

Spider (Araneae) Community Structure in an Intertidal Salt Marsh: Effects of Vegetation Structure and Tidal Flooding

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ABSTRACT The effects of vegetation structure and tidal flooding on the organization of a spider community were studied along an elevational gradient in an intertidal marsh. High marsh habitats were dominated by the grass *Spartina patens* (Ait.) Muhl., a species characterized by a low, matted profile and a complex layer of thatch. Another grass, *Spartina alterniflora* Lois., is more upright in structure, has a poorly developed thatch layer, and abounds in habitats that extend from the high marsh to much lower elevations. Along this elevational gradient, the structure of *S. alterniflora* changes from a short form on the high marsh to a tall form on the low marsh, and the frequency and duration of tidal flooding increases. Although more robust in structure during the summer months, the tall-form habitat of *S. alterniflora* is selectively destroyed and defaunated during the winter by shifting ice and storms and must be recolonized by spiders every spring from the more protected overwintering short-form habitat of *S. alterniflora* on the high marsh. In all, 21 species of resident spiders were sampled from the two grasses. The community of spiders in *S. patens* was less diverse than in *S. alterniflora* and consisted mostly of hunting spiders (Lycosidae, Gnaphosidae, Clubionidae, Thomisidae, Philodromidae, and Salticidae), which were more abundant in this low-profile grass. Web-building spiders (Dictynidae, Linyphiidae, Araneidae, and Tetragnathidae), which were rare in *S. patens*, occurred commonly in the more upright-structured *S. alterniflora* because of the abundance of sites for web attachment. Down the elevational gradient from short-form to tall-form *S. alterniflora*, the abundance of most hunting spiders and several web-building species decreased and was associated with an increase in the frequency and duration of tidal flooding. Winter defaunation of tall-form *S. alterniflora* contributed further to the depauperate spider community in this low marsh habitat. Thus, vegetation structure and elevational factors act in concert to influence the distribution, abundance, and community structure of spiders in intertidal marshes.

KEY WORDS Arachnida, *Spartina* architecture, spider community structure, tidal flooding

THE STRUCTURE of spider communities in natural as well as agricultural ecosystems has received considerable attention (e.g., Lowrie 1948, Barnes 1953, Duffey 1968, Sudd 1972, Uetz 1976, Culin & Yeargan 1983, LaSalle & DeLaCruz 1985, Spiller & Schoener 1988). This emphasis undoubtedly results from the fact that spiders are widely distributed and predominant predators in terrestrial ecosystems (Barnes 1953, Headstrom 1972, Moulder & Reichle 1972, Turnbull 1973, Nyffeler & Benz 1979, Foelix 1982, Sunderland et al. 1985) and because of their potential role as biological control agents (Specht & Dondale 1960, Whitcomb et al. 1963, Sunderland et al. 1985, Provencher & Vickery 1988; for a review see Riechert & Lockley 1984).

Despite our knowledge of spiders in terrestrial habitats, relatively few studies of spiders have been conducted in wetland ecosystems. Several investi-

gations on the diversity and structure of spider communities have been conducted in marshes along the Gulf coast of North America (Barnes 1953, Rey & McCoy 1983, LaSalle & DeLaCruz 1985), and along the North Sea in West Germany (Heydemann 1960a,b). Others have investigated spiders as part of the general trophic structure of marsh ecosystems (Marples 1966, Cameron 1972, Webb 1976, Pfeiffer & Wiegert 1981, Roderick 1987) or have focused on the regulatory role of spiders in the population dynamics of their prey (Greenstone 1978, Vince et al. 1981).

Studies of community change along altitudinal and successional gradients can elucidate how certain habitat factors influence community structure and organization (MacArthur 1965, Pianka 1966, Simberloff & Wilson 1969, Whittaker 1975). The main objective of our study was to describe changes in the spider communities associated with *Spartina* grasses along an elevational gradient from low- to high-marsh habitats. Along this elevational gradient, changes in several environmental factors oc-

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cur. First and foremost, the degree and frequency of tidal flooding increases with a decrease in elevation (Denno 1977, Bertness & Ellison 1987). Second, grass architecture changes along this elevational gradient; the amount of thatch (litter) and density of culms increase with elevation, whereas grass height decreases (Blum 1968, Redfield 1972, Denno 1977). Each of these environmental variables may influence the composition and structure of the spider communities in the various *Spartina* habitats. For example, changes in grass architecture along the gradient may constrain certain web-builders, and flooding frequency may alter the foraging ability of hunting spiders.

Based on elevational changes in plant architecture and tidal flooding, we test the following three hypotheses. First (Hypothesis 1), the degree and frequency of tidal flooding will selectively reduce populations of hunting spiders in low-marsh habitats because of their ground-dwelling habit. Flooding was shown to influence the distribution of hunting spiders in streamside forest (Uetz 1976) and intertidal marsh habitats (LaSalle & DeLaCruz 1985). In both studies, spider diversity and abundance were higher in habitats that were less frequently inundated by flood waters.

Second (Hypothesis 2), hunting spiders will be more abundant and diverse in habitats with a well-established layer of thatch on the marsh surface compared with areas with a reduced litter layer. Uetz (1975, 1976, 1979, in press) showed that spider diversity was correlated with the amount of litter accumulation in a deciduous forest ecosystem. Also, ground-dwelling spiders were more abundant in alfalfa, a perennial crop with a well-developed litter layer, compared with soybeans, an annual crop without an established litter layer (Culin & Yeargan 1983).

Third (Hypothesis 3), we expect changes in the height and culm density of *Spartina* to have the most influence on the abundance and diversity of web-building spiders. We expect habitats with short, dense and compact-growing grass (e.g., *S. patens* (Ait.) Muhl.) to support fewer numbers and species of web-building spiders because of the paucity of sites for web attachment. For example, in several field studies involving experimental manipulations of habitat structure, the abundance of web-building spiders was positively related to the number of attachment sites (Hatley & MacMahon 1980, Robinson 1981).

The structure of *Spartina* marshes is ideal for isolating the effects of grass architecture from tidal inundation on the organization of spider communities. Along an elevational gradient in *S. alterniflora* Lois. habitats, changes in flooding frequency are great, whereas changes in plant architecture are less extreme. Yet, a comparison on the high marsh between the spiders in *S. patens* and *S. alterniflora* provides a dramatic difference in plant architecture in habitats that are exposed to very similar patterns of tidal inundation.

Materials and Methods

Study Area and Habitats. Our research was conducted in an extensive intertidal marsh in the Mullica River–Great Bay estuarine system where Great Bay Boulevard crosses over Little Thorofare Creek near Tuckerton, Ocean Co., N.J. The main floral elements on this marsh are two cordgrasses, *S. alterniflora* (salt marsh cordgrass) and *S. patens* (salt meadow cordgrass), which often grow in expansive pure stands (Denno 1977). *S. alterniflora* has erect culms and forms stands with reduced culm density compared with *S. patens*.

Spartina alterniflora grows over an elevational gradient from 1.5 m below mean high water level up to mean high water level (Redfield 1972), along which one can distinguish three different growth forms (Fig. 1). At the lowest end of its tidal range along the depressed borders of tidal creeks and bay edges, tall-form *S. alterniflora* grows with culms reaching heights well >2 m (Adams 1963, Blum 1968). It is thought that greater tidal subsidy of nutrients and more oxygenated soils contribute to the robust structure of plants in these habitats (Adams 1963, Blum 1968, Redfield 1972, Bertness & Ellison 1987). Along tidal creeks, culms grow in reduced densities ($\sim 250/\text{m}^2$), and thatch rarely accumulates because it is quickly washed away by retreating tides (Denno & Grissell 1979). In the tall-form habitat of *S. alterniflora*, tidal flooding occurs twice daily, and plants growing at the lowest level in the tidal range may incur inundation 55% of the time (Redfield 1972). Further up the elevational gradient, tall-form *S. alterniflora* grades into stands of an intermediate growth form where the culms grow only 30–50 cm high (Niering & Warren 1980). Here, nutrient influx is reduced and the soil is less porous, resulting in slow tidal run off and partial anaerobic soil conditions (Adams 1963, Blum 1968, Redfield 1972, Niering & Warren 1980, Bertness & Ellison 1987). Under these conditions, plants grow slower and are less productive (Mendelssohn et al. 1981). The culms of *S. alterniflora* (intermediate form) are less robust and grow in denser stands ($\sim 2,400/\text{m}^2$) compared with tall-form *S. alterniflora* (Denno & Grissell 1979). In these habitats, tidal forces are dampened, allowing for the accumulation of a thin layer of thatch.

