely distributed geographically, altitudinally, and ecologically, and is most abundant in the vicinity of water (Lowrie 1973). This guild member was most often observed and collected in the rock-cobble adjacent to the stream. The only species largely restricted to the leaf litter was *P. uncata*. Lowrie (1973) found *P. uncata* under and on the bark of fallen

Table 7.—Frequencies of males and females (species pooled) by habitat from visual diurnal searches ($n = 152$). RC = rock-cobble, GW = grass-willow, SC = sand-cobble, GL = grass-litter, LL = leaf litter.

Sex	RC	GW	SC	GL	LL	Totals	$P <$
Females	44	29	1	18	30	121	0.001
Males	11	4	0	6	10	31	
Females with eggs	10	13	0	3	0	26	0.05

trees, but he only collected this species within the forest.

The higher overall ratio of males to females from pitfall collections probably reflects the greater activity of adult males as they search for sexually mature females. Peck & Whitcomb (1978) found that male cursorial spiders in a South Carolina pasture were less restricted than females to any one habitat because of increased male vagility during periods of breeding. The higher ratio of females to males visually observed during searches of each habitat can be attributed to searches conducted in late July, August, and September, when male activity was markedly reduced. Adult female wolf spiders with egg cases were more frequently observed in the open bare ground habitats (Table 6). Kronk & Riechert (1979) found that adult female *Lycosa santrita* utilized patches of bare ground and rock more
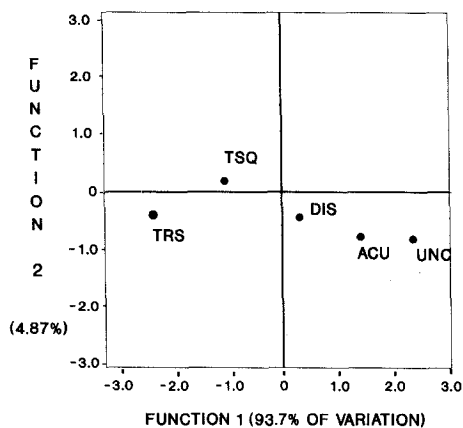

Figure 6.—Plot of mean discriminant function scores (functions 1 and 2) for the five most abundant guild members based on visual searches of five discrete habitats. TRS = *Pardosa tristis*, TSQ = *Pardosa tesquorum*, DIS = *Pardosa distincta*, ACU = *Alopecosa aculeata*, UNC = *Pardosa uncata*.

frequently than either sub-adult females or adult males of this species. For adult female wolf spiders, the open bare ground habitats may provide a more suitable environment for mate location and thermoregulation of developing eggs.

Guild species richness was highest in the two bare ground habitats (rock-cobble and sand-cobble), each with high diurnal variation in physical parameters (Table 1), and with the two highest levels of prey abundance. The more guild species represented and the greater abundance of lycosid spiders in the open-canopy habitats (with little or no leaf litter), could be attributed to greater prey availability, light intensity, and more suitable substrate in these habitats. Wolf spiders are visually oriented "sit-and-wait" predators (Foelix 1982; Riechert & Luczak 1982), and the ground surface is their principal habitat (Lowrie 1973). No guild members were observed moving vertically into the above-ground vegetation. Thus, more open, bare habitats with sufficient numbers of available prey that can be visually located more easily would lend support to Pianka's (1974) hypothesis that more productive (in this case, arthropod prey) habitats could support more species of foraging animals.

The species diversity of spiders in a number of ecosystem types has been positively correlated with factors such as litter depth, diversity of vegetation, and the overall structural complexity of the habitat (Uetz 1975; Hatley & MacMahon 1980; Abraham 1983). However, for lycosid hunting spiders, species diversity and individual species abundance is often higher in field borders (Doane & Dondale 1979) and disturbed habitats such as strip-clearcuts (Coyle 1981; Jennings et al. 1988). The higher measures of guild diversity (Table 3) from the open and less structurally complex habitats (rock-cobble and sand-cobble) would seem to support these observations. The relatively small diversity values (all less then 0.75) for all habitats is an indication of generally low species equitability. This could be a result of resource preemption (Southwood 1978) by one or more of the dominant or more abundant guild members such as *P. distincta* in the grass-willow, *P. tesquorum* and *P. tristis* in the rock-cobble, and *P. uncata* in the leaf litter habitat.

