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A COMPARISON OF CURSORIAL SPIDER COMMUNITIES ALONG A SUCCESSIONAL GRADIENT

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ABSTRACT

Wandering spiders from three communities representing points on a successional gradient (old field, oak and beech-maple forests) were sampled with pitfall traps and compared at the levels of species, family and guild. There was little similarity (species overlap) between communities. Species diversity was highest in the sub-climax forest and considerably lower in the mature beech-maple forest. This successional trend in species diversity is discussed in light of current hypotheses. Analysis of guild composition showed that, with succession, the relative abundance of wolf spiders decreased while that of vagrant web builders and crab spiders increased. Of the seven families sampled, only members of the Clubionidae occurred in fairly sizeable proportions in each community. Structure of the litter is discussed as a factor influencing cursorial spider abundance and distribution.

INTRODUCTION

There has been a sizeable amount of data of a descriptive nature collected on spider communities. Studies have revealed that specific plant associations harbor distinct spider faunas (Almquist 1973a, Chew 1961, Drew 1967, Duffey 1962, Elliot 1930, Kajak 1960, Muma 1973). Comparative studies have shown that spider community composition changes with vegetative succession. Changes in family and species composition with ecological succession have been reported by Gibson (1947), Dowdy (1950), Barnes (1953), Barnes and Barnes (1954) and Penniman (1975). Others (Berry 1967, Huhta 1971, Lowrie 1948) have also noted a general increase in species diversity through early and mid succession and a subsequent decrease in spider diversity in the climax community. This trend in diversity has been suggested for community development in general

(Margalef 1968, Odum 1969), and has been reported by workers studying organisms other than spiders, such as birds (Johnston and Odum 1956, Kricher 1973) and plants (Pielou 1966, Whittaker 1969, 1975).

Luczak (1959, 1963) and Duffey (1966, 1970) have suggested that physiognomy of plant communities is an important determinant of spider community composition, in that it influences microhabitats available to spiders. Others (Almquist 1970, 1973a, 1973b, Huhta 1971, Kuenzler 1958, Nørgaard 1951, Vogel 1972) have demonstrated the importance of microclimatic conditions in effecting observed spider distributions. Undoubtedly, these two factors are closely tied; one might expect changes in microclimate to accompany changes in plant structure. Therefore, changes in plant structure during succession should result in community compositional changes in resident spider faunas.

Guilds are ecological groupings of organisms which exploit a single or similar resources in a similar manner (Root 1967). Wandering, or cursorial spiders may be considered a "super-guild" or divided into several guilds depending upon their specific method of prey capture. Comparative studies of seral and climax communities which employ functional (rather than taxonomic) units of measure, such as guilds, may be useful because they deal with broad ecological roles common to most communities. This study examines the species composition, species diversity and guild structure of cursorial spiders in three communities along a successional gradient.

MATERIALS AND METHODS

Spiders were sampled from three isolated sites in western Michigan. An abandoned field (approximately 7 years old) located on the west side of Michigan State Route 40 near the City of Holland, contained the following dominant plants: *Solidago* spp. (golden rod), *Daucus carota* L. (Queen Anne's lace), *Carduus* spp. (thistle), *Vicia* spp. (vetch) and several sapling *Acer negundo* L. (boxelder). The site was rather heterogenous, and was bordered on the west by a small stream. Consequently there was an apparent gradient in humidity within the site. A second site, an edaphic sub-climax oak forest, was located 3 km NE of Fennville, near Allegan State Forest. It was characterized by *Quercus velutina* Lam. (black oak) and *Quercus alba* L. (white oak) in the canopy layer while *Vaccinium vacillans* Torr. (dryland blueberry) and *Viburnum acerifolium* L. (arrow-wood) were dominant shrubs. The herb layer was dominated by *Carex pensylvanica* Lam. (sedge) and *Pteridium aquilinum* (L.) Kuhn. (bracken fern). The third site was located in the Hope College Biological Field Station, 12 km SW of Holland. It was a beech-maple climax forest, the typical end point of Lake Michigan dune succession (Clements 1936, Cowles 1899, Olson 1958). Dominant trees within the canopy were *Fagus grandiflora* Ehrh. (beech), *Acer saccharum* Marsh (sugar maple), and to a lesser degree, *Prunus serotina* Ehrh. (black cherry) and *Quercus borealis* Michx. (northern red oak). *Viburnum* sp. was the dominant shrub while *Polygonatum biflorum* (Walt.) Eil. (true Solomon's seal) and *Mitchella repens* L. (Partridge-berry) dominated the herb layer.