On the high marsh near mean high water level, short-form *S. alterniflora* grows where culms grow at high density ($>3,000$ culms/ m^2) and reach heights of only 10–30 cm (Denno & Grissell 1979). Various environmental factors have been proposed to explain the stunted nature of plants on the high marsh. These include reduced soil porosity, high concentrations of salt, reduced tidal subsidy of nutrients, and anaerobic soil conditions (Adams 1963, Blum 1968, Redfield 1972, Mendelssohn et al. 1981, Bertness & Ellison 1987). In addition to these environmental influences, genetic factors also may contribute to architectural variation in *Spartina* clones along the elevational gradient (Gallagher et

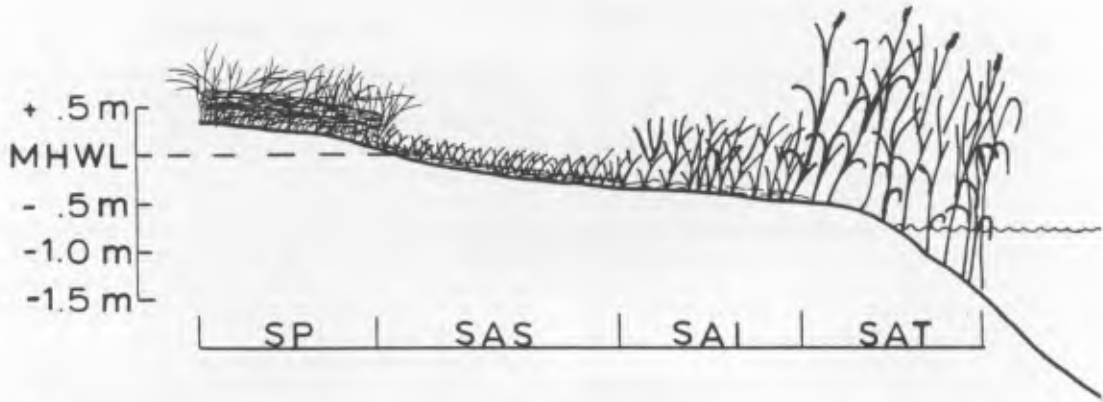


Fig. 1. Distribution of *Spartina* habitats along an elevational gradient (referenced to MHWL = mean high water level) during summer at Tuckerton, N.J. SP = *S. patens*; SAS = short-form *S. alterniflora*; SAI = intermediate-form *S. alterniflora*; SAT = tall-form *S. alterniflora*.

al. 1988). Short-form *S. alterniflora* habitats are characterized by a well-established thatch layer, which builds up under conditions of less severe tidal wash (Blum 1968, Denno & Grissell 1979). At mean high water level, short-form *S. alterniflora* habitats incur tidal flooding infrequently (<1% of the time) (Redfield 1972).

In addition to differences in architecture, the persistence of *S. alterniflora* plants differs along the elevational gradient. During the winter months, culms of tall-form *S. alterniflora* can be sheared off completely by the action of waves and shifting ice along tidal creek banks on the low marsh (Denno & Grissell 1979). The habitats of short and intermediate forms of *S. alterniflora* are not destroyed during winter and thatch remains in these habitats; consequently, spiders and their prey can overwinter effectively only in these habitats (Denno & Grissell 1979, Tallamy & Denno 1979). Following spring, after the culms of tall-form *S. alterniflora* have grown tall enough to outstrip all but the highest tidewaterers, the arthropod fauna recolonizes this temporary habitat by dispersing from overwintering habitats on the high marsh (Denno & Grissell 1979; Denno 1983, 1985; Denno et al. 1980, 1987).

On the high marsh just above mean high water level where tidal inundations are infrequent and soils are better drained, there is an abrupt transition from short-form *S. alterniflora* to a different marsh grass, *S. patens* (Adams 1963, Blum 1968, Redfield 1972, Denno 1977) (Fig. 1). *S. patens* has very slender culms with narrow blades that grow in very dense stands (up to 42,000/m²). As the season progresses, the culms of *S. patens* elongate, lodge over, and become matted on top of a persistent thatch layer (Blum 1968; Denno 1977, 1980). In contrast to that of *S. alterniflora*, the thatch of *S. patens* is complex and is composed of a dense entanglement of dead culms with layers from three or more previous growing seasons (Adams 1963, Blum 1968, Redfield 1972). The decomposition rate of *S. pa-*

tens is much slower than that for *S. alterniflora*, apparently because the lower layer of thatch is suspended by the dense crowns of individual plants and fails to contact the moist surface of the marsh (Blum 1968, Denno 1980).

Abrupt changes in environmental factors result in large, pure stands of *S. patens*, as well as short, intermediate, and tall-form *S. alterniflora* (Adams 1963, Redfield 1972). The result is a mosaic of large, irregularly shaped stands of *S. alterniflora* and *S. patens* that abut and interdigitate but rarely grow together (Blum 1968, Redfield 1972, Denno 1980). These relatively simple, naturally occurring monocultures are attractive for studying plant–arthropod interactions because of the absence of mixed vegetational effects (Denno et al. 1987).

Sampling. To determine patterns of spider diversity and abundance along the elevational gradient, two study plots (each 10 m² and separated by >100 m) were established in each of the four *Spartina* habitats (tall, intermediate, and short-form *S. alterniflora* as well as in *S. patens*; see Fig. 1). On a biweekly basis from early May until late October 1985 (11 dates in all), four samples were taken from each plot with a D-VAC suction sampler (D-VAC Company, Ventura, Calif.) (Dietrick 1961). Each sample consisted of four 15-s random placements of a D-VAC sampling head (0.0929 m²) on the vegetation surface. Arthropods were killed with ethyl acetate and transferred into jars containing 90% ethanol. Spiders were sorted to species and age class (adults and immatures) and counted. D-VAC sampling efficiently removes most spiders from low-profile vegetation; 97 ± 2% and 95 ± 2% of spiders are extracted from *S. alterniflora* and *S. patens*, respectively (H.G.D. & R.F.D., unpublished data).

Analysis. For each habitat, the absolute abundance (number per square meter) of all resident spider species was determined. Patterns of voltinism and reproduction (occurrence of spiderlings) were determined for the nine most abundant spider

species. In each of the four *Spartina* habitats, the richness (S) and diversity of the spider community were also determined. Spider diversity (H') was measured over the course of the season using the Shannon-Wiener information index (Shannon 1948):

$$H' = - \sum_{i=1}^S p_i \log_2 p_i \quad (1)$$

where H' is the amount of observed diversity in a community, S is the number of species (species richness), and p_i is the relative abundance of the i^{th} species. The greater the number of species (S) and the more even their abundances, the higher the diversity index H' will be. The maximum possible diversity for a community can be calculated as follows:

$$H_{\max} = \log_2 S. \quad (2)$$

Using the equitability index (Pielou 1966), the evenness of spider species representation in the *Spartina* habitats was calculated as

$$E = H' / H_{\max} \quad (3)$$

where H' is the observed diversity as defined in Equation (1), H_{\max} is the maximal possible diversity as defined in Equation (2), and E is the measurement of equitability. The equitability index ranges from 0 to 1, and the closer E is to 1, the more equally abundant are the species in the community under study.

The Berger-Parker index was used to estimate dominance (Berger & Parker 1970):

$$D = N_m / N_1, \quad (4)$$

where D is a measure of the dominance of the most abundant species in the community (range 0 to 1), N_m is the absolute abundance of the most common species in the community under consideration, and N_1 is the overall density of all the species in that community. The higher the proportion of a single species, the more unevenly distributed are the species in a community.

Because similar values for any one of the community indices (e.g., species diversity) can be obtained with a mutually exclusive set of spider taxa, these values do not indicate how similar the taxonomic compositions of spider communities are among the four *Spartina* habitats. Therefore, measurements of similarity were calculated using the Sørensen index of taxonomic similarity (Sørensen 1948, Bloom 1981):

$$C_i = 2S_c / (S_a + S_b) \quad (5)$$

where C_i is the measurement of taxonomic similarity (range 0 to 1), S_c is the number of species sampled throughout the entire year the two habitats a and b have in common, and S_a and S_b are the total numbers of species in habitats a and b, respectively. Because the Sørensen index of similarity does not take into account the relative abundances

of the species under consideration, we used a second similarity index (Kendall's rank correlation), whereby species are ranked according to their abundances. The rank abundance of the different species is used to calculate Kendall's τ (for details see Sokal & Rohlf 1981, Ghent 1963). Both indices are constrained between 0 (no taxonomic overlap) and 1 (taxonomic unity).

Data were examined for normality and homoscedasticity and, if necessary, were transformed before analysis. Analysis of variance (ANOVA) was the statistical model used to test for significant differences in all calculated community indices among the four *Spartina* habitats. Differences among habitat means for all community indices were tested using Duncan's multiple range test ($P < 0.05$) (Sokal & Rohlf 1981).

Results

Thirty-four spider species, 20 web-building and 14 hunting species, in 12 families were sampled from the four *Spartina* habitats at Tuckerton (Table 1). However, we considered only 21 of the 34 species to be residents on the marsh. Of the remaining 13 species, each was represented by four or fewer individuals and was found only on a single date. Because of their sporadic and rare appearance in samples, it is likely that these 13 species were transients; consequently, they were not included in our calculations of community statistics.

