

PREY OF TWO SYNTOPIC SPIDERS WITH DIFFERENT WEB STRUCTURES

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ABSTRACT

In order to determine the extent to which differences in web structure are correlated with divergence in diet, we collected and identified prey from the webs of two syntopic orb-weavers whose webs differ markedly in architecture. The species studied were the basilica spider *Mecynogea lemniscata*, and the labyrinth spider *Metepeira labyrinthea*. Two nearby allotopic populations were also compared. We determined the size and taxonomic category of the prey of both species, web height, and the type of vegetation supporting the web.

The diets of syntopic populations were very similar. No statistically significant differences were found between syntopic *Mecynogea* and *Metepeira* in either the types or size of prey collected from the webs. Allotopic populations differed in these aspects of the diet, but the overlap was substantial. *Metepeira* usually placed its web higher and on less rigid vegetation than did *Mecynogea*. However, the overlap was extensive, particularly when the species occurred together. Syntopic basilica and labyrinth spiders were significantly more similar than allotopic populations in where they placed the web.

Several authors have suggested that exploitative competition for prey between syntopic spiders has led to the evolution of differences in web structure as a means of competitive coexistence. The results of this study make it difficult to argue that avoidance of competition for food is the primary reason syntopic species have evolved different web structures.

INTRODUCTION

The type of web a spider spins is a component of its foraging behavior. Web design is a potentially important niche parameter if it influences a spider's diet, since species differences in web structure may lessen overlap in prey utilization and contribute to reduced interspecific competition. The argument that different types of spider webs have evolved in response to exploitative competition for prey rests upon the assumption, among others, that the structure of the web substantially influences the kinds of prey captured by its owner. The extent to which structural differences correlate with differences in diet is most directly approached by examining the prey of syntopic species that resemble each other in phenology and body size but differ in web architecture.

The basilica spider *Mecynogea lemniscata* (Walckenaer), and the labyrinth spider *Metepeira labyrinthea* (Hentz), are such species. They are syntopic in forested areas of central Maryland, USA, to the extent that on occasion a spider may construct its web within a few cm of the other species. Individuals of both species often remain at the same

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web site for several weeks. In Maryland these species mature during July and August, and females can live through October. Basilica spider females are larger at maturity than labyrinth spiders, though the difference is not substantial. Mean carapace widths (\pm s.e.) in a 1978 sample of *Mecynogea* and *Metepeira* were 2.16 ± 0.03 mm and 2.01 ± 0.04 mm, respectively (pers. obs.). Both species belong to the orb-weaving family Araneidae, but they spin dissimilar webs. The labyrinth spider constructs a typical vertically oriented orb with a viscid catching spiral. An irregular barrier web houses a retreat. *Mecynogea*'s web is much different and resembles a linyphiid snare. The basilica spider spins a horizontal orb that is modified into a dome under which the spider waits for prey. *Mecynogea*'s orb differs further from that of most other araneids in being non-viscid (Levi 1978). Orbs of adult female labyrinth and basilica spiders differ markedly in mesh size. Strands of the labyrinth spider's catching spiral form a series of variable rectangles, approximately 2 x 5 mm on average. Distances between the silk of the basilica spider's orb are smaller, about 1 mm or less. Thus openings in *Metepeira*'s web are approximately 10X larger than those of *Mecynogea*'s snare. We determined whether these substantial differences in web shape and mesh size are correlated with a divergence in diet.

STUDY AREAS AND METHODS

The research was conducted in three areas on the Patuxent Wildlife Research Center in Prince Georges County, Maryland, USA: two in which one species was rare (designated the allotopic *Mecynogea* and allotopic *Metepeira* areas) and a third, the syntopic area, where both species were abundant. We selected allotopic areas in addition to a site where both co-occurred because 1) a comparison of dietary differences in syntopy with the extent of divergence in diet between populations that inhabit different areas would provide information on the extent to which their diets might reflect spatial variation in the size and taxa of available prey, and 2) we wanted to examine the alternative possibility that diets diverge in syntopy due to differences in web placement, possibly resulting from interspecific competition. The allotopic *Mecynogea* area was a narrow 100-m zone of shrubs and young pine bordering both sides of a dirt road adjacent to a marsh. The allotopic *Metepeira* area was a 70 x 120 m portion of a lake-side oak-beech forest. Forest margin and marsh-side shrubs composed the syntopic area. It was discontinuous, with one sub-area beside a marsh, and another extending from either side of a dirt road between a pond and an open field. These sub-areas were 100 m apart and supported approximately equal numbers of both species.

