

Abundance and Community Structure of Forest Floor Spiders Following Litter Manipulation

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Summary. We conducted a field manipulation of forest litter to determine effects of litter structure (flat vs curly leaves) on forest floor spiders in natural and artificial leaf litter. Artificial litter made of vinyl, was nondecomposable and non-nutritive. In this way, we separated interactions of effects of litter as a nutritional base and as a spatially heterogeneous environment on litter-dwelling spiders.

Structural complexity of litter significantly affected abundances of some forest floor spiders. In particular, abundances of web-building spiders were lower in treatments of flat leaves. Litter nutritional content and structural complexity only slightly affected spider species composition and richness. Results suggest that litter depth is more influential than are litter structural complexity or nutritional content, in organizing forest floor spider communities.

Introduction

Arthropods of detrital food webs in forest leaf litter provide many opportunities for investigations in community ecology because of their small size, abundance and importance in nutrient cycling and energy flow of forest ecosystems. One group of litter-dwelling arthropods, the spiders, annually consume 43.8% of the arthropod biomass in Tennessee deciduous forests (Moulder and Reichle 1972). Spiders are important members of the detrital food web and are a stabilizing predatory influence on invertebrate communities (Riechert 1974). Therefore, understanding the ecology of spider communities may significantly enhance our understanding of energy and nutrient dynamics in forest ecosystems.

Faunas of ground-dwelling spiders differ between habitats (Luczak 1963; Duffey 1966; Bultman et al. 1982) and their diversity increases with increased litter depth and complexity (Lowrie 1948; Berry 1967; Huhta 1971; Jocqué 1973; Uetz 1975, 1976). Two problems accompany these comparative studies: first, correlations allow only inferences about the causal mechanisms operating and second, increases in litter structural complexity (flat vs curly leaves) were accompanied by increases in litter depth. This second difficulty results because most forests with thick litter layers

tend also to have structurally complex litter and vice versa. In a field manipulation of litter depth, Uetz (1979) found significant changes in spider guild composition and increases in species richness with increased litter depth. Changes in spider community structure reported by Uetz however, may result from factors concomitant with augmenting litter depth, such as a greater nutritional base or habitat space for detrital food web members or a combination of the two. A question yet unanswered by correlative or manipulative work is: what effect does litter structure have on forest floor spider abundance and community structure when effects of litter as a trophic base are controlled?

To answer this question, we conducted an experimental field study using natural and artificial leaves of varied structure and constant depth. The spider fauna inhabiting these artificial leaves of different structure (flat, natural and complex) was compared to that of natural leaves of similar structural configurations. By using artificial non-nutritive leaves as controls, we were able to separate the influences of litter structure and nutritional content on spider communities.

Methods and Study Site

Site Description

We chose the site of this study for its fairly homogeneous litter layer. Leaf litter, by its very nature, is variable in space and time. For a field manipulation of litter, a site with homogeneous litter is preferable. This allows a structural classification of litter within defined confidence limits and therefore allows construction of appropriate structural treatments. The site was a beech-maple forest located at YMCA Camp Kern near Morrow, Ohio, USA. It was a secondary forest dominated by large old beech trees (*Fagus grandiflora* Ehrh.). For a more complete description, see Bultman and Uetz (in review).

Litter Characterization

Structural configuration of leaves naturally occurring at the site were determined so that leaf treatments of varied structure could be assembled. On 6 April 1980 all leaves contained in ten 0.1 m² quadrats were collected and their structural configuration and species composition determined. The low variation in both taxonomic and structural

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Table 1. Mean taxonomic and structural composition of leaves on the forest floor of the study site, 6 April 1980. $N=10$ 0.1 m² quadrats

Species	Percent composition	Coefficient of variation
Species		
Beech	98	0.02
Other	2	1.23
Structure		
Falt	32	0.22
Bent	52	0.06
Twisted	6	0.81
Curled	10	0.83

classes (see C.V.'s in Table 1) indicates the high uniformity of the leaf litter in this forest. Natural litter depth was $4.4 \text{ cm} \pm 0.21$ ($\bar{x} \pm \text{C.V.}$).