The taxonomic composition of the spider community across the four *Spartina* habitats was quite similar as evidenced by the relatively high Sørensen indices, which ranged from 0.79 to 0.88 (Fig. 2). However, by measuring community similarity with Kendall's τ , which adjusts for differences in species abundance, habitat differences emerge. Now the assemblage of spiders in *S. patens* stands out as being considerably different in taxonomic composition than that in the three *S. alterniflora* communities ($\tau = 0.23, 0.31,$ and 0.13 for short, intermediate, and tall-form *S. alterniflora*, respectively) (Fig. 2). Kendall's τ , like the Sørensen index, revealed high taxonomic similarity among the spider communities in the three *S. alterniflora* habitats ($\tau \approx 0.70$ for all pairwise combinations of short, intermediate, and tall-form *S. alterniflora*) (Fig. 2).

The species richness of the spider community increased along an elevational gradient in the *S. alterniflora* habitats from 5.6 species in tall-form *S. alterniflora* to 9.2 species in short-form *S. alterniflora*; the *S. patens* habitat was intermediate, with an average of 7.2 spider species (Fig. 3A). An examination of the seasonal fluctuations in species richness shows that in early May, short- and intermediate-form *S. alterniflora* as well as *S. patens* harbored about six species each, whereas only one species was found in tall-form *S. alterniflora* (Fig. 4A). Although the number of species in tall-form *S. alterniflora* increased sharply over a period of 6 wk, species richness remained below the level in

Table 1. Spider species and their average annual densities in each of the four *Spartina* habitats at Tuckerton, N.J.

Species ^a	Average annual densities, no./m ² /yr ^b			
	SP	SAS	SAI	SAT
Web-builders				
Dictynidae				
* <i>Dictyna altamtra</i> Gertsch & Davis	1.74	25.13	42.89	8.90
Theridiidae				
<i>Achaearanea globosus</i> (Hentz)	0.03	—	—	—
Linyphiidae				
* <i>Grammonota trivittata</i> Banks	0.40	150.85	18.19	22.93
* <i>Erigone tenuipalpis</i> (Emerton)	0.31	12.44	2.84	1.16
<i>Floricomus crosbyi</i> Iviet & Barrows	0.03	—	—	—
<i>Pelecopsis excavatum</i> (Emerton)	0.03	—	—	—
sp. A	—	—	0.03	—
Araneidae				
* <i>Hyposinga variabilis</i> (Emerton)	0.64	15.93	8.53	1.99
* <i>Neoscona pratensis</i> (Hentz)	0.34	0.70	2.35	1.50
<i>Argiope trifasciata</i> (Forsk.)	—	—	0.03	—
<i>Acanthepeira</i> sp.	—	—	0.03	—
<i>Eustala emertoni</i> (Banks)	—	0.09	—	—
sp. B	—	—	0.03	—
sp. C	0.12	—	—	—
sp. D	0.03	—	—	—
sp. E	—	—	0.03	—
Tetragnathidae				
* <i>Glenognatha iveti</i> Levi	—	—	0.03	0.06
* <i>Glenognatha</i> n. sp.	0.67	6.85	7.89	0.40
* <i>Tetragnatha caudata</i> Emerton	—	0.03	—	0.09
*sp. F	0.06	—	0.03	0.06
Hunters				
Lycosidae				
* <i>Pardosa littoralis</i> Banks	64.13	2.45	24.73	11.37
* <i>Lycosa modesta</i> (Keyserling)	0.03	37.81	0.49	0.12
* <i>Pirata marxi</i> Stone	0.03	0.95	0.15	0.09
Oxyopidae				
sp. G	—	—	—	0.03
Gnaphosidae				
* <i>Zelotes pullis</i> (Bryant)	2.51	0.03	—	0.03
* <i>Callilepis</i> sp.	0.70	—	—	—
Clubionidae				
* <i>Clubiona saltitans</i> Emerton	0.67	10.45	4.3	1.13
<i>Clubiona nicholisi</i> Gertsch	—	0.06	—	—
Thomisidae				
* <i>Misumenops</i> sp.	0.25	0.03	—	0.09
Philodromidae				
* <i>Tibellus oblongus</i> (Walckenaer)	0.18	0.03	0.64	0.03
* <i>Thanatus striatus</i> C. L. Koch	3.33	0.03	0.12	—
Salticidae				
* <i>Marpissa pikei</i> (G. & E. Peckham)	—	0.15	0.70	0.21
* <i>Metacyrba undata</i> (DeGeer)	—	0.12	—	—
* <i>Sitticus palustris</i> (G. & E. Peckham)	3.88	0.92	0.12	—

^a *, resident species; 22 samples taken from two plots in each habitat on 11 dates from 7 May to 11 October 1985.

^b SP, *Spartina patens*; SAS, short-form *S. alterniflora*; SAI, intermediate-form *S. alterniflora*; SAT, tall-form *S. alterniflora*.

the three other habitats for the remainder of the season (Fig. 4A).

Spider diversity and equitability were highest in intermediate-form *S. alterniflora* (H' , 2.3; E , 0.75) and lowest in *S. patens* (H' , 1.2; E , 0.45) (Fig. 3 B and C). In intermediate-form *S. alterniflora* and *S. patens*, spider diversity and equitability remained rather constant throughout the season. This pattern contrasted with that for the short- and tall-form *S. alterniflora* habitats, where species diversity and equitability were low in spring, increased until midsummer, and then leveled out (Fig. 4 B

and C). Differences in spider diversity as well as equitability among the four *Spartina* habitats were reflected in the Berger-Parker index of dominance (Fig. 3D). Communities that were characterized by low diversity (e.g., *S. patens*) tended to be dominated by one or a few species. For example, 77% of all spiders sampled in the *S. patens* habitat belonged to a single species (*Pardosa littoralis* Banks) compared with only 40% in intermediate-form *S. alterniflora*. Over the course of the season, dominance values changed only slightly in intermediate-form *S. alterniflora* and more in *S. patens*, but

Kendall's Tau	Sørensen Index			
	SP	SAS	SAI	SAT
SP		0.80	0.81	0.79
SAS	0.23		0.85	0.88
SAI	0.31	0.71		0.84
SAT	0.13	0.70	0.70	

Fig. 2. Taxonomic similarity among the spider communities in the four *Spartina* habitats. SP, *Spartina patens*; SAS, short-form *S. alterniflora*; SAI, intermediate-form *S. alterniflora*; SAT, tall-form *S. alterniflora*. Pair-wise comparisons of habitats are measured by Sørensen's index (above the diagonal) and Kendall's tau (below the diagonal). Both indices are constrained between 0 (no taxonomic overlap) and 1 (taxonomic unity).

dropped considerably from about 1.0 to 0.5 in the short- and tall-form *S. alterniflora* habitats (Fig. 4D). Decreases in dominance occurred in tall-form *S. alterniflora* as more spider species colonized that temporary habitat and short-form *S. alterniflora* as populations of the rarer species increased (Fig. 4 A and D).

Total spider density was low during spring in tall- and intermediate-form *S. alterniflora* as well as in *S. patens* but was relatively high in short-form *S. alterniflora* (Fig. 4E). Populations increased in all four habitats, reaching a maximum during mid-June in intermediate-form *S. alterniflora* and mid-July in short-form *S. alterniflora* and *S. patens*. Maximum spider density did not occur until mid-August in tall-form *S. alterniflora*, and populations never attained the level they did in the other three habitats.

The spider community in *S. patens* differed from those in the three *S. alterniflora* communities in the proportion of hunting to web-building species (Fig. 5). About 95% of all spiders in *S. patens* belonged to the hunting guild (e.g., *P. littoralis*, and *Clubiona saltitans* Emerton), whereas only 23% of spiders were hunters in the *S. alterniflora* habitats. In particular, hunting spiders were rare in tall-form *S. alterniflora* (Fig. 5). Web-builders (e.g., *Grammonota trivittata* Banks, *Dictyna altamira* Gertsch & Davis, *Hyposinga variabilis* (Emerton), and *Erigone tenuipalpis* (Emerton)) that were rare in *S. patens* occurred abundantly in *S. alterniflora* (Fig. 5). In addition to the dominance of hunting spiders in *S. patens*, this community also contained several species (also hunters) that were never or rarely sampled in *S. alterniflora*. These were the two gnaphosids, *Zelotes pullis* (Bryant) and *Callilepis* sp., the philodromid *Thanatus striatus* C. L. Koch, and the salticid *Sitticus palustris* (G. & E. Peckham) (Table 1). Despite the