All three areas were censused in July 1978 and the site of every web with a female spider was marked with a numbered tag. In the two allotopic areas 72 *Mecynogea* and 89 *Metepeira* were located. We tagged 66 *Mecynogea* and 55 *Metepeira* web sites in the syntopic area. Females were studied since mature males wander and do not live as long as females.

Prey upon which spiders were feeding and insect exoskeletons left in the web were collected from occupied webs July through September. Each web was visited two to five times a day between 0700 and 1600. On a few occasions prey was collected later in the day, up to 2300 h. At the start of the study each web was visited on alternate days, but the decreased number of spiders later in the season made it possible to visit each occupied web several times a day. Collected prey was preserved in 70% ethanol and later identified to order, and to family whenever possible, using the keys of Jaques (1947), Borror and Delong (1964), and Borror and White (1970). We calculated a prey-size index equal to the product of the length and the square of the width.

Table 1.—Identity of prey collected from webs in two allotopic areas and the single syntopic area. Major families are distinguished for the more frequently represented orders.

	Allotopic Areas		Syntopic Area	
	<i>Mecynogea</i>	<i>Metepeira</i>	<i>Mecynogea</i>	<i>Metepeira</i>
Coleoptera				
Chrysomelidae	29	1	11	18
Curculionidae	3	47	2	10
Cantharidae	10	3	6	4
Scarabaeidae	0	3	0	3
Scolytidae	0	4	1	2
Staphylinidae	1	2	1	1
Other Families	5	2	3	1
Unidentified Family	0	19	2	4
Total Coleoptera	48	81	26	43
Hymenoptera				
Formicidae	37	18	16	11
Ichneumonidae	1	7	4	6
Sierolomorphidae	0	2	3	0
Pompilidae	0	4	0	2
Halictidae	0	2	0	4
Braconidae	2	2	0	0
Other Families	2	8	0	1
Unidentified Family	0	15	1	5
Total Hymenoptera	42	58	24	29
Homoptera				
Cicadellidae	9	3	9	7
Flatidae	7	3	9	4
Aphididae	2	1	1	3
Delphacidae	4	0	0	0
Other Families	2	2	3	2
Unidentified Family	2	0	0	0
Total Homoptera	26	9	22	16
Diptera				
Tabanidae	2	2	0	3
Other Families	5	2	4	2
Unidentified Family	4	0	3	3
Total Diptera	11	4	7	8
Odonata	10	5	1	5
Lepidoptera	9	4	5	1
Hemiptera	4	1	3	0
Orthoptera	1	0	1	1
Neuroptera	1	0	0	1
Unidentified Order	8	8	5	7
Unidentified Larvae	2	0	3	1

Our primary goal was to document the extent to which diets of the syntopic populations differed. Since we also wanted to determine whether syntopic populations of *Mecynogea* and *Metepeira* differed more than allotopic populations in where they placed their webs, we also recorded web height and the type of substrate to which the spider attached the supporting silk. Substrates were scored on a subjective scale of rigidity ranging from 1 to 8: live pine (1), live vine (greenbrier, *Smilax*) (2), mixed live and dead vines (3), dead vine (4), live shrub (5), live deciduous twigs (6), mixed live and dead deciduous twigs (7) and dead deciduous twigs (8).

Data were analyzed with the use of UCLA Biomedical Computer Programs [multiway frequency tables (BMDP3F) and analysis of variance (BMDP2V)] and nonparametric techniques (Conover 1971).