Experimental Design and Sampling

Leaf treatments whose composition was structurally less complex (78% flat; 22% bent), equally complex (32% flat; 52% bent; 6% twisted; 10% curled) or more complex (50% twisted; 50% curled) than those at the study site were assembled for both natural and artificial non-nutritive leaves. Artificial leaves were constructed of vinyl plastic of 0.254 mm thickness. Environmental conditions within artificial litter did not differ from those within natural leaves (Bultman and Uetz, in review). Odors from plastics may affect (attract or repel) litter-dwelling arthropods; the particular vinyl used was chosen for its lack of odor. Laboratory reared spiders were neither repelled by nor attracted to it (T. Bultman, personal obs.). Leaf treatments were housed in 2.54 cm mesh chicken-wire baskets whose area was 0.1 m² and whose sides were equal to the study site mean litter depth. The 6 treatments were replicated 24 times and placed on the forest floor 15 May 1980 using a randomized block design. Spiders colonizing baskets were removed monthly for 4 months with the exception that sampling did not occur within 36 h after a rain. Allowance for this drying period was necessary because the spider fauna is noticeably inactive following a rain. Sampling was accomplished by sieving spiders from litter. Bultman and Uetz (in review) give a more detailed account of sampling techniques.

Statistical Techniques

This study was designed specifically for statistical testing by analysis of variance (ANOVA). Probability level of significance attached to statistical tests throughout was $P < 0.05$. To insure that our sampling techniques adequately sampled spiders in the forest litter, we constructed species-samples effort curves. Because these curves appeared to reach an asymptote after sampling 24 replicate baskets per treatment per date (i.e., Fig. 1) we concluded our sampling methods adequately sampled the spider fauna.

Spider species diversity and its two components of diversity were calculated for the 6 treatment types. The two components of species diversity are species richness (s) and even-

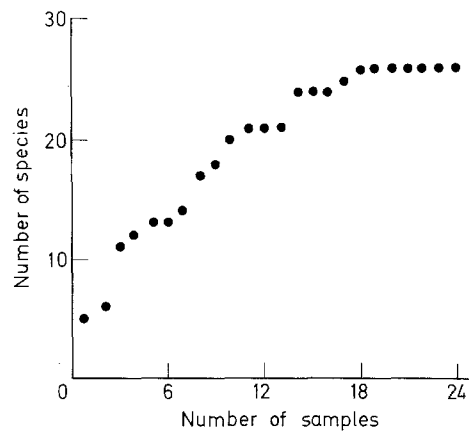


Fig. 1. Species-area curve for spiders collected in July, 1980 from structurally complex - natural litter

ness (J). The Shannon (1948) index of diversity takes the form:

$$H' = - \sum_{i=1}^s p_i \log_2 p_i$$

where P_i is the proportion of total individuals in species i , and s is the number of species. An estimate of evenness is J (where $J = H'_{\text{obs}}/H'_{\text{max}}$) (Pielou 1966). For calculations of diversity, data were standardized to account for missing data of disturbed baskets using the formula: $S_i = N_i (T/T - D)$, where S_i is the number of individuals of species i after standardization, N_i equals the number of individuals of species i , D is the number of disturbed baskets and T equals the total number of baskets (24). This standardization was done for all treatments.

To further assess differences between treatments in spider community structure we calculated from standardized data after log transformation [$\log_{10}(X+1)$] (Clifford and Stephenson 1975) percent similarity values using the formula:

$$PS = 1 - 0.5 \sum |P_a - P_b|$$

where P_a is the proportion of a given species in treatment A and P_b is the proportion of a given species in treatment B (Whittaker 1975).

We also analyzed guild compositional changes between treatment types. We assigned spiders to guilds (Root 1967) which are functional groups based, in the case of spiders, on foraging method. Spider guild systems may reflect, depending upon information available on foraging method, gross (Balogh and Loksa 1948) or slight (Post and Riechert 1977; Rovner 1980) differences in spider foraging behavior. A gross feature of spider foraging is the use or lack of use of webs in prey capture. A simple dichotomous system based on web use distinguishes the 'macro-guilds' web-building and hunting spiders. Within this we also recognized five spider guilds, members of which comprised >90% of all spiders collected. Members of the wolf spider guild are 'sit and wait' type predators which frequently change sites (Ford 1977). A second guild, the running spiders, are active, pursuing predators (Gertsch 1979). Members of the three remaining guilds build webs: the scattered line, sheet web and vagrant web-building spiders.