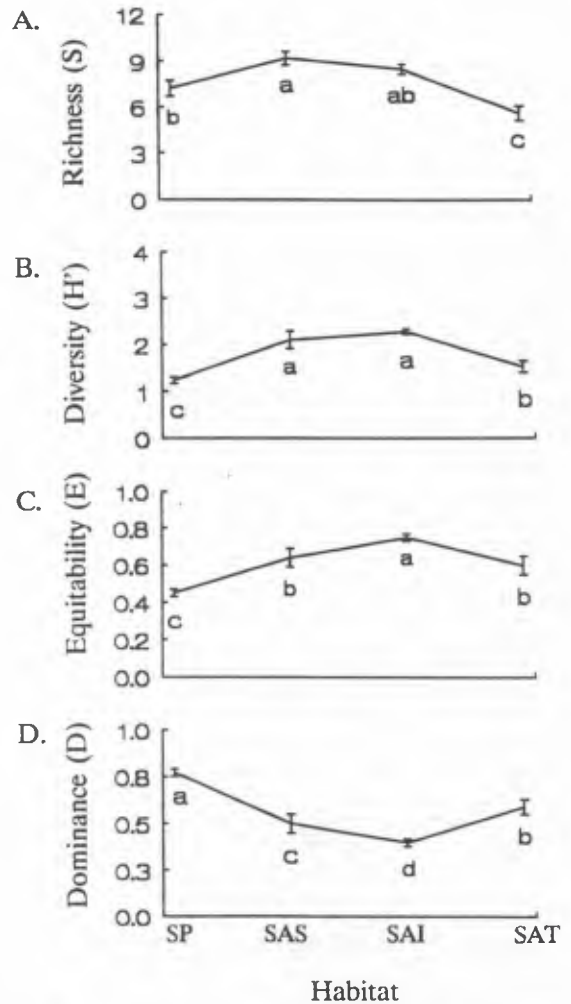


Fig. 3. Species richness (A), diversity (B), equitability (C), and dominance (D) of the spider community in the four *Spartina* habitats along an elevational gradient at Tuckerton, N.J. SP, *S. patens*; SAS, short-form *S. alterniflora*; SAI, intermediate-form *S. alterniflora*; SAT, tall-form *S. alterniflora*. Means (\pm SE, $n = 22$) with different letters are significantly different ($P < 0.05$).

unique occurrence of many species in either *S. patens* or *S. alterniflora*, a few hunters (e.g., *P. littoralis*) ranged across all habitats and were sampled in both *S. patens* and *S. alterniflora* (Fig. 6G).

The species composition in the three *S. alterniflora* communities was similar, but spider species varied in abundance among the three habitats (Fig. 5 B-D). For example, *G. trivittata*, *D. altamira*, and *P. littoralis* were the three most abundant spiders (about 80% of all individuals) in all three *S. alterniflora* habitats. Generally, however, many spider species, including both hunters and web-builders, decreased in abundance along the elevational gradient from short- to tall-form *S. alterniflora* (Fig. 6 A-D, H and I). These included the web-builders *G. trivittata*, *E. tenuipalpis*, *H. var-*

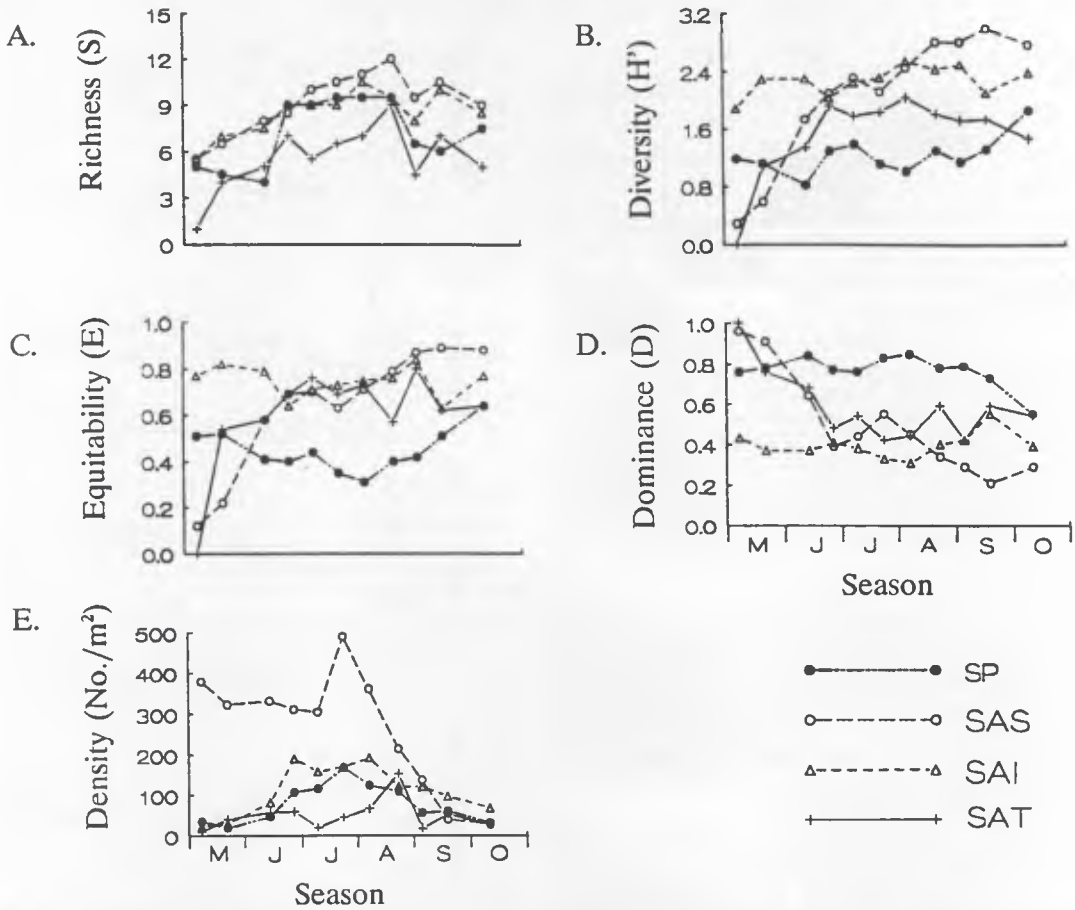


Fig. 4. Seasonal fluctuations in the species richness (A), diversity (B), equitability (C), dominance (D), and total abundance (E) of the spider community in the four *Spartina* habitats at Tuckerton, N.J. SP, *S. patens*; SAS, short-form *S. alterniflora*; SAI, intermediate-form *S. alterniflora*; SAT, tall-form *S. alterniflora*. Plotted are the means of two plots in each habitat sampled on 11 dates from 7 May to 11 October 1985.

abilis, and *Glenognatha* n. sp. and the hunters *Lycosa modesta* (Keyserling) and *C. saltitans*. Two exceptions were the web-builders *D. altamira* and *Neoscona pratensis* (Hentz), which were most abundant in intermediate-form *S. alterniflora* (Fig. 6 E and F). Across the four habitats sampled, no resident spider species occurred most abundantly in tall-form *S. alterniflora*.

Nine species of spiders were sufficiently abundant to obtain detailed information on their population dynamics and natural history. *G. trivittata* and *E. tenuipalpis* are small (2–3 mm) aerial sheet-weavers in the family Linyphiidae. Webs are oriented horizontally, are convex in shape, and are suspended close to the marsh surface in short-form *S. alterniflora* by an irregular network of threads. Information on prey capture for these species is difficult to obtain because webs are not sticky, and prey can easily escape if they are not seized immediately. The araneids *H. variabilis* (4–6 mm) and *N. pratensis* (10–15 mm) build vertically-oriented, regular webs in short- and intermediate-

form *S. alterniflora*. Planthoppers (mostly the migratory forms of *Prokelisia*) constituted 94 and 70% of the prey captured in the webs of *N. pratensis* and *H. variabilis*, respectively (H.G.D., unpublished data). *D. altamira* is a small (2–3 mm) dictynid which builds a lacy, irregular web supported by a framework of threads. On occasion in intermediate-form *S. alterniflora*, planthoppers and small Diptera were seen in the webs, but observations were too few to establish patterns of prey capture. *Glenognatha* n. sp. is a small (2–3 mm), previously undescribed tetragnathid (Hormiga & Döbel in press) which builds horizontal webs close to the marsh surface. Of the three common hunting spiders, the two lycosids *P. littoralis* (5–6 mm) and *L. modesta* (10–12 mm) captured mostly (60–70% of all prey) planthoppers in the genera *Prokelisia* and *Delphacodes*. *C. saltitans* (4–5 mm) was too shy for us to observe feeding because it would scurry rapidly back into its retreat.

The population dynamics of these nine dominants differed dramatically among the four *Spar-*

tina habitats (Fig. 7). For example, most web-builders occurred abundantly during May and June in short-form *S. alterniflora* on the high marsh but were rare at this time in tall-form *S. alterniflora*, suggesting that spiders overwintered successfully only at higher elevations on the marsh (Fig. 7 A-E). As the season progressed, these species colonized tall-form *S. alterniflora*, and their populations grew to a maximum in mid-August. By contrast, hunting spiders, which were abundant in both *S. patens* and short-form *S. alterniflora* from June through August, failed to colonize tall-form *S. alterniflora* successfully, and their populations never increased in this habitat (Fig. 7 G-I).