RESULTS

Prey Captured.—Coleoptera, Hymenoptera, Homoptera and Diptera were the major insect orders captured by *Mecynogea* and *Metepeira* (Table 1), with beetles and hymenopterans comprising over half of the prey found in the webs of each species. Differences between the diets of allotopic populations were statistically significant, but the diets of *Mecynogea* and *Metepeira* in syntopy did not differ significantly in the relative proportions of these prey orders (Fig. 1). However, the apparently greater similarity in prey captured when the species are syntopic is not statistically significant ($\chi^2 = 5.59$, $p > 0.2$, for the 3-way interaction term in the 2 x 5 x 2 contingency table of spider species x prey order x area. The size of the interaction term indicates whether the extent to which the two spiders differ in the relative proportion of prey in the diet is similar for the syntopic and allotopic comparisons).

Diets of the two syntopic spider populations also closely resemble each other in terms of the relative representation of the families of prey (Table 1). At this level of resolution the prey of allotopic populations does appear more different than the prey in syntopy, particularly for the two most numerous families of Coleoptera. Allotopic *Mecynogea* captured many chrysomelids but very few curculionids, whereas allotopic *Metepeira* exhibited the opposite pattern. However, in syntopy these differences between the basilica and labyrinth spiders' diets decreased. When together, both species snared substantial numbers of chrysomelids, and the apparent specialization of *Metepeira* on curculionids disappeared.

Prey of allotopic *Metepeira* tended to be larger than that of the allotopic *Mecynogea* population [Fig. 2; χ^2 (median test) = 5.88, $p = 0.02$]. However, in syntopy the median prey sizes were more similar and did not differ significantly [$\chi^2 = 2.55$, $p = 0.11$]. We tested for differences in prey size with a nonparametric procedure because the data are skewed, though a shortcoming of nonparametric approaches is the lack of convenient procedures to test for interactions between treatments (Conover, 1971). Although large deviations from normality can make an Analysis of Variance (ANOVA) too conservative, the small value of the interaction term in the 2 x 2 ANOVA of log (prey size) (Table 2) suggests that the greater similarity in prey size in syntopy would also be judged statistically non-significant by an equivalent nonparametric test. Note that the overall effect of species in the ANOVA (p of $F = 0.09$) is in general agreement with the results of the two nonparametric comparisons.

Web Placement.—The heights above the ground at which both species built their webs overlapped, particularly in the syntopic area (Fig. 3). *Metepeira* placed its web significantly higher in the vegetation than did the basilica spider (Table 2). This difference between the species in mean web height was significantly less in syntopy, as indicated by the significant interaction term in the ANOVA.

Both species used similar vegetation for supporting their webs, but they differed in the relative proportions of types of substrate selected. (Fig. 4). The labyrinth spider usually spun its web on more rigid substrate. The difference between syntopic populations was significantly less than for the allotopic comparison (Fig. 4; $\chi^2 = 24.4$, $p < 0.001$, for the 3-way interaction term in the 2 x 4 x 2 contingency table of spider species x substrate x

Table 2.—Two-way ANOVA of log (prey size) and web height. Treatments are species (*Mecynogea*, *Metepeira*) and area (allotopic, syntopic). A significant interaction term (species x area) indicates that the species are more alike in syntopy than allotopy. A logarithmic transformation of prey size was required to make variances homogeneous and reduce the skewness of the data distribution. No transformation of web height was necessary.

Source	d.f.	M.S.	F	Significance
Log (Prey Size)				
Species (S)	1	0.958	2.81	0.09
Area (A)	1	0.050	0.15	0.70
S x A	1	0.128	0.38	0.54
Error	486	0.341		
Web Height				
Species (S)	1	254.42 x 10 ³	178.92	<0.001
Area (A)	1	0.50 x 10 ³	0.35	0.55
S x A	1	9.24 x 10 ³	6.49	<0.01
Error	200	1.42 x 10 ³		

area. Contiguous classes of substrate scores were pooled in order to yield expected values > 5 for the contingency table analysis).