Spider communities in these sites were sampled with pitfall traps. Polypropylene cup traps (15 cm dia.) were fitted within a metal sleeve which was placed in the ground flush with the soil surface. A preservative (ethylene glycol) was placed in the bottom of the traps to a depth of about 5 cm. To prevent the accumulation of rain and leaves, the traps were covered with a square wooden roof, raised 3 cm above the soil surface by four legs. Six pitfall traps were placed approximately 6 m apart along a transect within each study site. This appears to be the minimum number (of 15 cm dia. traps) necessary for accurate

sampling of cursorial spiders (see Uetz and Unzicker 1976). Traps were emptied weekly for 12 weeks from June to September 1977. Adult spiders were identified to species and, when possible, juveniles were separated and counted as morphospecies. These identifications were used in community comparisons at the guild, family and species levels.

The validity of pitfall trapping has been questioned because weather factors, differential species activity and trap placement all influence results (Greenslade 1964, Turnbull 1973, Southwood 1966). Proponents (Brey Meyer 1966, Gist and Crossley 1973) defend the method because it allows continuous sampling and is not limited to specific habitats. Recently it has been shown to be an adequate estimator of the number of species of cursorial spiders over a wide range of habitats (Uetz and Unzicker 1976). Although it does not give a true estimate of density, it does sample the number of cursorial spiders moving in an area for a given time (or the "active density" (Uetz 1977).)

Spider species diversity in each community was calculated using the total information content index of Shannon (1948). The Shannon index (H') has been used in previous studies dealing with pitfall trapping of cursorial spiders (Jocqué 1973, Uetz 1975, 1976, 1979, Uetz *et al.* 1979) and appears to be the best available index for pitfall samples (see Pielou 1966). It takes the form:

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

where p_i = proportion of total individuals in species i , and s = number of species. J' (H'/H'_{\max}), the estimate of the component of evenness, was also calculated. The Bray-Curtis similarity index,

$$\frac{\sum_{i=1} |N_{1i} - N_{2i}|}{\sum_{i=1} N_{1i} + N_{2i}}$$

where N_{1i} and N_{2i} are the numbers of the i^{th} species in communities 1 and 2, after log transformation of the data ($1n[X + 1]$) (see Clifford and Stephenson 1975), was calculated for spiders by community and by guild.

RESULTS

A total of 568 individuals was collected and included 41 species and 7 families of wandering spiders (Table 1). The old field samples contained the most individuals (243), representing 21 species and 5 families. Those from the oak forest contained 142 individuals and 21 species while the samples from the beech-maple forest contained 183 individuals and 11 species. Samples from each forest contained representatives from 5 different families.

Calculated species diversity and evenness indices increase slightly from the old field to the oak forest and then decrease in the beech-maple forest (Table 1). Each community, as a whole and by guilds, is quite dissimilar from the others as indicated by values of the Bray-Curtis similarity index (Table 2). However, the two forests are more similar to each

Table 1.—Abundance and diversity of wandering spiders over the successional gradient.

	Old Field	Oak	Beech-Maple
VAGRANT WEB BUILDERS			
Agelenidae			
<i>Cicurina brevis</i> (Emerton)		3	2
<i>C. pallida</i> Keyserling			1
<i>C. robusta</i> Simon		3	2
Hahniidae			
<i>Neoantistea magna</i> (Keyserling)			80
RUNNING SPIDERS			
Gnaphosidae			
<i>Drassyllus aprilius</i> (Banks)		2	
<i>D. depressus</i> (Emerton)	6		
<i>Herpyllus ecclesiasticus</i> Hentz		1	
<i>Litophyllus temporarius</i> Chamberlin		1	
<i>Sergiolus decoratus</i> Kaston	4		
<i>Zelotes hentzi</i> Barrows		1	
<i>Z. subterraneus</i> (C. L. Koch)	2	8	
Clubionidae			
<i>Agroeca</i> sp.		28	3
<i>Castianeira cingulata</i> (C. L. Koch)		15	3
<i>C. gertschi</i> Kaston	4		
<i>C. variata</i> Gertsch	5		
<i>Clubiona abbotii</i> (L. Koch)	17		
<i>C. johnsoni</i> Gertsch		1	
<i>Micaria elizabethae</i> Gertsch	2		
<i>M. pulicaria</i> (Sundevall)	13		
<i>Phrurotimpus alarius</i> (Hentz)		19	24
<i>P. borealis</i> (Emerton)		1	33
WOLF SPIDERS			
Lycosidae			
<i>Lycosa frondicola</i> Emerton		2	
<i>L. gulosa</i> Walckenaer		24	
<i>L. modesta</i> (Keyserling)		1	
<i>Pardosa modica</i> (Blackwall)	1		
<i>P. moesta</i> Banks	75		
<i>P. saxatilis</i> Emerton	29	9	
<i>Pirata minutus</i> Emerton	19		
<i>Schizocosa avida</i> Walckenaer	1		
<i>S. bilineata</i> (Emerton)	36		
<i>S. ocreata</i> (Hentz)		2	2
<i>S. crassipalpa</i> Roewer	4		
<i>S. saltatrix</i> (Hentz)		1	
<i>Trabea aurantiaca</i> (Emerton)	6		
<i>Trochosa terricola</i> Thorell	7		
CRAB SPIDERS			
Philodromidae			
<i>Thanatus striatus</i> C. L. Koch	2		

