

Web placement, web structure, and prey capture in orb-weaving spiders*

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Summary

Studies of syntopic orb-weaving spiders in grassland and forest habitats suggest that placement and fine structure of webs play important roles in determining the prey characteristic of a species.

Differences in mesh size and habitat utilization may facilitate coexistence in congeneric *Argiope* species in Illinois prairies. The two species specialize on different sized prey, and also exploit taxonomically different prey resources. Habitat differences between these congeners may be related to the movement of different sized insects in vegetation.

Prey size of several spider species is correlated with the mesh size of their webs. Comparison of species in two forests shows that habitat utilization patterns diverge among congeners or within groups of species whose webs are similar in mesh size. Window-pane trap sampling shows different sizes and taxa of insects in different spaces in vegetation. Differences in microhabitat may allow species to exploit different prey resources and avoid competition.

Introduction

Orb-weaving spiders, found in the families Araneidae, Tetragnathidae, and Uloboridae, are well

known because of their intricately designed webs. The orb-web appears to function as a prey catching device in two ways: 1) as an aerial net, seining "planktonic" flying insects; and 2) as an extension of the perceptual field of the poor-sighted spiders, improving prey detection by transmitting vibrations. Kullmann (1972) has argued effectively that the orb-web is a case of evolutionary convergence, having arisen independently in both cribellate and ecribellate spiders as an efficient design for capturing flying insects with a minimum of silk and energy expended.

The orb-weaving spider families constitute a "guild", an ecological group denoting organisms which exploit the same or similar resources in a similar manner (Root, 1967). Orb-weaving spiders tend to be "sit-and-wait" predators (Schoener, 1971) changing location infrequently once established (Enders, 1975). Because of the dependence of predatory success on web location, pronounced habitat or microhabitat specificity might be expected. Vertical stratification of webs has been suggested as a mechanism allowing coexistence of congeneric species in this guild (Enders, 1974).

The results presented here are from current studies exploring the ecological significance of web placement and design. Habitat distribution and prey utilization of syntopic species in prairie and forest environments in Illinois, U.S.A., will be examined as they relate to coexistence within the orb-weaving guild. The studies are preliminary, but contain interesting and statistically significant results that hopefully merit presentation at this time.

Methods and study areas

The data presented here were collected in several contrasted habitats in East Central and Southern Illinois, U.S.A. Spiders of the genus *Argiope* were studied in a tallgrass prairie remnant on a railroad right-of-way near Mayview, Ill. The vegetation is heterogeneous, and is composed of a variety of prairie and old field species (*Andropogon gerardi* Vitm.; *A. scoparius* Michx.; *Sorghastrum nutans* (L.); *Spartina pectinata* Link.; *Silphium terebinthinaceum* Jacq.; *Aster pilosus* Willd.). The prairie area is mostly open, except in some areas where patches of willow (*Salix* sp.) and cattail (*Typha* sp.) provide limited shade. Soil ranges from wet to dry, depending on local drainage, and this influences vegetative composition.

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Orb-weaving spiders were also studied in two forested areas. Brownfield woods, located near Urbana in East-Central Illinois, is a 60-acre tract of mature forest on prairie soil. The area is dominated by oaks (*Quercus macrocarpa* Michx.; *Q. rubra* L.), sugar maple (*Acer saccharum* Marsh.), basswood (*Tilia americana* L.) and slippery elm (*Ulmus rubra* Muhl.). The canopy is mostly closed, resulting in reduced vegetative growth at ground level and widely spaced saplings and shrubs. Destruction of elms by Dutch elm disease has left openings in the canopy in some areas, resulting in a patchy distribution of light on the forest floor, and some patchiness in understorey vegetation. In general, the soil is moist, made so by a shallow drainage stream within the interior of the woodlot. An abundance of mosquitoes and other Diptera arise from these damp places, providing prey for orb-weaving spiders (and also making life miserable for arachnologists).