DISCUSSION

Bristowe (1941) discusses how different snares capture different types of prey as part of his argument that the diversity of spider hunting habits reflects evolution to avoid exploitative competition for food among species occupying the same habitat. Robinson (1981) suggests that in the spider community he studied, specialization on different-sized prey permits coexistence within a guild. Both a spider's size and its web characteristics are important predictors of the size and type of prey the spider will capture (Bristowe 1943, Enders 1975, Chacón and Eberhard 1980, Riechert and Luczak in press). Uetz *et al.* (1978) argue that these aspects of a web-builder's foraging behavior, in particular the spacing of the web's mesh, reflect specialization on different sizes and taxa of prey and hence permit coexistence among competing syntopic species.

Two basic assumptions underlie arguments relating differences in web structure to competitive coexistence: 1) exploitative interspecific competition for food is important in spider communities, and 2) different webs capture different kinds of prey. Although many spiders are food-limited in nature, the few experimental studies of competition that have been conducted so far have not uncovered evidence of major interspecific competition in spider communities (Wise, in press). Absence of significant interspecific competition over ecological time does not rule out its possible role in causing the evolution of differences in prey specialization. However, establishing that competition actually has caused the evolution of niche differences is difficult (Connell 1980); furthermore, other hypotheses can explain why species differ in trophic characters (e.g., Strong 1980). The second assumption, that differences in web structure lead to differences in prey captured, can be tested directly. The results of this study suggest that two species with markedly different webs do not necessarily capture markedly different prey.

Syntopic populations of the basilica and labyrinth spiders exhibited remarkable overlap in diet, especially considering the species differences in mesh size and web morphology. One might expect that the non-sticky sheet web of *Mecynogea* would capture a different array of insect taxa than the sticky, vertically oriented orb of *Metepeira*. On the contrary, the overlap in prey taxa was high. Pianka's (1973) index of niche overlap was 0.96 for the syntopic populations. Although *Mecynogea* is slightly larger than *Metepeira*,