Results and Discussion

Abundances of Spiders

In each month but June web-building spiders were significantly more abundant in artificial litter than in natural litter (Table 2 and Fig. 2). A dominant web-builder, *Neoantistea magna* (see Appendix) commonly made webs in artificial

Table 2. F ratios of 2-way analysis of variance on abundance of web-building and hunting spiders

Month	Source of variation	Web-builders F value	Hunters F value
June	Structure	0.22	0.22
	Artificial	3.79*	8.21*
	Structure* artificial	0.17	3.60*
July	Structure	8.77*	3.17*
	Artificial	29.47*	0.34
	Structure* artificial	4.99*	0.08
Aug	Structure	5.29*	1.59
	Artificial	34.23*	6.22*
	Structure* artificial	1.92	0.80
Sept	Structure	0.25	2.63
	Artificial	30.40*	2.68
	Structure* artificial	0.77	1.20

* $P < 0.05$

leaves (T. Bultman, personal obs.). Artificial leaves were more rigid than natural leaves and they may have provided superior sites for web attachment. If this is true, significant effects of litter type (natural/artificial) for web-building spiders (Table 2) are misleading; web-builders sought architectural, not nutritional, qualities of artificial leaves.

Unlike web-builders, hunting spiders were significantly more abundant in natural litter in June and August (Table 2 and Fig. 2). There are several possible reasons for this. Because there were more web-building spiders in artificial leaves, presence of greater amounts of silk webs may have deterred hunting spiders from these leaves. Also, greater abundances of potential prey (Collembola and/or Diptera) in natural leaves may suggest hunting spiders were aggregating in areas of high prey density (Bultman 1981).

Web-building spiders occurred in significantly greater abundance in treatments of greater structural complexity in July and August (Fig. 2 and Table 2). Others have obtained similar results with shrub layer spiders by providing frames meeting structural requirements of web-building species (Colebourne 1974; Schaefer 1978; Robinson 1981). An explanation for why structure does not effect web-building spider abundances in June and September is that environmental parameters influencing spider populations may change seasonally (Bultman and Uetz, in review). Uetz (1979) previously suggested structure is of major importance to litter-dwelling spiders during mid-summer while environmental parameters such as prey abundance, temperature and humidity conditions, are more important in early