The second forest area was Dysert's woods, located on the Little Cache River in Southern Illinois near Vienna. The forest is fairly heterogeneous, and occupies a ravine with steep, deeply eroded sides of sandstone and limestone. Spiders were studied in the vegetation of the ravine forest itself, rather than the many habitats associated with rock faces, etc. Within the ravine, the vegetation was composed of white oak (*Quercus alba* L.), red oak (*Q. rubra* L.), beech (*Fagus grandifolia* L.), and hornbeam (*Carpinus caroliniana* Walt.). Patchy light distribution results in a heterogeneous understorey similar to Brownfield Woods. The major physical difference between the two forests is topography; the ravine forest is somewhat patchier in a horizontal sense. Despite differences in tree species composition, physical structure of the vegetation is similar.

Measurements of habitat parameters of spiders were made in the field with a metre stick. Height was measured as the distance from the ground to orb hub (where the spider sits). Length of the bridge thread (usually the uppermost frame thread) was recorded as the distance between supporting vegetation. Measurements of web fine structure (mesh size) were taken from webs in the field in the *Argiope* studies, or from web photographs in the forest studies. Photographs were taken in the field using 35mm high contrast black and white film, with strobe flash from the side or beneath the web, as suggested by J. W. Burgess

(pers. comm.). Photographs were printed natural size, and measured. The distance between sticky threads in the catching spiral, representing the mesh size, was measured to the nearest 1/10mm with dial calipers in both cases.

Prey insects were collected from spider webs, brought back to the laboratory, measured (body length) and identified to order. Independent estimates of abundance, size and composition of prey were made from field collections. In the Illinois prairie study, sweep-netting was used to collect potential spider prey. This method has inadequacies due to bias (Turnbull, 1973; Lowrie, 1971) but was the most practical method in this grassland study. In the Brownfield Woods study, potential prey were collected from different microhabitats by window-pane traps. The traps consisted of a 32 x 32 cm (1000cm²) plexiglass sheet, mounted vertically above a 30 x 24 x 5 cm aluminium pan containing soapy water. Three traps were mounted at different heights above the

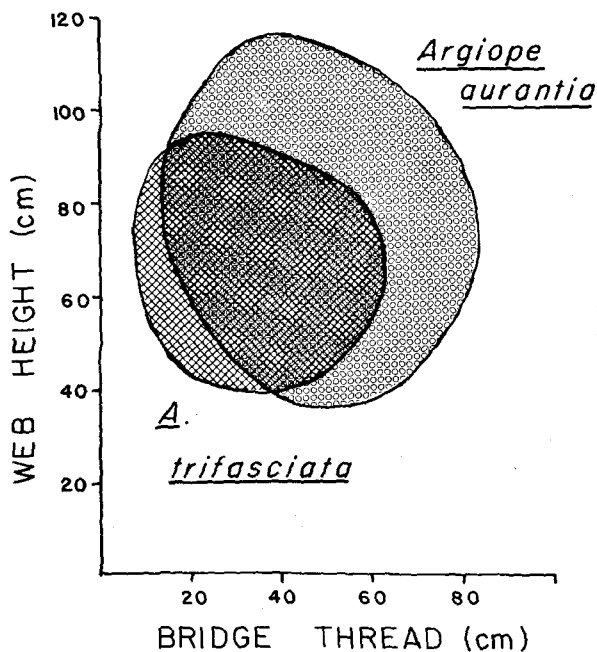


Fig. 1: Habitat utilization of *Argiope* spp. in an Illinois prairie. Shaded areas represent scatter diagrams of web/habitat measures for each species. Sample size: *A. aurantia*, $n = 121$; *A. trifasciata*, $n = 151$ (webs recorded).