Table 1.—(Cont.)

	Old Field	Oak	Beech-Maple
Thomisidae			
<i>Ozyptila conspurcata</i> Thorell	4		
<i>Xysticus elegans</i> Keyserling		9	2
<i>X. ferox</i> (Hentz)	5	6	
<i>X. fraternus</i> Banks		5	31
<i>X. luctans</i> (C. L. Koch)	1		
N	243	142	183
S	21	21	11
H' (base 2)	3.380	3.575	2.306
J'	0.770	0.814	0.677

other than to the old field, and the oak forest is more similar to the old field than is the beech-maple forest.

Some differences between communities are apparent in the analysis of guild composition (Figure 1). The wolf spider guild declines sharply over the successional gradient. In addition, the vagrant web-building spiders are absent in the old field but dominate in the climax community. A steady increase in the relative abundance of crab spiders occurs over the successional sequence. In contrast, the running spiders show no distinct trends with succession. Family composition (Figure 2) tends to follow guild composition, but the sizable contributions of the Clubionidae and Hahniidae to the relative abundance of their guilds are apparent. Individuals of the Hahniidae were all of the species *Neoantistea magna* (Keyserling) (Table 1).

Dominance-diversity curves (Whittaker 1975) for the three communities graphically show differences in community structure (Figure 3). The curves for the old field and oak forest approach lognormal distributions. In contrast, community structure of the beech-maple forest yields a curve approaching a geometric series.

DISCUSSION

Each of the plant communities is distinct in its cursorial spider species composition (Table 1). In fact, no species overlap occurs between the old field and the climax forest (Table 2). These results are in accord with those of previous researchers, who have found disparate communities when sampling dissimilar habitats along a successional gradient (Berry 1967, Huhta 1971, Lowrie 1948). These workers have also suggested that spider communities may show a pre-climax peak in species diversity.

Odum (1969) proposed that the mechanism for a pre-climax peak in species diversity is the mixing of transitional species. In climax communities, diversity may decline somewhat because transitional species, which cannot adequately compete with better adapted climax species, are forced out. Similarity values (Table 2) give some evidence in support of this mechanism. The oak forest contains some species which are common to the old field and some which are common to the beech-maple (and hence, contains some transitional species). Consequently, the oak forest is more similar to the old field and the beech-maple forest than the old field is to the beech-maple forest. Cannon (1965),

Table 2.—Bray-Curtis similarity values (after log transformation) calculated for spider communities in the three study sites.

GUILDS	SITES		
	O-F/OAK	OAK/B-M	O-F/B-M
Vagrant Web Builders	.00	.44	.00
Running Spiders	.07	.47	.00
Wolf Spiders	.15	.22	.00
Crab Spiders	.32	.55	.00
Total	.14	.43	.00

studying forests and old fields in south central Ohio, has obtained similar results. A somewhat different mechanism has been put forth by Auclair and Goff (1971). In forests of the Great Lakes regions they found that some plant species within the climax community are competitively superior (i.e., the shade tolerant beech and sugar maple) and become dominant. As a consequence, species diversity may decline considerably in older climax forests. Loucks (1970), studying similar forests, proposed that considerable declines in diversity are prevented by periodic burning. These perturbations act to return the forest to an earlier sere in which diversity is higher.