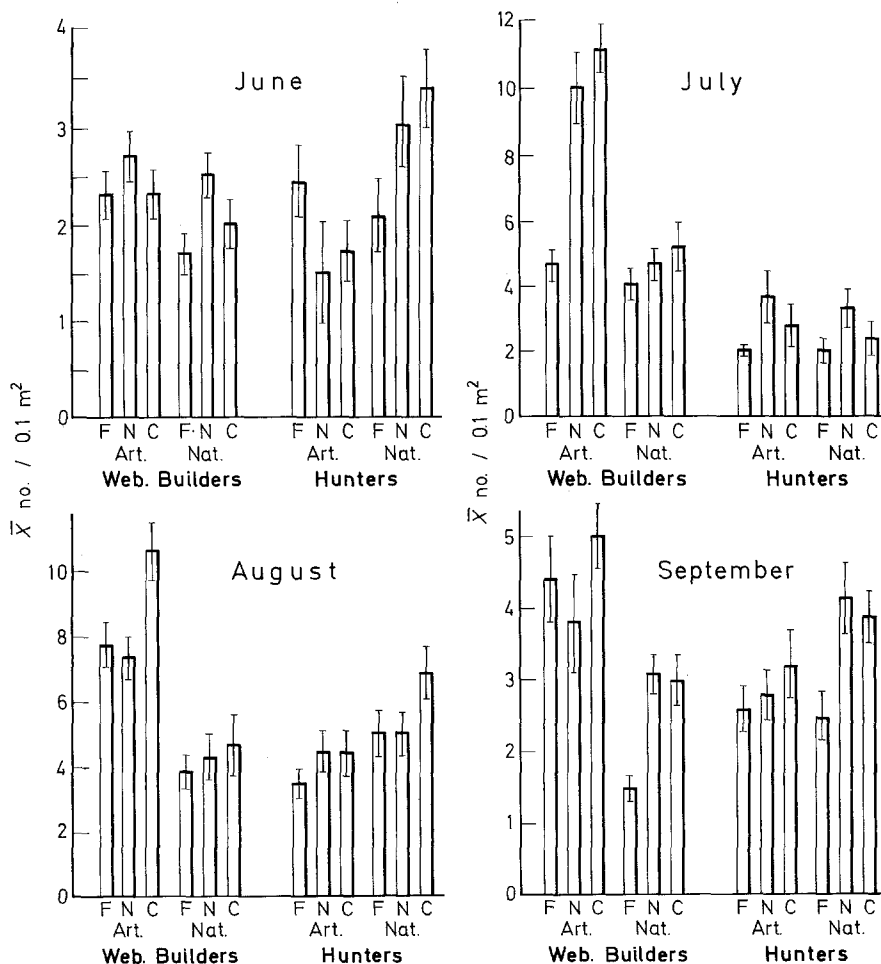


Fig. 2. Mean number of web-building and hunting spiders collected per sample. Bars represent 1 standard error of the mean. F, N, and C represent falt, natural and complex leaf structures respectively. Art. and Nat. represent artificial and natural leaves, respectively

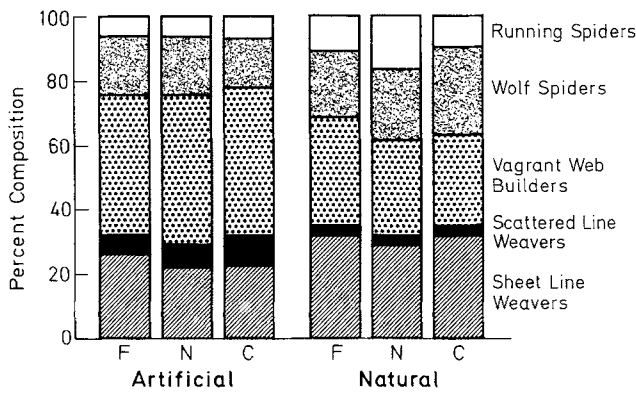


Fig. 3. Relative abundance of dominant spider guilds per treatment type, using notation in Fig. 2

and late summer. Also, most litter spiders show mid-summer peaks in population density. If these spiders respond to litter complexity we expect their responses to be most pronounced during periods of high density, when space may become limiting.

Hunting spiders may also respond to litter complexity, but previous work has not separated effects of litter structure, depth and nutritional content (Duffey 1975; Uetz 1979; Bultman et al. 1982). Results presented here give little support to this contention. Structure is a significant effect only for July (Table 2). More striking are higher abundances of these animals in natural litter (Fig. 2).

In conclusion, as initially anticipated, we found a positive relationship between litter structural complexity and web-building spider abundances during mid-summer. Unlike web-builders, hunting spiders showed no clear response to litter structural complexity. This lack of response by hunting spiders may be real, but hunting spiders are far more mobile than web-builders (Gertsch 1979) and our treatment basket size (0.10 m²) may be too small to detect patterns of hunting spider abundance with litter complexity.

Community Structure

Guild composition (Fig. 3) was independent of structural treatments within and between artificial and natural litter types (G-test, Sokal and Rohlf 1969). Dissimilar spider communities occur in habitats with different litter depth and complexity (Gibson 1947; Lowrie 1948; Dowdy 1950; Berry 1967; Huhta 1971; Penniman 1975; Bultman et al. 1982). If these changes in community structure are primarily caused by alterations in litter complexity and not litter depth or nutritional content, then we would expect similar changes in community structure between our structural types (flat, natural and complex) for both natural and artificial treatments. Our results suggest litter depth influences spider guild composition more than do litter structural complexity or nutritional content.