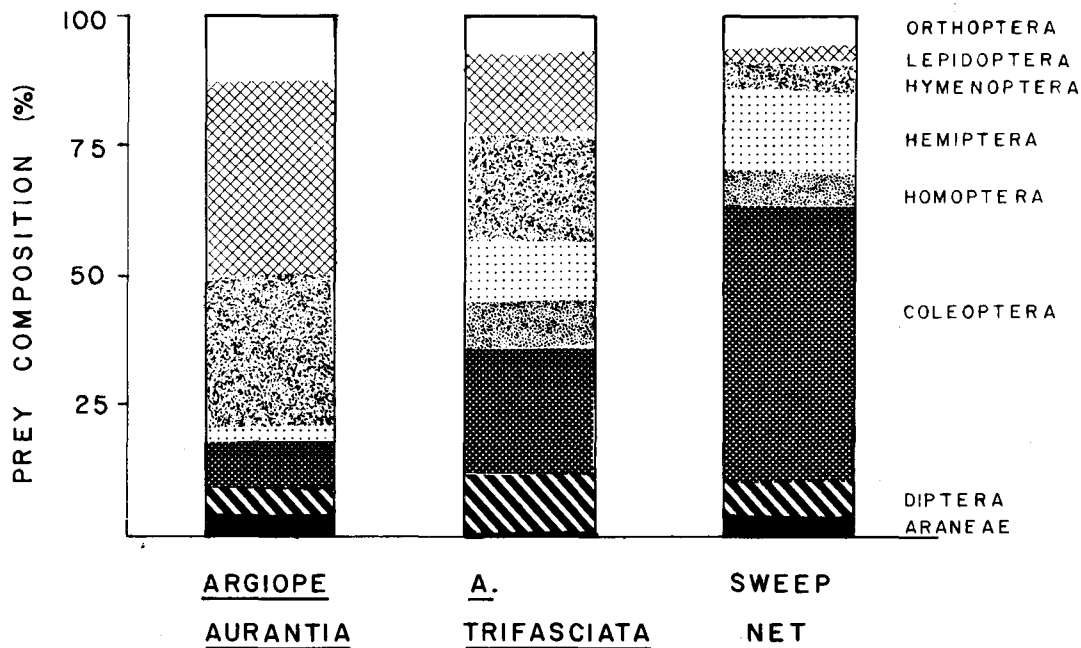


Fig. 2: Taxonomic composition (by orders) of the prey collected from webs of *Argiope aurantia* (n = 202) and *A. trifasciata* (n = 400) and of insects collected in the prairie habitat by sweep net (n = 1056).

end of the season (at adulthood) might make competition unimportant may not apply here. In general, adult female spiders increase their food uptake prior to egg-laying. If prey were a limiting resource for populations of *Argiope*, the increased nutritional ground (0-60 cm; 60-140 cm; 140-200 cm) between two wooden stakes. Groups of three traps were placed in three densities of vegetation (low, medium and high), approximating microhabitats where spiders build webs. Window-pane traps also have their limitations in sampling potential prey of orb-weaving spiders (Robinson & Robinson, 1970, 1973), but are preferable in a forest setting to the sweep net technique. Prey collections from 24-hour, 48-hour and week-long trapping periods in August and September were analysed.

Results and Discussion

Coexistence in *Argiope* spiders

Argiope aurantia Lucas and *A. trifasciata* (Forskål) are two common orb-weavers found in grassland-type habitats (old fields, road margins, prairies, etc.) in North America. Co-occurrence of these species with

high overlap in habitats has been mentioned frequently in the literature (Fitch, 1963; Muma & Muma, 1949; Enders, 1974; Tolbert, 1976). Enders (1974) found that *A. aurantia* and *A. trifasciata* were vertically segregated during earlier instars, but not in adulthood. He concluded that as density was greatly reduced over the growing season, competition between species was not important in the adult stage. Enders hypothesized that differences in vertical stratification of webs during immature stages allowed coexistence of these otherwise similar congeners.

In our studies (Uetz & Schemske, in prep.), we found a high degree of habitat overlap in these two species during the adult stage (Fig. 1). The two species overlap greatly in vertical web placement, but differ significantly ($p < 0.01$) in bridge thread length. *A. aurantia* builds webs in more open and slightly higher spaces in the vegetation than does *A. trifasciata*. The hypothesis that reduced densities by the requirements of adults might offset any decrease in competition resulting from reduced density. Densities recorded on eight 200 m² transects ranged from 0.07 to 0.39 individuals/m² for *A. aurantia* and 0.16 to 0.59 individuals/m² for *A. trifasciata* (more than

twice the density reported by Enders). In addition, we have observed great changes in the abundance of these two species (alternately) from year to year. Łuczak (1963) observed similar changes in orb-weaver populations, and suggests that interspecific competition is the cause. Thus, coexistence of these species as adults requires further explanation.