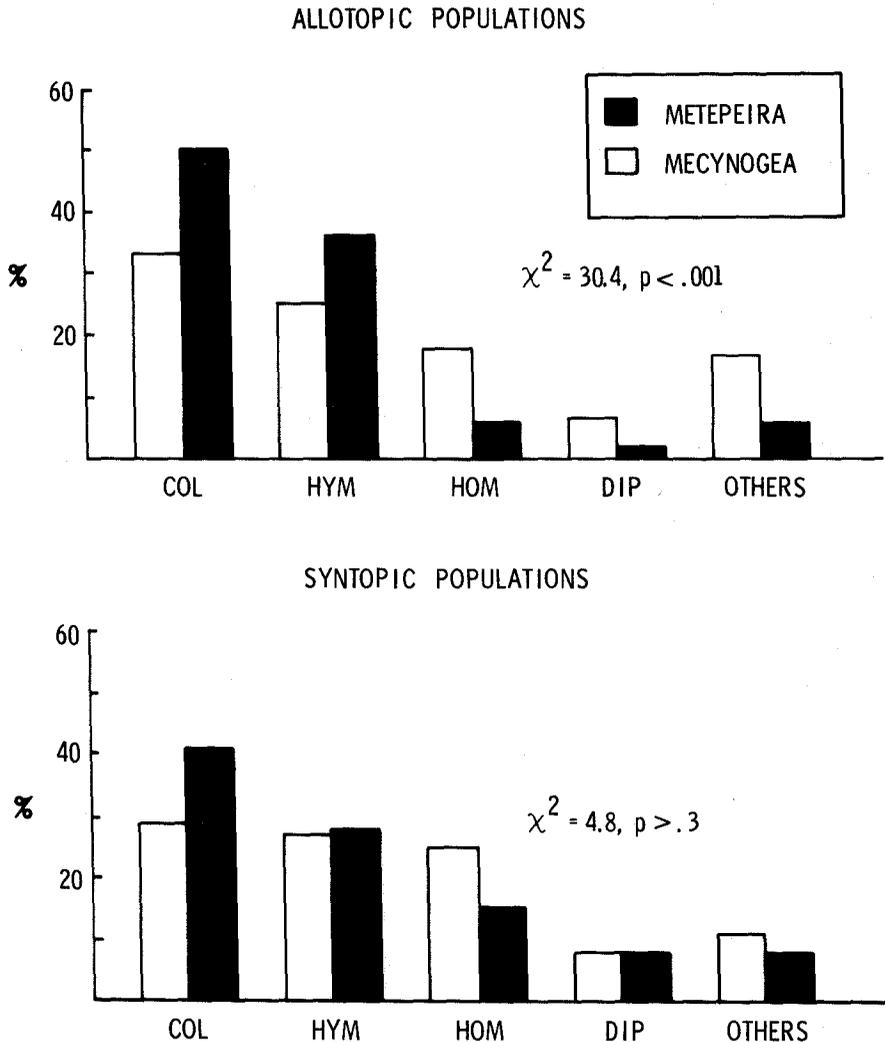


Fig. 1.—Relative representation of the major orders of prey in the webs of *Mecynogea* and *Metepeira* in allotopic and syntopic populations. Larvae, and prey which could not be identified to order, are not included. For *Mecynogea* 149 and 90 prey were identified from allotopic and syntopic populations, respectively; corresponding totals for *Metepeira* were 162 and 106. COL = Coleoptera, HYM = Hymenoptera, HOM = Homoptera, DIP = Diptera, and OTHERS = Odonata, Lepidoptera, Hemiptera, Orthoptera and Neuroptera. The χ^2 statistic is a test of independence of species and prey order in a 2×5 contingency table. The statistic tests whether *Mecynogea* and *Metepeira* differed significantly in the relative proportions of the major insect orders found in their webs. Numbers of prey in the latter orders were combined because analyzing any of them separately produced an expected value < 5 in at least one of the two contingency tables of species \times prey order.

the much finer mesh of the former's web suggests that it might have more small insects in its diet. Such does not appear to be the case. Our schedule of examining webs may have allowed the basilica spider to consume very small prey entirely without being detected. However, predictions from optimal foraging theory and studies of the feeding behavior of other orb-weavers (Schoener 1971, Riechert and Luczak 1982) suggest that such small, energetically poor prey would not comprise the major portion of a mature basilica spider's diet.

We undoubtedly failed to detect some small prey of both species. Furthermore, the spiders may not have extracted the same fraction of the available energy from the different types of prey that did comprise our samples. Also, we collected prey primarily during daylight hours. Thus the insects observed being fed upon and the discarded exoskeletons collected from the webs reflect the diet of each species but are not identical to it. This lack of complete correspondence presents no problem of interpretation, though, because the goal of the research was to compare the filtering properties of webs with markedly different structures. The aim was to uncover the effect of web structure upon diet, not to measure the actual diet of each species.

The similarity of the diets of the basilica and labyrinth spiders cannot lead to a general conclusion that web characteristics play no role in setting a spider's diet. In a recent review article, Riechert and Luczak (1982) summarize many of the studies that demonstrate the extent to which different species of web builders, though polyphagous, tend to