Spider species richness is also not strongly affected by litter complexity or nutritional content. Species richness depends upon litter complexity only in August and differs between nutritional types only in June (Duncan's multiple range test, Table 3). In light of our results, demonstration of increased spider species richness with increased litter depth (where depth and complexity were not separated) by correlative (Lowrie 1948; Berry 1967; Huhta 1971; Uetz

Table 3. Duncan's multiple range test for mean values of spider species richness. Notation as in Fig. 2

	Structural type			Nutritional type	
	F	N	C	Art.	Nat.
June*	4.043	3.857	4.630	3.735	4.642
July	4.957	5.830	6.043	5.814	5.400
Aug**	6.500	6.795	7.844	7.077	7.000
Sept	5.348	5.553	6.136	5.986	5.353

* Significant differences in species richness between artificial/natural treatments only in June ($F_{1,129} = 6.36, P < 0.05$)

** Only in August were significant differences found in species richness between structural treatment types (flat vs curly, $F_{2,131} = 3.44, P < 0.05$)

1975) and experimental (Uetz 1979) research, suggests that litter depth, as habitat space, influences species richness more than litter structural complexity. Litter spatial heterogeneity appears a more important determinant of species richness in web-building than in hunting spiders but its effect is still minimal. The significant effect of litter structure on species richness during August is due to increases in species richness of sheet line weaving spiders ($F_{2,131} = 7.03, P < 0.001$). Species richness of hunting guilds (wolf and running spiders) is not significantly affected by litter structure.

As litter depth increases, its vertical layers (in differing stages of decomposition) become more distinct (Anderson 1975, 1978). Vertical partitioning of deep litter may be a means by which spider species richness changes with litter depth. Workers have demonstrated a positive relationship between vegetational layering or patchiness and species diversity of birds (MacArthur and MacArthur 1961; MacArthur et al. 1966; Recher 1969; Karr and Roth 1971; Willson 1974; Roth 1976), lizards (Pianka 1967), old field insects (Murdoch et al. 1972) rodents (Rosenzweig and Winakur 1969; M'Closkey 1976; Dueser and Brown 1980) and fish (Gorman and Karr 1978). This relationship is a general one for many animal taxa. As novel layers or patch types are added to a habitat, pronounced increases in animal species diversity usually occur. Increases in habitat structural complexity within vegetational layers may increase faunal diversity slightly (Karr 1971) but major changes in diversity usually occur with increases in between-habitat variation. If litter-dwelling spiders can respond to fine-scale vertical variation in litter structure (Anderson 1975, 1978) then we expect increases in species richness with increased litter depth.

Alternatively, changes in litter depth may affect spider species richness not because of increased layering but rather because of increased litter volume. Increased volume may lead to increased population sizes and therefore lowered extinction rates (MacArthur and Wilson 1967). Under this hypothesis, major changes in species richness would not be expected in the present study (and indeed we did not find them) because litter depth and therefore volume was held constant while structural heterogeneity was manipulated.

Community matrix analysis (Table 4) mirrors results of guild compositional analysis; that is, as with guild structure, we found little differences between all six treatment types

Table 4. Community matrix based on percent similarity of spider species. A and N refer to artificial and natural treatments respectively, while f, n, and c refer to flat, natural and complex structural treatments

	Af	Nf	An	Nn	Ac	Nc
Af	–					
Nf	0.723	–				
An	0.738	0.716	–			
Nn	0.734	0.735	0.759	–		
Ac	0.738	0.709	0.793	0.738	–	
Nc	0.708	0.744	0.725	0.771	0.715	–

Table 5. Araneae species diversity (H') and evenness (J) for treatment types. Notation as in Fig. 1

		Treatments					
		Artificial			Natural		
		F	N	C	F	N	C
June	H'	3.377	3.429	3.724	4.022	3.650	4.221
	J	0.482	0.505	0.539	0.594	0.513	0.572
July	H'	2.933	2.802	2.947	3.999	3.388	3.325
	J	0.385	0.331	0.341	0.447	0.424	0.417
Aug	H'	3.405	3.307	3.271	3.852	3.573	3.615
	J	0.413	0.390	0.376	0.485	0.451	0.433
Sept	H'	3.596	3.662	3.894	3.720	3.921	3.902
	J	0.462	0.477	0.498	0.511	0.506	0.512

at the species level (see Appendix for species list). All similarity values are $>70\%$. Matrices of individual sampling months also showed no differences between treatment types. This supports our previous contention that litter structural heterogeneity weakly affects spider community organization.