May (1981) suggested that models of species abundance such as those represented by rank abundance plots were the best means of providing accurate measures of species diversity. The majority of communities studied by ecologists follow a log normal distribution model of species abundance (Sugihara 1980). Magurran (1988) emphasized that any variable under the influence of the random variation of several factors, can result in that variable being normally distributed. None of the species rank abundance plots differed significantly from the log normal model. The best fit to a log normal abundance curve of an observed frequency distribution was for the rock-cobble habitat (Fig. 3 and Table 3), where guild species diversity, species richness, and prey abundance were the highest. A large component of the arthropod community in a high-elevation riparian system in which air temperature and light intensity remain relatively low during the day, possibly at limiting levels, may find the more open, bare ground habitats optimal during periods of activity.

The low value of proportional similarity for the rock-cobble and leaf litter habitats (Table 4) was expected given the differences in physical parameters, prey abundance, and the relative abundance of guild members (particularly *P. uncata*, and *P. tesquorum*) between these habitats. The high proportional similarity ($PS = 82.4$) between the leaf litter and grass-litter habitats is largely the result of a high degree of habitat selectively displayed by *P. uncata* for these habitats.

As expected, the highest correlations between air temperature, incident solar radiation and mean abundance (species pooled) were for the more open-canopied rock-cobble and sand-cobble habitats (Table 5), with the lower correlations noted for the closed-canopied grass-litter and leaf litter habitats. The small coefficient of correlation between spider abundance and prey abundance in the rock-cobble can be explained by the drop in spider activity after a midsummer peak in activity (Fig. 1), and a continued high number of arthropod prey in pitfall collections through September. The extremely small coefficient of correlation ($r = 0.01$) between prey and spider abundance in the leaf litter habitat could be attributed to low arthropod diversity (at least those defined as available prey) in a habitat with little or no understory production. Bultman et al. (1982) studied spider assemblages along a successional gradient, and found that spider species diversity decreased in a mature beech-maple forest, presumably with minimal understory.

The species diversity of wandering spiders was found to be proportional to an increase in litter depth along a successional gradient (Huhta 1965). In a similar study, both the total abundance of

spiders and spider species diversity increased in the deep leaf litter of a mature forest (Uetz 1979). The low positive correlation between spider abundance and prey abundance in the leaf litter habitat may be an indication that pitfall trapping is not the best means for measuring spider density in a habitat with a vertical dimension provided by leaf litter. This vertical habitat dimension may account for less lateral movement by wolf spiders, and thus a reduction in pitfall rates of capture. Peck & Whitcomb (1978) suggested that pitfall trapping bias can be minimized by trapping over longer periods and pooling the results.

The early diurnal times of activity for *P. tristis* and *P. distincta* (Fig. 4) in the streamside habitats (rock-cobble and grass-willow) were probably a function of higher air temperatures, substrate temperatures, and light intensities much earlier in the day in these habitats. On several occasions, adult *P. tristis* were observed on the top surface of rocks at 0800 h, during midsummer, when air temperatures were as low as 3–5 °C. The negative correlation between overall activity and incident solar radiation is an indication of the extremely high light intensities (maximum of 8100 f.c.) and substrate (rock surface) temperatures (maximum of 35.4 °C) characteristic of the rock-cobble in mid-afternoon. Riechert & Tracy (1975) and Riechert (1976) have shown that spiders will avoid thermal stress by selecting more thermally favorable microenvironments in order to maximize feeding activity. Several personal observations suggest that individuals of *P. tristis* were thermoregulating by moving to the top surface of rocks in the morning and retreating to the underside of rocks in the afternoon. The more continual diurnal activity of *P. uncata* was predictable given this species association with the less physically extreme (Table 1) grass-litter and leaf litter habitats. *Pardosa distincta* was also active through the afternoon, which could be attributed to the availability of cover or retreats in the structurally more complex habitats of the grass-willow and grass-litter habitats. These retreats would allow the spiders to avoid light and temperature extremes in these open habitats at midday. Individuals of this species were often observed in large numbers on and in the vicinity of large ant colony mounds. Incident solar radiation was limiting to spider activity as it increased to high levels during the day in the more open habitats, and was probably limiting, with associated low air and substrate temperatures, in the more closed-canopied habitats until light intensity increased to optimal levels in the late morning and early afternoon (Fig. 5).