Of the four web-builders that occurred most abundantly in short-form *S. alterniflora*, three were bivoltine (*G. trivatatta*, *E. tenuipalpis*, and *H. variabilis*) (Fig. 8 A-C) with peaks of juvenile abundance in May-June and again in July-August. *Glenognatha* n. sp., the only univoltine species in short-form *S. alterniflora*, produced juveniles during July-August (Fig. 8D). The two web-builders in intermediate-form *S. alterniflora* (*D. altamira* and *N. pratensis*) were univoltine with juveniles prevalent during June-July and September, respectively (Fig. 8 E and F). All web-builders (with the exception of *N. pratensis*) overwintered as adults. Hunting spiders were all univoltine; juveniles were common from June through August (Fig. 8 G-I). However, differences in overwintering strategies were evident. *P. littoralis* overwintered as juveniles, whereas most *L. modesta* and *C. saltitans* spent the winter in the adult stage.

Discussion

Our data show that the spider community in *S. patens* is very different from the communities in the three *S. alterniflora* habitats. The *S. patens* community consisted almost exclusively of hunting spiders. We attribute the scarcity of web-builders in *S. patens* to the architecture of the grass. The matted nature of *S. patens* and the tendency for culms to lodge results in few upright attachment sites for spider webs (Hypothesis 3 supported). It is very unlikely that any factor associated with elevation, such as frequency of tidal flooding, is responsible for the dramatic difference in the composition of the spider communities between *S. patens* and short-form *S. alterniflora*. On mid-Atlantic marshes, these habitats are separated by only a few centimeters in elevation, and patterns of tidal inundation are very similar (Adams 1963, Blum 1968, Redfield 1972, Denno 1977). Although the structure of *S. patens* may exclude many web-builders, it may provide specific microhabitats or foraging space (thatch) (or both) for certain hunting spiders which do not occur in *S. alterniflora* (Hypothesis 2 supported). For example, gnaphosids depend upon dense vegetation in which to build their tunnellike retreats; they emerge from these tunnels to hunt (Kaston 1978). The complex-struc-

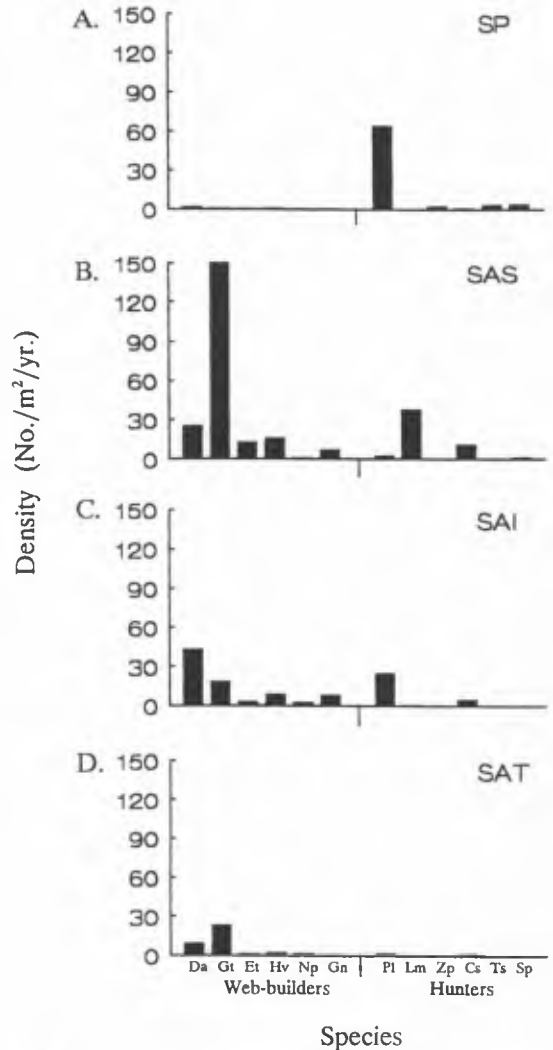
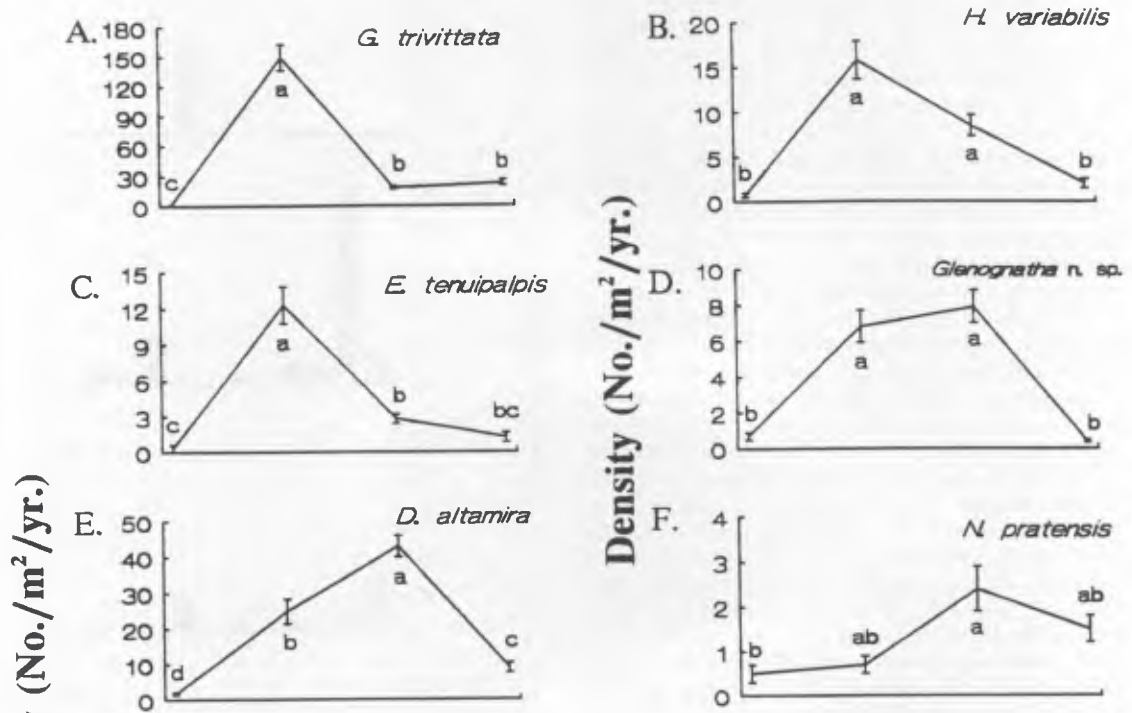


Fig. 5. Absolute abundance (number per square meter per year) of the 12 most common web-building and hunting spider species in the four *Spartina* habitats at Tuckerton, N.J. Habitat symbols: SP, *S. patens*; SAS, short-form *S. alterniflora*; SAI, intermediate-form *S. alterniflora*; SAT, tall-form *S. alterniflora*. Species symbols: Da, *Dictyna altamira*; Gt, *Grammonota trivittata*; Et, *Erigone tenuipalpis*; Hv, *Hyposinga variabilis*; Np, *Neoscona pratensis*; G, *Glenognatha* n. sp.; Pl, *Pardosa littoralis*; Lm, *Lycosa modesta*; Zp, *Zelotes pullis*; Cs, *Clubiona saltitans*; Ts, *Thanatus striatus*; Sp, *Sitticus palustris*. Plotted are the mean number of individuals per species in two plots of each habitat sampled on 11 dates from 7 May to 11 October 1985.

tured thatch of *S. patens* provides such microhabitats and may explain why *Z. pullis* and *Callilepis* sp. are restricted to *S. patens*. Generally, the matted structure of *S. patens* is easily negotiated by most hunting species. Wolf spiders the size of *P. littoralis* (5-6 mm) easily pass through the matted culms. However, very large hunters like *L. modesta* (10-12 mm) cannot enter the dense structure