Examination of 602 prey items collected from *Argiope* spp. webs during the same time of year shows significant differences in size characteristics and taxonomic composition. *A. aurantia*, the larger of the two species, feeds on prey with a mean body length of 16.33 ± 0.72 (2 S.E.) mm. *A. trifasciata*, which is slightly smaller, feeds on prey with a mean body length of 10.23 ± 0.56 mm. Differences in prey size are significant (t-test; $p < 0.01$). Taxonomic composition of the prey of these two species is also different (Fig. 2), in contrast to the observations of Bilsing (1920). The prey of *A. aurantia* consists mainly of Lepidoptera, Hymenoptera, and Orthoptera (ca 75% in these three orders), reflecting its tendency to specialize on larger prey. The prey of *A. trifasciata* is comprised of smaller insects of the orders Hemiptera, Homoptera, Coleoptera and Diptera (ca 50% of prey are of these orders). Differences in taxonomic composition of prey between these species are statistically significant (G-test, $p < 0.01$). The prey of both species differs from the composition of that available (sweep net sampling), as was found for other orb-weavers (Kajak, 1965).

An important question needs to be raised at this point. Is prey composition a reflection merely of the habitat exploited, or of the size specialization of the spider, or both? *A. aurantia* and *A. trifasciata* exhibit consistent (and significant) differences in web fine structure (Uetz & Schemske, in prep.). Risch (1977) suggests that mesh size of webs is a reflection of body size, and as such, determines prey size. He found greater similarity of mesh size between webs of species within the same genus than between genera. Mesh size (measured as the distance between turns of the sticky spiral) appears to be positively correlated with prey size in the small sample of species for which we have measurements of prey and web structure (Fig. 3). One aberrant data point in Fig. 3, the disproportionately small prey of *Leucauge venusta* (Walckenaer), may be explained by the tendency of this species to incline its web from the vertical by ca

45° . Since prey generally fly in a horizontal plane, this orientation effectively reduces the mesh size from 1.96 mm to 1.31 mm. Robinson & Robinson (1970) caution interpretation of this simple relationship, in that there is often an inverse relationship between spiral area and mesh size (e.g., *Argiope argentata* (Fabr.) vs. *Nephila maculata* (Fabr.), which respectively build small, large-meshed and large small-meshed webs). Still, Risch's suggestion seems plausible.

Enders (1974) suggests that differences in vertical habitat utilization allow coexistence of the two *Argiope* species discussed here because various prey types fly at different heights in grassland vegetation. We might add that a horizontal component of habitat stratification is also important. Our observations would support this, in that the hymenoptera and lepidoptera common in the diet of *A. aurantia* fly in the upper parts of prairie vegetation (where there are flowers), while the orthoptera jump in the larger open spaces. Smaller Hemiptera, Homoptera and Coleoptera common in the diet of *A. trifasciata* are more likely to be found within the vegetation.

Coexistence of these congeneric orb-weavers may be facilitated by differences in prey utilization. Web

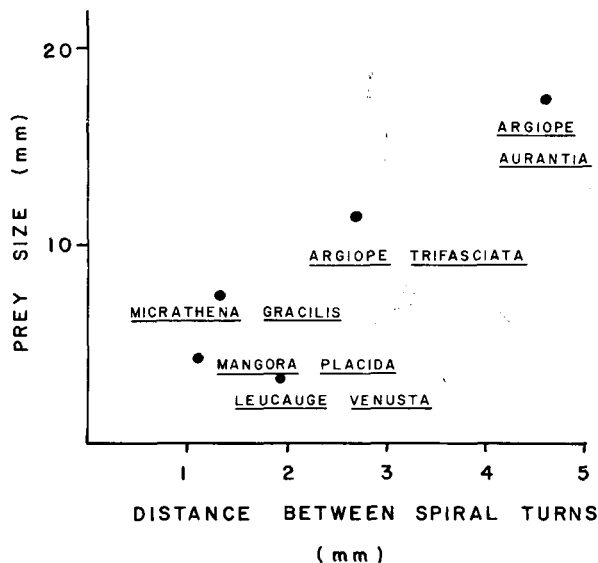


Fig. 3: Relationship between body length of prey (collected from webs) and mesh size (distance between turns of sticky spiral) of orb-webs.

placement and web structure could each play important roles in determining the characteristics of the prey a species utilizes. It is unclear to what extent each of these influences the prey of *Argiope* spp., although there is evidence to suggest that mesh size of webs is related to prey size specialization. Examination of larger species assemblages of orb-weavers in more complex habitats may shed further light on this question.