Results from the visual searches of habitats were consistent with monthly pitfall collections for the five dominant or most abundant guild members (*P. tristis*, *P. distincta*, *P. tesquorum*, *P. uncata*, and *A. aculeata*) indicating that these species were spatially segregating among habitats. In addition, the visual searches suggested that habitat type (substrate) selected and the time of diurnal activity best distinguished between the five dominant guild members (Table 8 and Fig. 6). In addition to studies focusing on interspecific differences, intraspecific variation in spatial and temporal partitioning of habitats by wandering spiders should receive more attention. Kronk & Riechert (1979) addressed intraspecific differences in habitat choice and diurnal time of activity of the wolf spider *Lycosa santrita* Chamberlin & Ivie in a desert riparian habitat. They found that penultimate and adult males of this species differed in preference for substrate types (i. e., bare ground, leaf litter, grass, or rock).

While causal evidence is lacking, results of this study suggest that among members of a small guild of cursorial wolf spiders with similar if not identical methods of hunting, species tend to segregate spatially among discrete riparian habitats and are diurnally active at different times of the day within their "preferred" habitats. Peak seasonal activity occurred during midsummer (July) for all guild species, with males more abundant in May and June collections and less frequent in samples from September and October. The midsummer peak of activity for all eight guild members is typical for temperate arthropod communities (Evans & Murdoch 1968; Root 1973). This measured increase in activity was in part a result of the abundance of males in collections during this period.

More information on the sympatric or syntopic associations of wandering spiders from pitfall trapping and analyses of microhabitat selection is needed (Lowrie 1973), particularly in undisturbed systems such as riparian zones that are subject to agricultural and recreational development along with other types of habitat alteration.

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LITERATURE CITED

Abraham, B. J. 1983. Spatial and temporal patterns in a sagebrush steppe spider community (Arachnida: Araneae). J. Arachnol., 2:31–50.

Brower, J. E. & J. H. Zar. 1984. Field and Laboratory Methods for General Ecology. Wm. C. Brown, Iowa.

Bultman, T. L., G. W. Uetz & A. R. Brady. 1982. A comparison of cursorial spiders along a successional gradient. J. Arachnol., 10:23–33.

Bultman, T. L. & G. W. Uetz. 1982. Abundance and community structure of forest floor spiders following litter manipulation. Oecologia, 55:34–41.

Coyle, F. A. 1981. Effects of clearcutting on the spider community of a southern Appalachian forest. J. Arachnol., 9:258–298.

Doane, J. F. & C. D. Dondale. 1979. Seasonal captures of spiders (Araneae) in wheat field and its grassy borders in central Saskatchewan. Canadian Ent., 111: 439–445.

Duffey, E. 1966. Spider ecology and habitat structure. Senckenb. Biol., 47:45–49.

Duffey, E. 1970. Habitat selection by spiders in salt-marsh in Gower. Nature in Wales, 12:15–23.

Evans, F. C. & W. W. Murdoch. 1968. Taxonomic composition, trophic structure, and seasonal occurrence in a grassland insect community. J. Anim. Ecol., 37:259–273.

Foelix, R. F. 1982. Biology of Spiders. Harvard University Press, Cambridge.

Greenstone, M. H. 1984. Determinants of web spider species diversity: vegetation structural diversity vs. prey availability. Oecologia, 62:299–304.

Hatley, C. L. & J. A. MacMahon. 1980. Spider community organization: seasonal variation and the role of vegetation architecture. Environ. Entomol., 9:632–639.

Huhta, V. 1965. Ecology of spiders in the soil and litter of Finnish forests. Ann. Zool. Fennici, 2:260–308.

Jennings, D. T. & J. B. Dimond. 1988. Arboreal spiders (Araneae) on balsam fir and spruces of east-central Maine. J. Arachnol., 16:223–235.

Jennings, D. T. & D. J. Hilburn. 1988. Spiders (Araneae) captured in Malaise traps in spruce-fir forests of west-central Maine. J. Arachnol., 16:85–94.

Jennings, D. T., M. W. Houseweart, C. D. Dondale, & J. A. Redner. 1988. Spiders (Araneae) associated with strip-clearcut and dense spruce-fir forests of Maine. J. Arachnol., 16:55–70.

Kronk, A. W. & S. E. Reichert. 1979. Parameters affecting the habitat choice of Lycosa santrita Chamberlin and Ivie. J. Arachnol., 7:155–166.