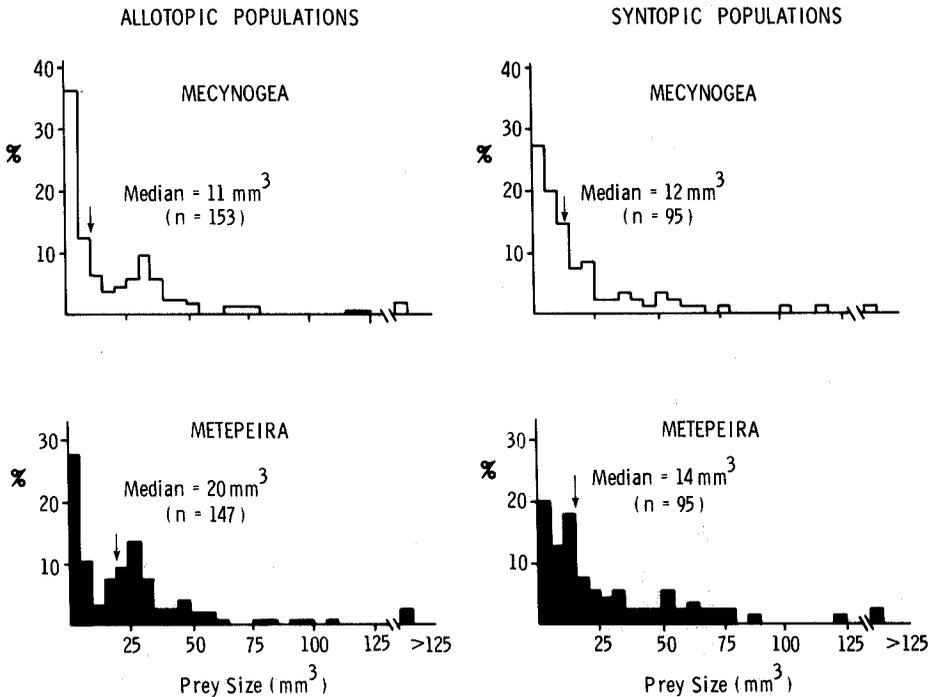


Fig. 2.—Sizes of prey captured by *Mecynogea* and *Metepeira* in the allotopic and syntopic populations. Prey size differed significantly between the allotopic populations (p of $\chi^2 < 0.05$, median test); however, differences between syntopic *Mecynogea* and *Metepeira* populations were not statistically significant (p of $\chi^2 > 0.1$, median test). [Note that the number of prey identified to order (Fig. 1) does not equal the number whose size was determined, because some prey could be identified to order but not measured accurately, or vice versa.]

capture different prey. They point out, though, the difficulty in evaluating the web's role in determining the observed dietary differences, since most of the studies were conducted by different investigators at different times or places and thus cannot be compared directly. Several recent studies do permit one to generalize about the extent to which the diets of syntopic web-builders differ. Uetz *et al.* (1978) found that the size and taxa of prey differed significantly between two similar old-field spiders, *Argiope aurantia* and *A. trifasciata*. The investigators related these differences at least partly to the larger body size and mesh size of *A. aurantia*. On the other hand, Taub (1977) found that the diets of these species overlapped broadly and did not differ significantly in taxa of prey. Taub did find that *A. aurantia* tended to feed on larger prey, and she presents some data which suggest that the filtering properties of the webs may contribute partly to differences in mean prey size. Brown (1981) studied these *Argiope* spp. in different areas and found that the extent to which the diets differed was variable. He found no pattern to suggest that their diets are substantially and consistently different. Other studies also conclude that the diets of closely related syntopic orb-weavers overlap extensively. Kajak (1965) found that syntopic *A. cornutus* and *A. quadratus* select basically the same taxa and size of prey. *Araneus quadratus* and *Argiope bruennichi* also capture prey taxa in the same proportions when the spiders co-occur (Nyffeler and Benz 1978). The pattern emerging from these studies is that diets of closely related syntopic species are very similar, and that even when they differ statistically, the diets still broadly overlap.