Spider species diversity (H') shows no trend with structural complexity within natural and artificial treatments (Table 5). Mean species diversity from natural leaves (3.76) however, is considerably higher than that from artificial leaves (3.36). Differences in diversity between natural and artificial treatments are significantly different (Mann-Whitney U test, $P < 0.05$). As with species diversity, evenness is also significantly higher in natural than in artificial treatments. There is no difference however, between spider species richness in natural and artificial litter.

Species diversity in artificial leaves was less than in natu-

ral leaves because dominant species became more abundant in artificial litter (see Appendix), and therefore evenness and total diversity declined. Dominant species in both artificial and natural litter were primarily web-builders. We feel differences in diversity between the two leaf types (natural/artificial) are a result of greater rigidity or the artificial material as compared to natural leaves and are unrelated to differences in nutritional content between leaf types.

Conclusions

Influence of the litter habitat on spider communities is clearly complex, involving a concert of potentially interacting variables. Litter-dwelling spiders are influenced by variation in litter habitats (Uetz 1979). Variation in litter depth influences several variables: litter complexity, prey abundance, temperature and humidity. Probable pathways between important variables associated with litter depth are diagrammed in Fig. 4.

In the present study, roles of litter as a structurally heterogeneous habitat and as a trophic base were decoupled from each other through field experiments controlling litter complexity and nutritional content. Litter complexity significantly affects abundances of web-building but not hunting spiders (Table 2); this may be related to the former group's need for web-attachment sites. Unlike abundance, community structure of litter-dwelling spiders is only slightly affected by the complexity and nutritional content of litter. In light of previous work, it appears that depth of litter, rather than its leaf heterogeneity or nutritional content more strongly affects community parameters of species diversity and composition. In reference to Fig. 4, we feel pathway 'A' is more important than pathways 'B' or 'C' in determining parameters of spider community organization. The means by which this occurs may be through vertical layering of litter or by the contribution of depth to total litter volume, and its influence on population sizes and extinction rates.

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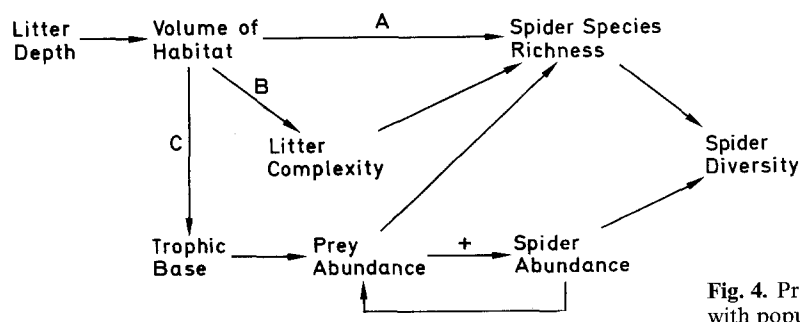


Fig. 4. Probable interaction pathways of several litter parameters with populations of spiders and their prey