Web-builders



Hunters

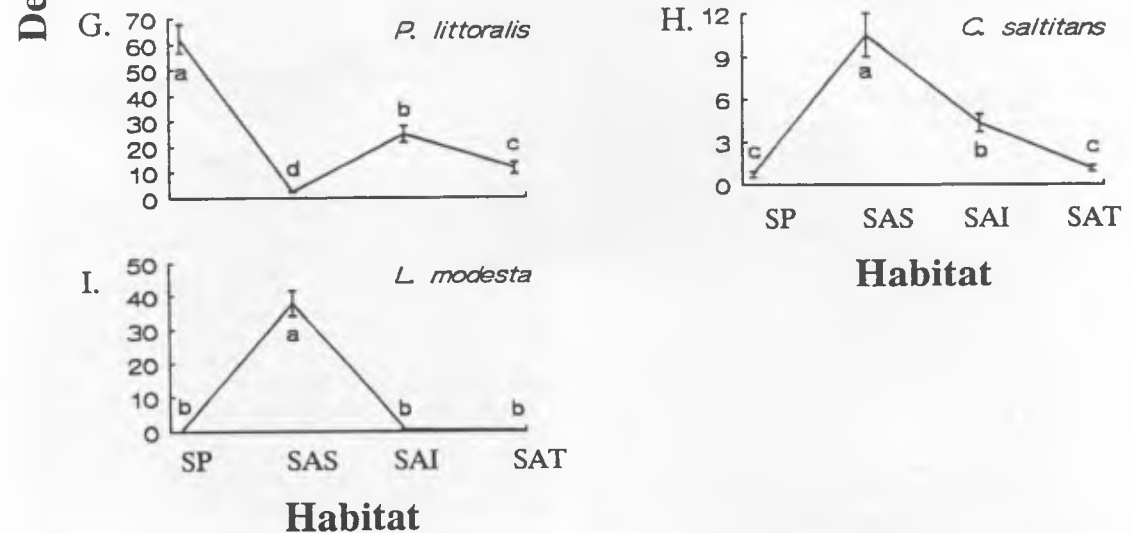
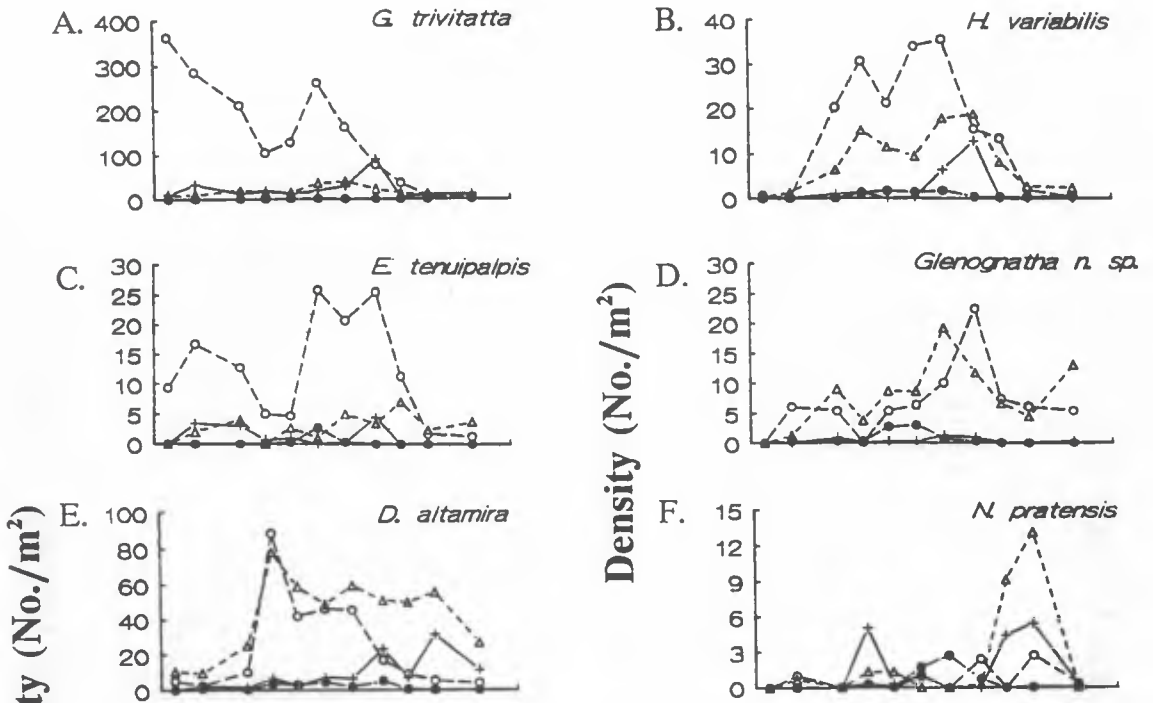
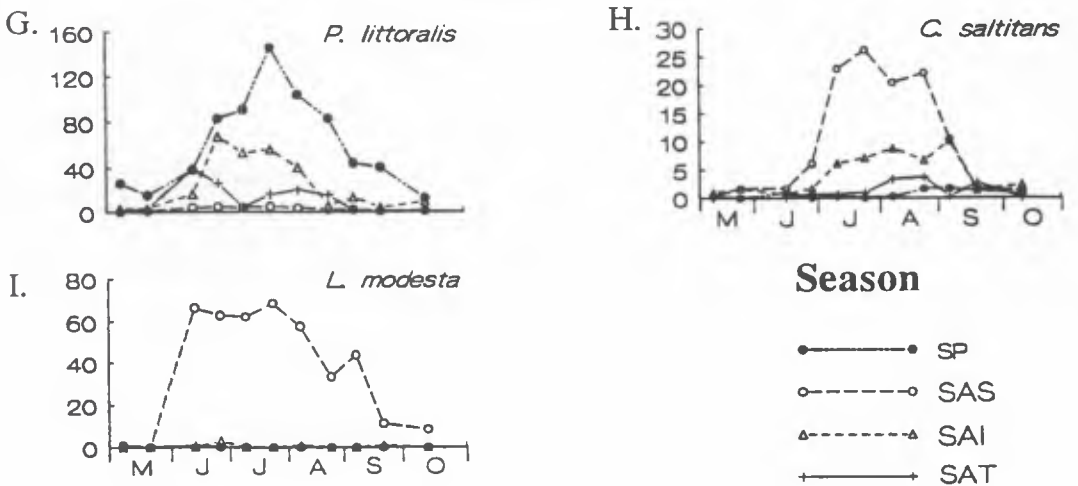


Fig. 6. Annual mean densities (number per square meter per year) of *G. trivittata* (A), *H. variabilis* (B), *E. tenuipalpis* (C), *Glenognatha* n. sp. (D), *D. altamira* (E), *N. pratensis* (F), *P. littoralis* (G), *C. saltitans* (H), and *L. modesta* (I) in the four *Spartina* habitats along an elevational gradient at Tuckerton, N.J. SP, *S. patens*; SAS, short-form *S. alterniflora*; SAI, intermediate-form *S. alterniflora*; SAT, tall-form *S. alterniflora*. Means (\pm SE, $n = 22$) with different letters are significantly different ($P < 0.05$).

Web-builders



Hunters



Season

Fig. 7. Seasonal abundance (number per square meter) of *G. trivittata* (A), *H. variabilis* (B), *E. tenuipalpis* (C), *Glenognatha n. sp.* (D), *D. altamira* (E), *N. pratensis* (F), *P. littoralis* (G), *C. saltitans* (H), and *L. modesta* (I) in the four *Spartina* habitats at Tuckerton, N.J. SP, *S. patens*; SAS, short-form *S. alterniflora*; SAI, intermediate-form *S. alterniflora*; SAT, tall-form *S. alterniflora*. Plotted are the means of two plots for each habitat sampled on 11 dates from 7 May to 11 October 1985.