Habitat utilization in forest orb-weavers

In forest environments, a diverse assortment of orb-weaving species may be found. The patchiness inherent in forest vegetation provides opportunities for vertical and horizontal stratification of species. Examination of habitat distribution of species in Brownfield woods suggests that species with similar mesh sizes are separated by habitat (Fig. 4). *Mangora placida* (Hentz), *Micrathena gracilis* (Walckenaer), *Leucauge venusta* and *Cyclosa conica* (Pallas) all have webs with mesh sizes in the range of 1.0 – 2.0 mm. All show considerable separation in their habitat utilization patterns, with the exception of *Cyclosa*. However, *C. conica* is temporally segregated from *Mangora*, as it appears very late in the growing season

(September). The other species, *Neoscona* sp. and *Hyptiotes cavatus* (Hentz), overlap considerably with these species, but have a larger mesh and (presumably) exploit larger prey. They are separated from each other in habitat utilization.

In a more diverse assemblage of orb-weaving species (Dysert's Woods in Southern Illinois) differences are apparent in the habitat utilization patterns of some of the species discussed above (Fig. 5). Three species of the genus *Micrathena* are present. *Micrathena gracilis* occupies a position considerably lower in the vegetation here than it does in Brownfield Woods. *M. sagittata* (Walckenaer), whose body size and mesh size are most similar to *M. gracilis*, occupies a different microhabitat. *M. mitrata* (Hentz), the smallest of the three species, occupies a position between the other two, with some overlap with each. *Mangora placida* also occupies a lower position in the vegetation here, perhaps due to the presence of *Metepeira labyrinthea* (Hentz), (a spider with very similar mesh size) in the upper, more dense portion of the vegetation. Three species with large-meshed webs (3-7 mm), *Araneus marmoreus* Clerck, *Neoscona* sp. and *Verrucosa arenata* (Walckenaer) are present, and overlap very little with each other in habitat utilization. However, both *Araneus* and *Verrucosa* overlap considerably in microhabitats with smaller-meshed species.

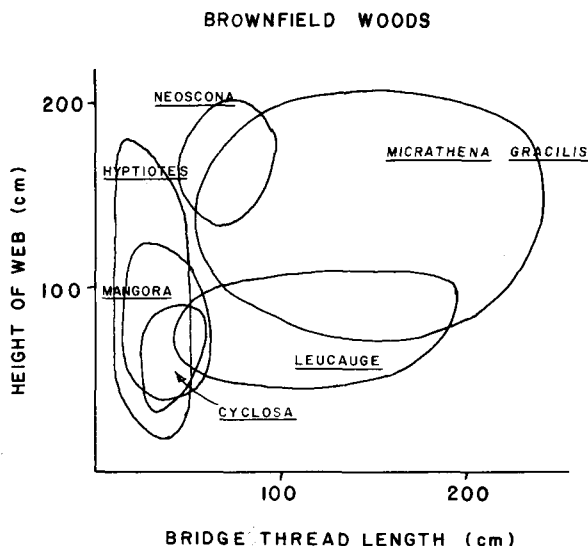


Fig. 4: Habitat utilization of spider species in a central Illinois forest. Lines enclose scatter diagrams of web/habitat measures for species as indicated. $N > 25$ in all cases.