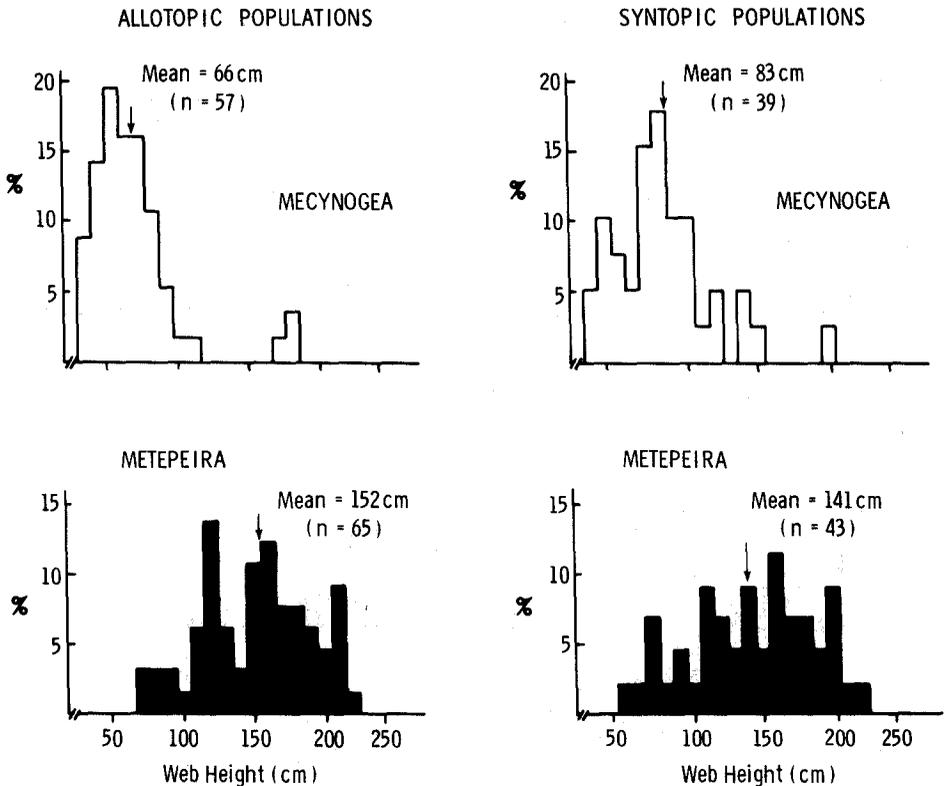


Fig. 3.—Height of the web from the ground of *Mecynogea* and *Metepeira* in the allotopic and syntopic populations. In both populations *Metepeira* built its web significantly higher than *Mecynogea* (p of $\chi^2 < 0.001$ for median test for both allotopic and syntopic comparisons).

The previous research discussed above has compared the prey of species with webs more similar in structure than those spun by *Mecynogea* and *Metepeira*. Riechert recently compared the prey capture of three quite different syntopic web-builders: a scattered-line weaver, a sheetline weaver, and an orb-weaver which inhabit sandstone rock faces. A chi-square test of the taxonomic composition of the prey that encountered these webs and were attacked by the spiders revealed statistically significant differences among the three species. However, substantial overlap in several major prey taxa did occur, and examining the prey taxa that account for the dietary differences suggests that "... location on the cliff face rather than web type itself is responsible for the filtering" (Riechert and Luczak 1982). They suggest that different types of webs capture different prey taxa because the webs require different habitat features for their construction. Any partitioning of prey taxa would thus result primarily from webs being placed in different micro-habitats rather than from different filtering properties. In our study spiders in the syntopic populations captured similar prey even though the species differed significantly in micro-habitat utilization. The large overlap in the diets of the basilica and labyrinth spiders in syntopy contrasts with Riechert's finding of statistically significant differences in the diets of syntopic species. The greater similarity in diets uncovered in our study may reflect a greater homogeneity of physical features, and hence prey distribution, at slightly