Web-builders

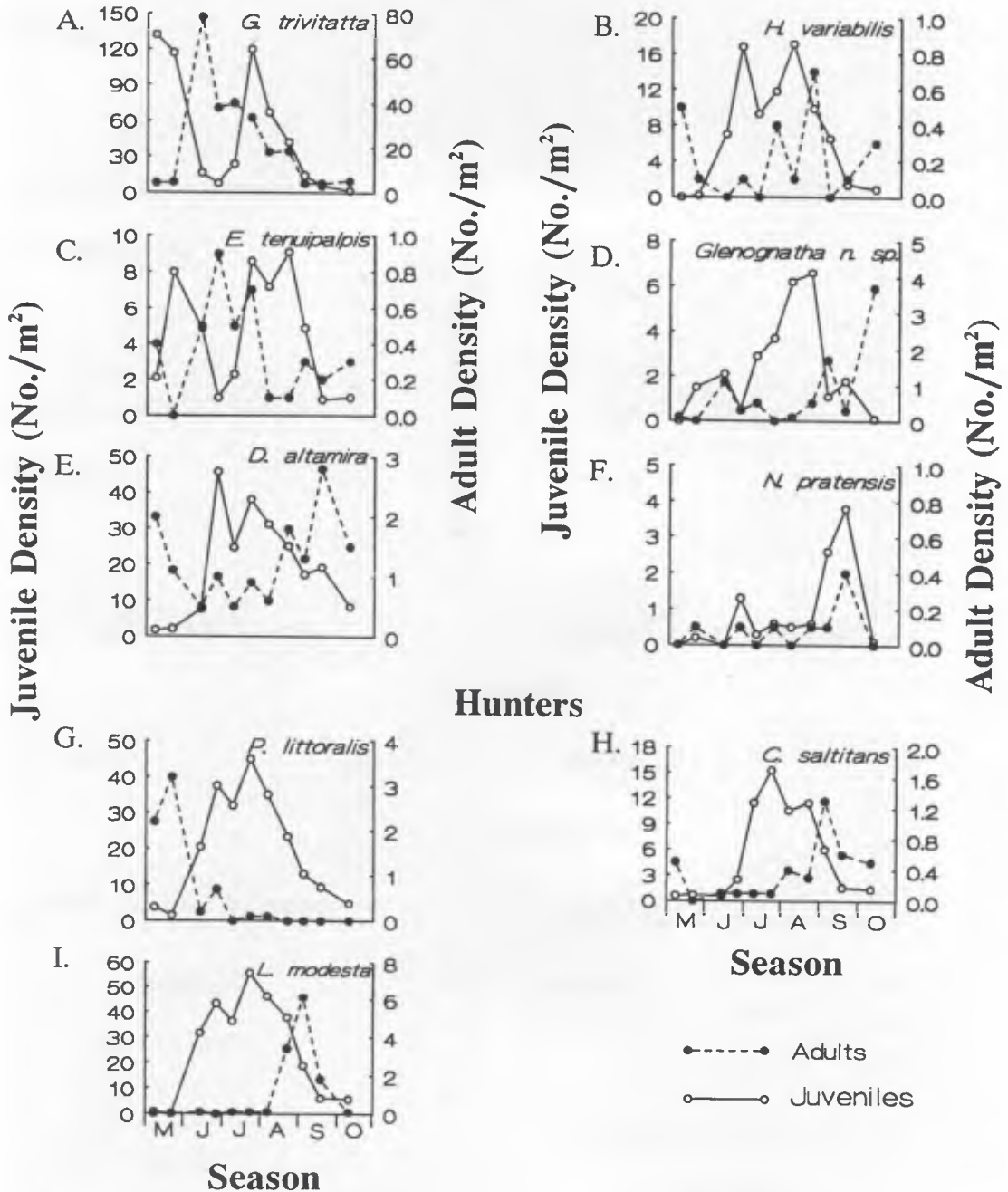


Fig. 8. Seasonal abundance (number per square meter, averaged across all habitats) of the adults and juveniles of *G. trivittata* (A), *H. variabilis* (B), *E. tenuipalpis* (C), *Glenognatha n. sp.* (D), *D. altamira* (E), *N. pratensis* (F), *P. littoralis* (G), *C. saltitans* (H), and *L. modesta* (I) at Tuckerton, N.J.

of *S. patens* easily and remain mostly on top of the matted culms to forage. This may explain the preference of *L. modesta* for more open-structured habitats like short-form *S. alterniflora*.

Although the taxonomic composition of the spider community in the three *S. alterniflora* habitats was similar, there are noteworthy differences in the abundance of species. For example, the relative

rarity of hunting spiders in tall-form *S. alterniflora* is most likely caused by the combined effects of frequent tidal flooding and the lack of thatch in this habitat. Flooding interferes directly with the ground-foraging habit of most hunting spiders, even though species such as *P. littoralis* are able to walk on the surface of the water (H.G.D., unpublished data). As a general pattern, the population densities of several hunting spiders (*L. modesta*, *C. saltitans*, and *S. palustris*) tended to decrease down the elevational gradient from short- to tall-form *S. alterniflora*, suggesting that tidal inundation limits their distribution to the high marsh (Hypothesis 1 supported). Also, by artificially manipulating the biomass of thatch in short-form *S. alterniflora*, Döbel (1987) showed that hunting spiders like *P. littoralis* avoid thatch-free patches for foraging, even though prey is abundant there. Furthermore, thatch is an important correlate with spider density in deciduous forest habitats (Uetz 1975). The relative lack of thatch in tall-form *S. alterniflora* also may contribute to the rarity of ground-foraging species in this habitat.

Most web-building species also were rare in tall-form *S. alterniflora* and several increased in density with elevation (e.g., *G. trivitatta*, *E. tenuipalpis*, and *H. variabilis*). Even though the occurrence of a physical gill allows some web-building species to withstand submergence (Rovner 1986, 1987), we never observed this phenomenon in salt marsh spiders. Although tidal flooding is implicated, it cannot be the only factor that influences the abundance of web-builders in tall-form *S. alterniflora*. We expected the tall culms of tall-form *S. alterniflora* to compensate somewhat for the low elevation of this habitat, allowing web-builders to construct their webs in the upper canopy of the grass. However, winds blow constantly throughout much of the year in coastal marsh habitats, and spider webs may be easily destroyed by the whipping action of tall-form *S. alterniflora* culms and leaf blades. In particular, the short culms of short-form *S. alterniflora* are not as affected by winds, and webs can be seen remaining in this habitat after having been destroyed in tall-form *S. alterniflora* (H.G.D., unpublished data).

In addition to the direct effects of flooding and vegetation structure on spiders in the tall-form *S. alterniflora* habitat, its temporary nature also is very influential in dictating population dynamics and community structure. Because no spider species is able to overwinter on the exposed creek banks where tall-form *S. alterniflora* grows, this habitat must be colonized from persistent high marsh habitats every year. The low species richness as well as the low overall abundance of spiders in the tall-form *S. alterniflora* habitat during spring (Fig. 4 A and E) documents the ephemerality of tall-form *S. alterniflora*. As the season progresses, spider (mostly web-builders) richness and abundance increase. However, several species (e.g., *G. trivitatta*, *H. variabilis*, and *D. altamira*) do not reach max-

imum abundance in tall-form *S. alterniflora* until fall, >1 mo after maximum population size is achieved in the other habitats (Fig. 7 A, B, and E).

As pointed out previously, the low richness and abundance of spiders in tall-form *S. alterniflora* is not solely a reflection of the colonization process of temporary habitats. Wolf spiders such as *P. littoralis* colonize tall-form *S. alterniflora* rapidly in spring (Fig. 7 G), but their populations simply do not build for a variety of reasons. Conditions may not be conducive for population growth (tidal flooding), but storm conditions may reduce spider populations in tall-form *S. alterniflora* directly and selectively. For example, 1 d before sampling on 9 July, a strong storm with heavy precipitation affected the marsh and its spider fauna, possibly causing the lower densities of several spider species (e.g., *P. littoralis* and *N. pratensis*) compared with samples taken before and after this particular date (first July sampling date shown in Fig. 7 F and G) (National Oceanic and Atmospheric Administration 1985). Consequently, a combination of harsh conditions and mandatory recolonization of this temporary habitat results in the depauperate spider community in tall-form *S. alterniflora*.

Because spiders (especially hunters) can show strong numerical (aggregative) responses to increases in prey density (Kobayashi 1975, Kenmore 1980, Bultman & Uetz 1982, Rypstra 1983, Kenmore et al. 1984, Döbel 1987), it could be argued that spiders avoid tall-form *S. alterniflora* because prey are rare. In fact, planthoppers, the most preferred prey of all spiders studied (Döbel 1987), colonize tall-form *S. alterniflora* habitats in spring, and by midsummer, populations can exceed those in short- and intermediate-form *S. alterniflora* by one order of magnitude (Denno & Grissell 1979). Also, planthoppers and leafhoppers are extremely abundant in *S. patens*, and densities are similar to those found in *S. alterniflora* (Denno 1976, 1977). Consequently, differences in prey availability are not likely responsible for the low densities of most spider species in tall-form *S. alterniflora* or for differences in habitat selection in general.

Several web-building species (e.g., *D. altamira* and *N. pratensis*) were most abundant at midelevations on the marsh in intermediate-form *S. alterniflora*, making arguments that are based solely on tidal influence problematical. In these cases, structural differences (culm density and height) between intermediate and short-form *S. alterniflora* likely contribute to patterns of habitat selection. Interactions between web-builders for attachment sites also may contribute to habitat divergence (see Wise 1984; Spiller 1984, 1986). For example, of the two most abundant web-builders, *D. altamira* occurred most commonly in intermediate-form *S. alterniflora*, whereas *G. trivitatta* was most abundant in short-form *S. alterniflora*. However, in their shared short-form *S. alterniflora* habitat, the similar population fluctuations of these two species from July through October does not suggest any

competitive displacement between these spiders for web sites (see Fig. 7 A and E). Species interactions may be involved in differences in habitat selection between the two lycosids. For example, experimental manipulations with three co-occurring species of wolf spiders in a European salt marsh implicate interspecific interactions (Schaefer 1974). In our study, *P. littoralis* was least abundant in short-form *S. alterniflora*, the habitat where *L. modesta* occurred most commonly. Even though the preferred prey items of both spiders are planthoppers, it is likely that the larger (10–12 mm) and more aggressive *L. modesta* simply drives the smaller (6 mm) *P. littoralis* from short-form *S. alterniflora*. However, only careful field experiments will elucidate the underlying causes for differences in habitat selection between these species pairs.

In summary, our results suggest that differences in plant architecture between *S. patens* and *S. alterniflora* best explain the divergent spider communities in these habitats. Hunting spiders are more abundant in *S. patens*, and web-builders predominate in *S. alterniflora*. We suggest that the availability of thatch in *S. patens* facilitates efficient foraging by ground-dwelling species in that habitat, and that web-builders find sites for web attachment in *S. alterniflora* that do not occur in *S. patens*. The spider communities of the *S. alterniflora* habitats are taxonomically similar, but certain species select specific habitats along an elevational gradient from short- to tall-form *S. alterniflora*. Some web-building species and most hunting spiders decrease in abundance down this elevational gradient, resulting in a spider community in tall-form *S. alterniflora* that is composed of a few rare species. The duration and frequency of tidal flooding and the probability of habitat destruction during winter increase down the elevational gradient from short- to tall-form *S. alterniflora* and together act to influence the distribution, abundance, and community structure of spiders on intertidal *S. alterniflora* marshes. Our findings support the general notion that habitat structure and physical factors are important in determining the organization of spider communities.