Appendix

Species list	Number per treatment type ¹					
	Af	Nf	An	Nn	Ac	Nc
Hackled band weavers						
Dictyniidae						
<i>Dictyna muraria</i> Emerton	1	4	2	3	4	3
Amaurobiidae						
<i>Callobius sp.</i>	5	1	2		1	
Sheet line weavers						
Linyphiidae						
<i>Bathypantes pallida</i> (Banks)	3	1		1	5	2
<i>Centromerus cornupalpis</i> (O. P.-Cambridge)	30	17	23	43	19	23
<i>C. latidens</i> (Emerton)	2	2	3	2	3	1
<i>Ceraticelus fissiceps</i> (O. P.-Cambridge)	4	2	2		2	1
<i>Ceratinopsis atolma</i> Chamberlin			2	1	1	1
<i>Corniculari sp.</i>		1			2	
<i>Eperigone maculata</i> Emerton	12	6	8	13	18	8
<i>E. tridenta</i> Emerton					1	
<i>Erigone autumnalis</i> Emerton	1					
<i>Helophora insignis</i> (Blackwall)	50	75	36	72	40	71
<i>Islandia sp.</i>	1					1
<i>Lepthyphantes zebra</i> (Emerton)	33	13	39	14	36	24
<i>Meioneta unimaculata</i> (Banks)			1	2		2
<i>Microneta viaria</i> (Blackwall)	39	42	39	27	56	82
<i>Neriene variabilis</i> (Banks)	14	16	17	18	36	25
<i>Prolinyphia marginata</i> (C.L. Koch)		3	2	3	3	4
AAA			2	1		1
BBB	2	2	2	2	2	1
CCC		1				
DDD					1	1
EEE				1		
FFF	19	24	42	46	44	43
Scattered line weavers						
Mysmenidae						
<i>Mysmena guttata</i> (Banks)	14	11	24	3	17	5
Theridiidae						
<i>Euryopis limbata</i> (Walckenaer)		1		1	1	
<i>Pholcomma hirsutum</i> Emerton	3	2	1	2	6	2
<i>Steatoda albomaculata</i> (DeGeer)	15	8	21	18	35	20
<i>Theridion frondeum</i> Hentz	16	8	29	7	46	5
AAA			1	1	1	
BBB				1		
CCC			1	1	1	1
Vagrant web builders						
Hahniidae						
<i>Hahnia flaviceps</i> Emerton		7		6	2	6
<i>Neoantistea magna</i> (Keyserling)	340	168	439	213	488	234
Agelenidae						
<i>Agelenopsis pennsylvanica</i> (C.L. Koch)	8	10	8	8	17	6
<i>Circurina robusta</i> Simon	2	8	7	8	1	14
<i>Wadotes calcaratus</i> (Keyserling)	19	22	13	23	16	27
<i>Tegenaria sp.</i>	1					
Wolf Spiders						
Pisauridae						
<i>Dolomedes sp.</i>		1				
<i>Pisaurina mira</i> (Walckenaer)	9	6	5	7	5	3
<i>P. brevipes</i> (Emerton)				1		
Lycosidae						
<i>Lycosa helluo</i> Walckenaer	1				2	
<i>Pirata minutus</i> Emerton	103	97	136	118	119	116
<i>Schizocosa ocreata</i> (Hentz)	34	42	41	61	49	50

¹ Notation as in Table 4

Species list (continued)

Species list	Number per treatment type ¹					
	Af	Nf	An	Nn	Ac	Nc
Running spiders						
Gnaphosidae						
<i>Drassyllus virginianus</i> Chamberlin	2	1	1		2	8
<i>Litopyllus temporarius</i> Chamberlin	2	6	4	2	2	5
Clubionidae						
<i>Castianeira cingulata</i> (C.L. Koch)	10	5	8	13	7	9
<i>Clubiona</i> sp.		1	4	2	5	3
<i>Phrurotimpus alarius</i> (Hentz)	25	47	23	81	23	88
<i>P. borealis</i> (Emerton)	5	11	7	13	10	19
Anyphaenidae						
<i>Anyphaena celer</i> (Hentz)	8	2	12	13	14	7
Philodromidae						
<i>Philodromus marxi</i> Keyserling	3		1	2	1	
Crab spiders						
Thomisidae						
<i>Xysticus fraternus</i> Banks	10	27	22	24	5	34
<i>X. ferox</i> (Hentz)	4	4				4
<i>Tamarus angulatus</i> (Walckenaer)			1			3
Jumping spiders						
Salticidae						
<i>Eris marginata</i> (Walckenaer)	3	1	6	4	10	1
<i>Marpissa lineata</i> (C.L. Koch)	1	2				3
<i>Zygoballus bettini</i> G. & E. Peckham	1	1	3	2	2	

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