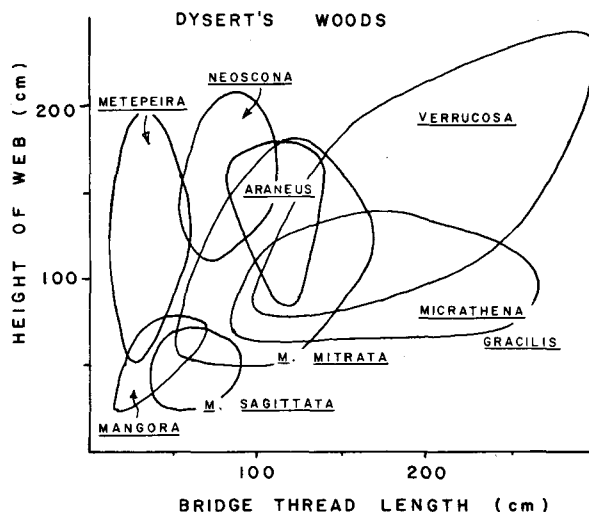


Fig. 5: Habitat utilization of spiders in a southern Illinois forest. (same as Fig. 4).

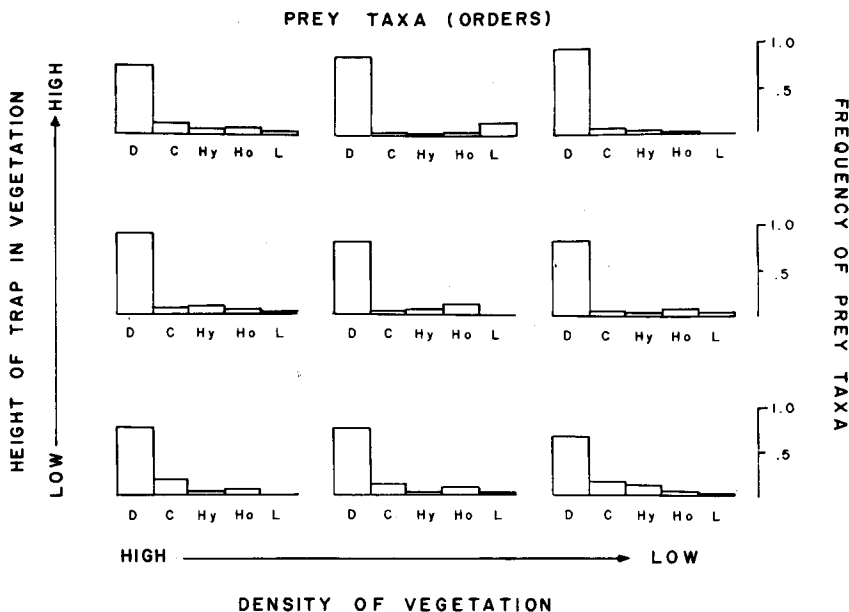


Fig. 6: Composition of prey taxa in different spaces of the forest vegetation in Brownfield Woods, as sampled by window-pane traps in late August. D = Diptera; C = Coleoptera; Hy = Hymenoptera; Ho = Homoptera; L = Lepidoptera. (Sample size for each is listed as prey abundance in Table 1).

It is possible that choice of different microhabitats by spider species would result in exploitation of different prey resources. Window-pane traps placed at different heights and densities of vegetation collected different combinations of prey taxa which show different size distributions (Figs. 6 and 7, respectively). If prey were distributed randomly throughout the environments that spider species share, we would expect height and density of vegetation to be independent of each other with regard to the abundance, composition and size distribution of prey collected at each site. Significant differences (at $p < 0.05$) were found for abundance (no./1000cm²/wk.), composition (orders), and size classes (0-4 mm, 4-10 mm, and > 10 mm) of prey using the G-test (Sokal & Rohlf, 1969) indicating the non-randomness of prey distribution. Subsequent crosswise comparisons site-by-site and group-by-group further confirm these results. The distribution of prey resources for orb-weaving spiders is likely to vary greatly from location to location within the forest vegetation. Habitat segregation would allow species to exploit different prey resources and avoid competition, as has been pre-

viously suggested in the literature (Tretzel, 1955; Turnbull, 1960; Enders, 1974).