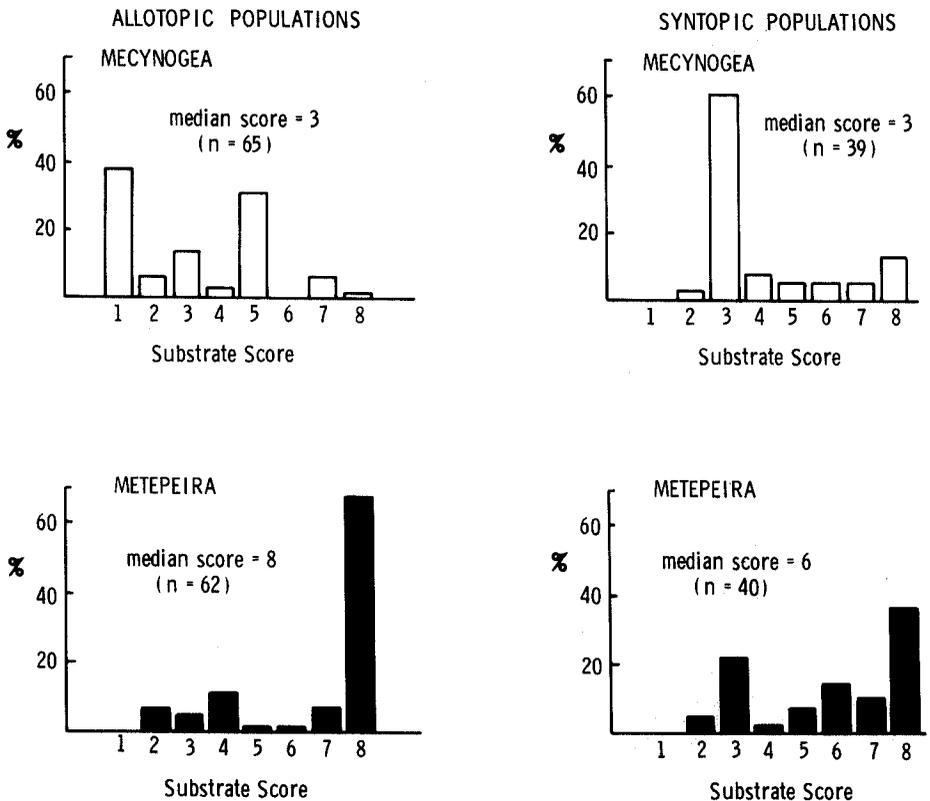


Fig. 4.—Utilization of different substrates for web construction by *Mecynogea* and *Metepeira* in the allotopic and syntopic populations. Rigidity of the substrate increases with increasing score. (Refer to text for details of the scoring procedure.) *Metepeira* built its web on more rigid substrate than did *Mecynogea* in both allotopic and syntopic populations (p of $\chi^2 < 0.001$ for median test for both comparisons).

different heights and areas of a forest compared with differences in prey distribution associated with the more marked physical discontinuities of rock faces.

Other research also suggests that differences in microhabitat utilization and factors other than web properties are the major causes of dietary differences. Olive (1980) discovered that the diets of *Argiope trifasciata* and *Araneus quadratus* converged when the spiders built their webs in more similar microhabitats as the season progressed. In a two-year study, Horton and Wise (1983) found that the diets of *Argiope trifasciata* and *A. aurantia*, though statistically different, were more similar in 1980 than the previous year in the same field and time of season. Mean web heights and spider sizes were also closer in 1980, which may explain much of the convergence in diet.

Our results are consistent with the conclusion that differences between microhabitats influence prey capture more than differences in web structure. Syntopic populations of *Mecynogea* and *Metepeira* were more similar than the allotopic populations in web height and the type of vegetation used for web support. Convergence of these niche parameters in the two species was statistically significant. Prey size and taxonomic composition of the diet were also more similar when the species were syntopic, though the apparent convergence was not statistically significant for either aspect of the diet. These differences in the statistical significance of the convergence in syntopy reflect the fact that parameters of the feeding niche were more similar for allotopic populations than were aspects of the spatial niche; hence for the sample size of this study, almost identical diets in syntopy would have been required for the convergence to be significant statistically.

Divergence in one or more niche parameters in syntopy is often cited as indirect evidence of interspecific competition. Our study provides no such evidence of competition. On the contrary, the results indicate that the species not only fail to shift their niches in response to the presence of the other, but that major parameters of the niche converge in syntopy. A manipulative field experiment conducted the same year in a nearby area uncovered no evidence of interspecific competition between *Mecynogea* and *Metepeira* (Wise 1981).

Studies of prey partitioning conducted to date lead to several generalizations. Statistical differences do sometimes exist between syntopic web builders in size and type of prey captured. These differences reflect differences in spider size and web mesh. Differences also result from different attack behaviors once the prey has hit the web (Olive 1980). However, separation is partial when statistically significant. Broad overlap in diet is the general pattern, even when web architecture is quite different. The location of the web, its size, and the behavior of the spider on the web appear to affect a spider's diet more than the filtering properties of its web. It thus becomes difficult to argue that avoidance of exploitative competition for food is the primary reason syntopic species have evolved structurally different webs.

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