Lowrie, D. C. 1948. The ecological succession of spiders of the Chicago area dunes. Ecology, 29:334–351.

Lowrie, D. C. 1973. The microhabitats of western wolf spiders of the genus Pardosa. Ent. News, 84: 103–116.

Lowrie, D. C. 1985. Preliminary survey of wandering spiders of a mixed coniferous forest. J. Arachnol., 13:97–110.

Luczak, J. 1959. The community of spiders of the ground flora of pine forests. Ekol. Polska, 8:199–228.

Luczak, J. 1963. Differences in the structure of communities of web-building spiders in one type of environment (young pine forests). Ekol. Polska, A, 11: 159–221.

Ludwig, J. A. & J. F. Reynolds. 1988. Statistical Ecology: A Primer on Methods and Computing. John Wiley & Sons.

MacArthur, R. H. 1972. Geographical Ecology. Princeton University Press, Princeton.

Magurran, Anne E. 1988. Ecological Diversity and its Measurement. Princeton University Press, Princeton.

May, R. M. 1981. Patterns in multi-species communities. Pp. 197–227, In Theoretical Ecology: Principles and Applications. (R. M. May, ed.). Blackwell Scientific Publications, Boston.

Moulder, B. C. & D. E. Reichle. 1972. Significance of spider predation in energy dynamics of forest-floor arthropod communities. Ecol. Monogr., 42: 473–498.

Muma, M. H. & K. E. Muma. 1949. Studies on a population of prairie spiders. Ecology, 30:485–503.

Pianka, E. 1969. Habitat specificity, speciation and species density in Australian desert lizards. Ecology, 50:498–502.

Pianka, E. R. 1974. Niche overlap and diffuse competition. Proc. Nat. Acad. Sci., 71:2141–2145.

Pielou, E. C. 1966. The measurement of diversity in different types of biological collections. J. Theoret. Biol., 13:131–144.

Riechert, S. E. 1974. Thoughts on the ecological significance of spiders. Bioscience, 24:352–356.

Riechert, S. E. 1976. Web-site selection in a desert spider. Oikos, 27:311–315.

Riechert, S. E. & C. R. Tracy. 1975. Thermal balance and prey availability: basis for a model relating web-site characteristics to spider reproductive success. Ecology, 56:265–284.

Rivas, L. R. 1964. A reinterpretation of the concept "sympatric" and "allopatric" with the proposal of additional terms "syntopic" and "allotopic". Systematic Zool., 13:42–43.

Root, R. B. 1973. Organization of a plant-arthropod association in simple and diverse habitats: the fauna

of collards (*Brassica oleracea*). Ecol. Monogr., 43: 95–124.

Roth, V. D. 1985. Spider Genera of North America. American Arachnol. Soc.

Rypstra, A. L. 1986. Web spiders in temperate and tropical forests: relative abundance and environmental correlates. American Midl. Nat., 115:42–51.

Schoener, T. W. 1971. Theory of feeding strategies. Ann. Rev. Ecol. Syst., 2:369–404.

Sokal, R. R. & F. J. Rohlf. 1981. Biometry (2nd ed.). W. H. Freeman & Co., San Francisco.

Southwood, T. R. E. 1978. Ecological Methods. Chapman & Hall, London.

SPSS Inc. 1985. SPSS, Advanced Statistics Guide. McGraw-Hill Book Co., New York.

Sugihara, G. 1980. Minimal community structure: an explanation of species abundance patterns. American Nat., 116:770–787.

Turnbull, A. L. 1973. Ecology of the true spiders. Ann. Rev. Entomol., 18:305–348.

Uetz, G. W. & J. D. Unzicker. 1976. Pitfall trapping in ecological studies of wandering spiders. J. Arachnol., 3:101–111.

Uetz, G. W. 1975. Temporal and spatial variation in species diversity of wandering spiders (Araneae) in deciduous forest litter. Environ. Entomol., 4:719–724.

Uetz, G. W. 1977. Coexistence in a guild of wandering spiders. J. Anim. Ecol., 46:531–542.

Uetz, G. W. 1979. The influence of variation in litter habitats on spider communities. Oecologia, 40:29–42.

Wolda, H. 1981. Similarity indices, sample size and diversity. Oecologia, 50:296–302.

Zar, J. H. 1984. Biostatistical Analysis (2nd ed.). Prentice-Hall, New Jersey.