The beech-maple forest exhibits a much lower value of cursorial spider species diversity than the other two communities (Table 1) despite a deep and well-developed litter layer. Species diversity of wandering spiders has been found to increase with increased litter depth in sub-climax oak-hickory and oak-tuliptree-maple forests (Uetz 1979) and over succession with increased litter depth (Huhta 1971). Our results fit this trend and

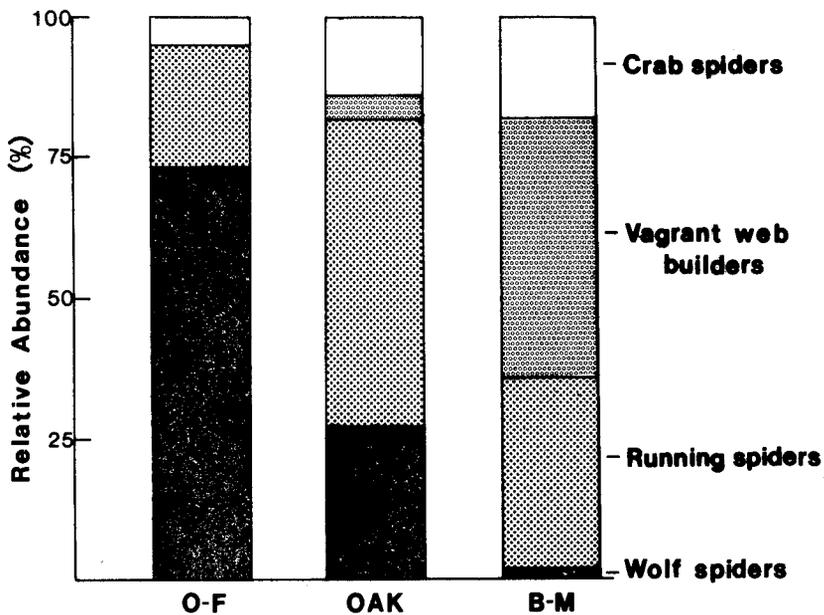


Fig. 1.—Guild composition of spider communities from the three study sites. O-F = Old Field and B-M = Beech-Maple.

suggest further that with extremely deep litter (i.e., like that of beech-maple forests) diversity declines. Dominance-diversity curves (Figure 3) graphically show the decrease in spider diversity (i.e., a steep slope) in the climax community. Similar results have been obtained in work on forest succession at Brookhaven, New York (Whittaker 1975). The dominance of the hahniid, *Neoantistea magna*, may be a major factor influencing the slope of the curve, in that it was the most abundant species trapped and occurred only in the beech-maple forest. The absence of fire in this preserve may explain the observed decline in spider diversity, although we have no historical data. In contrast, the high diversity of the old field may be explained in part from the fact that it has been undisturbed for at least 7 years and has a diversity of plant species and structures. Nicholson and Monk (1974) have found old fields on the Georgia piedmont to double in plant species richness within the first decade of succession.

Recently, spiders have been subdivided into increasingly finer guild systems (for example, see Post and Riechert 1977). Unfortunately, the present paucity of knowledge of foraging methods of some families of spiders makes the development of highly resolved guild systems difficult. The present system delineates four guilds, based upon gross differences in foraging behavior within the cursorial spider community. Members of the wolf spider guild are "sit and wait" type predators which change sites frequently (Ford 1977). Crab spiders, while also being "sit and wait" type predators, are differentiated because of morphological differences (the first two pairs of legs are laterigrade rather than prograde). Because the foraging methods of the Clubionidae and Gnaphosidae are not well known, they have been put into a separate guild, the running spiders. They appear to be active pursuing predators, according to Gertsch (1979). The vagrant web builders are represented by some members of the Agelenidae and Hahniidae (Uetz 1975), and while they