The importance of habitat segregation in reducing competition (by allowing species to exploit different prey resources) depends on whether or not spiders compete for food. No data are currently available to document this. However, Wise (1975) found prey to be a limiting resource for adult female linyphiid spiders, and there is evidence that spiders experience chronic food shortages in nature (Anderson, 1974). Conversely, a high degree of habitat specificity among web building spiders has been documented, presumably related to habitat structure and its importance to web architecture (see Turnbull, 1973). Riechert & Tracy (1975) suggest that thermal characteristics of web sites are more important than prey abundance, because of the limits that the thermal environment places on spider activity (and prey capture). Obviously, a variety of explanations could be made for differences in habitat exploitation patterns of orb-weavers. Further research is necessary to determine whether differences in spider prey are attributable to habitat specialization, or whether dif-

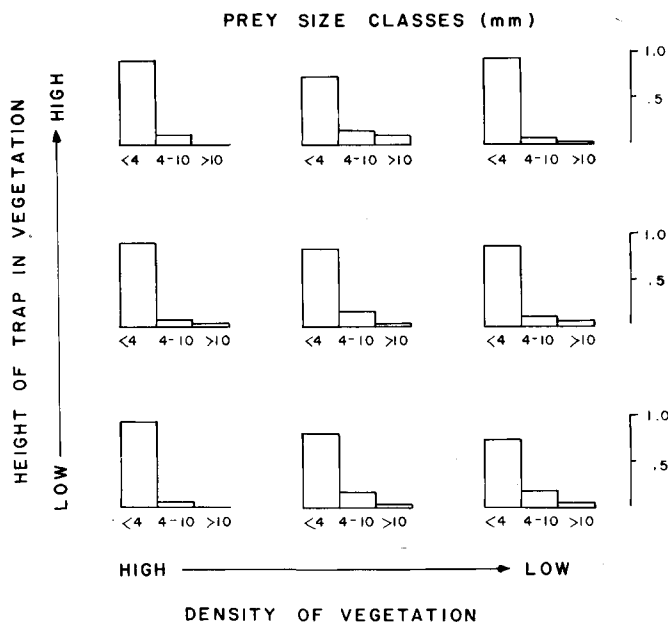


Fig. 7: Frequency distributions of prey in three size classes (< 4.0mm, 4.0-10.0mm, > 10.0mm) in different spaces of the forest vegetation in Brownfield Woods, as sampled by window-pane traps in late August.

ferences in spider habitats are attributable to specialization for prey occurring in different places.

Spiders are not distributed randomly throughout the forest vegetation, and there are many places where the overlap of species' habitat distribution results in higher species density than others (Figs. 4

Height of Trap	Vegetation Density		
	High	Medium	Low
140-200 cm			
prey abundance	133	85	115
no. of spider spp.	2	2	1
60-140 cm			
prey abundance	160	96	109
no. of spider spp.	4	3	2
0-60 cm			
prey abundance	232	162	110
no. of spider spp.	4	4	1

Table 1: Prey abundance (no./1000 cm²/week) as sampled by window-pane traps, and the number of spider species in different spaces in forest vegetation at the Brownfield Woods site.

and 5). In the Brownfield Woods site, species packing (in habitat) appears to be influenced by prey abundance. There are more species present in areas of higher prey density than in areas of lower prey density (Table 1). This relationship is marginally significant statistically (Spearman rank correlation coefficient, $R_s = 0.620$; $0.10 > p > 0.05$), but biologically interesting. Further study is needed before we can understand species packing in orb-weavers.

Conclusion

MacArthur & Levins (1964) suggest that animals which expend proportionately more energy searching for prey (searchers) should specialize for habitat. Animals which expend proportionately more energy in pursuing prey (pursuers) should specialize for prey size. Enders (1974) has inferred that larger orb-weavers like *Argiope* are searchers, since congeners appear to coexist by vertically stratifying habitats. He also infers that smaller orb-weavers are pursuers, since they often occur in arrays of differing body sizes (as in Łuczak, 1963). The logic of inferring foraging strategies of spiders from patterns of resource utilization, especially from a limited data base, is tenuous at

best. An orb-weaver's major foraging expense is the energy required to construct a web. We might assume this activity to be analogous to "searching" the environment for prey. Therefore, we would expect to see specialization for habitat as the primary mechanism allowing coexistence. In these studies, we have seen evidence of both prey size specialization and habitat stratification in a wide variety of orb-weaving species. The results suggest that the relative importance of prey size selectivity vs. habitat specificity in permitting coexistence in orb-weaving spiders has yet to be resolved.

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