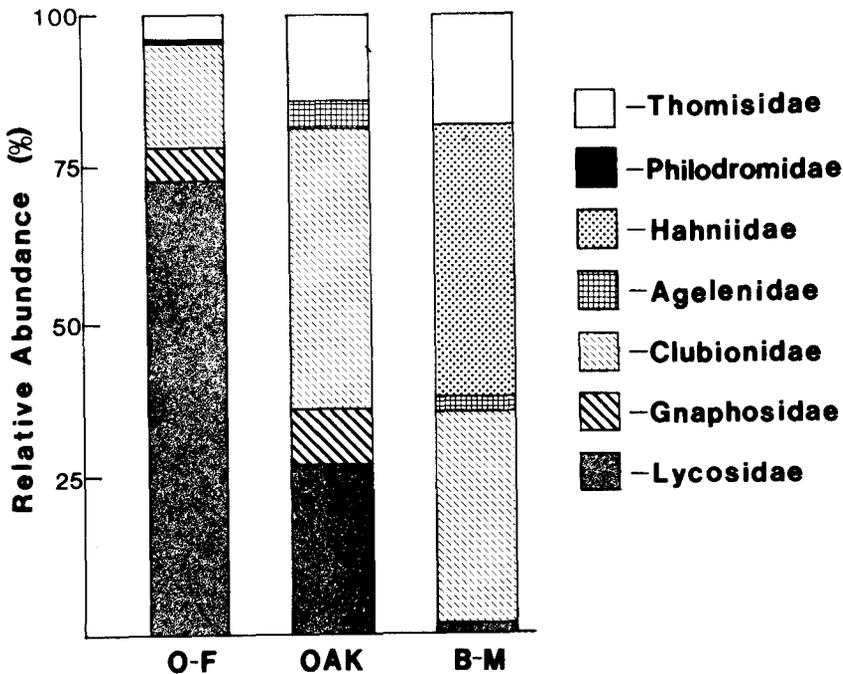


Fig. 2.—Family composition of spider communities from the three study sites.

are known to spin small webs, they also leave their webs and wander through and over the litter while foraging.

Guild composition in the three communities studied show some interesting trends (Figure 1). Members of the wolf spider guild dominate in the old field but then fall dramatically along the successional gradient. This scarcity of the wolf spider fauna in beech-maple forests has also been noted, although not to this degree, by Lowrie (1948). Members of the Lycosidae are typical field inhabitants and have been collected there in large numbers by several workers (Berry 1967, 1970, Doane and Dondale 1979, Peck 1966, Whitcomb *et al.* 1963). They seem best suited for locomotion in habitats where little litter accumulates. Uetz (1979) has found that augmenting natural litter depth results in a decrease in the relative dominance of wolf spiders while removal of litter increases their dominance. The development of a thick and intricate litter system during succession may prevent lycosids from dominating the cursorial spider community of climax forests.

Increases in the relative abundance of the crab spiders and vagrant web builders are also noticeable. These spiders live within the litter and have previously been found to increase in dominance with the addition of litter (Uetz 1979). Family compositional changes (Figure 2) show that differences in vagrant web builders are, for the most part, due to the occurrence of hahniids in the climax community. In fact, differences in the relative abundance of both guilds are primarily determined by single species (Table 1): *Neoantistea magna* and *Xysticus fraternus* Banks. *N. magna* was the most commonly collected species in a study of beech forest in central Ohio (Penniman 1975) and appears to be a dominant typical of the climax forest.

An increase in spider abundance has also been correlated with an increase in litter depth (Berry 1967, Hagstrum 1970, Lowrie 1948). Unfortunately no litter data are available from the study sites. However, it seems certain that the development and modification of the litter, which normally occurs with succession, is an important factor influencing the abundance of these spiders. Increased litter depth may enhance resource

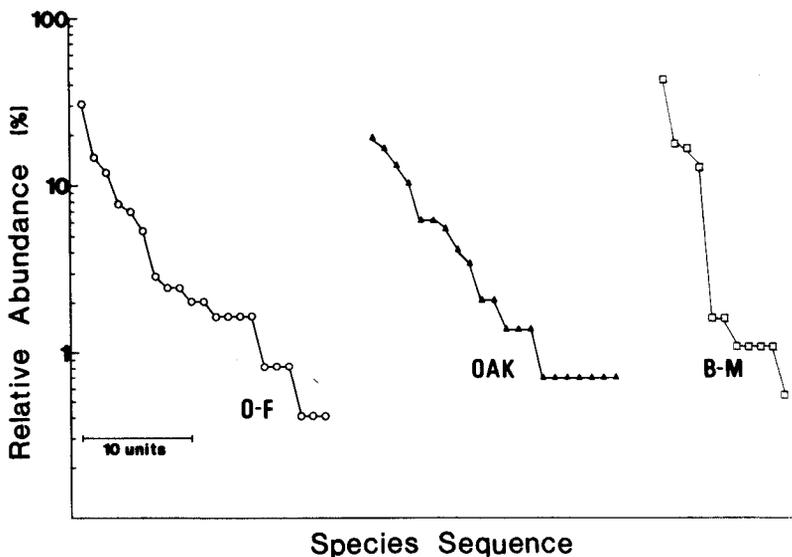


Fig. 3.—Dominance-diversity curves for spiders sampled from old field, oak and beech-maple communities.

partitioning by members of these guilds by increasing prey densities and/or microhabitat diversity, which may in turn allow a reduction of inter- and intraspecific competition and predation. While we have no quantitative litter data, this study does provide strong indirect evidence that cursorial spider abundance and distribution are closely correlated with litter development.

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