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References Cited

- Adams, D. A. 1963. Factors influencing vascular plant zonation in North Carolina salt marshes. *Ecology* 44: 445–456.
- Barnes, R. D. 1953. The ecological distribution of spiders in non-forest maritime communities at Beaufort, North Carolina. *Ecol. Monogr.* 23: 315–337.
- Berger, W. H. & F. L. Parker. 1970. Diversity of planktonic Foraminifera in deep-sea sediments. *Science* 168: 1345–1347.
- Bertness, M. D. & A. M. Ellison. 1987. Determinants of pattern in a New England salt marsh plant community. *Ecol. Monogr.* 57: 129–147.
- Bloom, S. A. 1981. Similarity indices in community studies: potential pitfalls. *Mar. Ecol. Prog. Ser.* 5: 125–128.
- Blum, J. L. 1968. Salt marsh spartinas and associated algae. *Ecol. Monogr.* 38: 199–221.
- Bultman, T. L. & G. W. Uetz. 1982. Abundance and community structure of forest floor spiders following litter manipulation. *Oecologia* 55: 34–41.
- Cameron, C. N. 1972. Analysis of insect trophic diversity in two salt marsh communities. *Ecology* 53: 58–73.
- Culin, J. D. & K. V. Yeargan. 1983. Comparative study of spider communities in alfalfa and soybean ecosystems: ground-surface spiders. *Ann. Entomol. Soc. Am.* 76: 832–838.
- Denno, R. F. 1976. Ecological significance of wing-polymorphism in Fulgoroidea which inhabit tidal salt marshes. *Ecol. Entomol.* 1: 257–266.
1977. Comparison of the assemblages of sap-feeding insects (Homoptera-Hemiptera) inhabiting two structurally different salt marsh grasses in the genus *Spartina*. *Environ. Entomol.* 6: 359–372.
1980. Ecotope differentiation in a guild of sap-feeding insects on the salt marsh grass, *Spartina patens*. *Ecology* 61: 702–714.
1983. Tracking variable host plants in space and time, pp. 291–341. In R. F. Denno & M. S. McClure [eds.], *Variable plants and herbivores in natural and managed systems*. Academic, New York.
1985. Fitness, population dynamics and migration in planthoppers: the role of host plants, pp. 623–640. In M. S. Rankin [ed.], *Migration: mechanisms and adaptive significance*. Contributions in marine science, vol. 27. Marine Science Institute, University of Texas at Austin, Port Aransas, Tex.
- Denno, R. F. & E. E. Grissell. 1979. The adaptiveness of wing-dimorphism in the salt marsh-inhabiting planthopper, *Prokelisia marginata* (Homoptera: Delphacidae). *Ecology* 60: 221–236.
- Denno, R. F., M. J. Raupp, D. W. Tallamy & C. F. Reichelderfer. 1980. Migration in heterogeneous environments: differences in habitat selection between the wing forms of the dimorphic planthopper, *Prokelisia marginata* (Homoptera: Delphacidae). *Ecology* 61: 859–867.
- Denno, R. F., M. E. Schauff, S. W. Wilson & K. L. Olmstead. 1987. Practical diagnosis and natural history of two sibling salt marsh-inhabiting planthoppers in the genus *Prokelisia* (Homoptera: Delphacidae). *Proc. Entomol. Soc. Wash.* 89: 687–700.
- Dietrick, E. J. 1961. An improved back pack motor fan for suction sampling of insect populations. *J. Econ. Entomol.* 54: 394–395.
- Döbel, H. C. 1987. The role of spiders in the regulation of salt marsh planthopper populations. M.S. thesis, University of Maryland, College Park.
- Duffey, D. 1968. An ecological analysis of the spider fauna of sand dunes. *J. Anim. Ecol.* 37: 641–674.
- Foelix, R. F. 1982. *Biology of spiders*. Harvard University Press, Cambridge, Mass.
- Gallagher, J. L., G. F. Sommer, D. M. Grant & D. M.

- Seliskar, 1988.** Persistent differences in two forms of *Spartina alterniflora*: a common garden experiment. *Ecology* 69: 1005–1008.
- Ghent, A. W. 1963.** Kendall's "Tau" coefficient as an index of similarity in comparisons of plant or animal communities. *Can. Entomol.* 95: 568–575.
- Greenstone, M. H. 1978.** The numerical response to prey availability of *Pardosa ramulosa* (McCook) (Araneae: Lycosidae) and its relationship to the role of spiders in the balance of nature. *Symp. Zool. Soc. Lond.* 42: 183–193.
- Hatley, C. A. & J. A. MacMahon. 1980.** Spider community organization: seasonal variation and the role of vegetation architecture. *Environ. Entomol.* 9: 632–639.
- Headstrom, R. 1972.** Spiders of the United States. Barnes, South Brunswick, N.Y.
- Heydemann, B. 1960a.** Die biozönotische Entwicklung vom Vorland zum Koog. Vergleich.-ökolog. Untersuchungen an der Nordseeküste 1. Spinnen (Araneae) Abhandlungen der Akademischen Wissenschaftlichen Literatur Mainz. Mathematik und Naturwissenschaften, Klasse NR. 11.
- 1960b.** Verlauf und Abhängigkeit von Spinnensukzessionen im Neuland der Nordseeküste. *Verh. Dtsch. Zool. Ges.* 47: 431–457.
- Hormiga, G. & H. G. Döbel. In press.** A new *Glenognatha* (Araneae: Tetragnathidae) from New Jersey, with redescription of *G. centralis* and *G. minuta*. *J. Arachnol.*
- Kaston, B. J. 1978.** How to know the spiders. Brown, Dubuque, Iowa.
- Kenmore, P. E. 1980.** Ecology and outbreaks of a tropical insect pest of the green revolution: the rice brown planthopper *Nilaparvata lugens* (Stål). Ph.D. dissertation, Division of Biological Pest Control, Entomological Sciences, University of California, Berkeley.
- Kenmore, P. E., F. O. Cariño, C. A. Perez, V. A. Dyck & A. P. Gutierrez. 1984.** Population regulation of the rice brown planthopper (*Nilaparvata lugens* Stål) within rice fields in the Philippines. *J. Plant Prot. Tropic* 1: 19–37.
- Kobayashi, S. 1975.** The effect of *Drosophila* release on the spider population in a paddy field. *Appl. Entomol. Zool.* 10: 268–274.
- LaSalle, M. W. & A. A. DeLaCruz. 1985.** Seasonal abundance and diversity of spiders in two intertidal marsh plant communities. *Estuaries* 8: 381–393.
- Lowrie, D. C. 1948.** The ecological succession of spiders of the Chicago area dunes. *Ecology* 29: 334–351.
- MacArthur, R. H. 1965.** Patterns of species diversity. *Biol. Rev.* 40: 510–533.
- Marples, T. 1966.** A radionuclide tracer study of arthropod food chains in a *Spartina* salt marsh ecosystem. *Ecology* 47: 270–277.
- Mendelsohn, L. A., K. L. McKee & W. H. Patrick. 1981.** Oxygen deficiency in *Spartina alterniflora* roots: metabolic adaptation to anoxia. *Science* 214: 439–441.
- Moulder, B. C. & D. E. Reichle. 1972.** Significance of spider predation in the energy dynamics of forest-floor arthropod communities. *Ecol. Monogr.* 42: 473–498.
- National Oceanic and Atmospheric Administration (NOAA). 1985.** Storm data 27(7). National Climatic Data Center. Asheville, N.C.
- Niering, R. S. & W. A. Warren. 1980.** Vegetation patterns and processes in New England salt marshes. *BioScience* 30: 301–307.
- Nyffeler, M. & G. Benz. 1979.** Zur ökologischen Bedeutung der Spinnen der Vegetationsschicht von Getreide- und Rapsfeldern. *Z. Angew. Entomol.* 87: 348–376.
- Pfeiffer, J. W. & R. G. Wiegert. 1981.** Grazers on *Spartina* and their predators, pp. 87–112. In L. R. Pomeroy & R. G. Wiegert [eds.], *The ecology of a salt marsh*. Springer, New York.
- Pianka, E. R. 1966.** Latitudinal gradients in species diversity: a review of concepts. *Am. Nat.* 100: 33–46.
- Pielou, E. C. 1966.** The measurement of diversity in different types of biological collections. *J. Theor. Biol.* 13: 131–144.
- Provencher, L. & W. Vickery. 1988.** Territoriality, vegetation complexity, and biological control: the case for spiders. *Am. Nat.* 132: 257–266.
- Redfield, A. C. 1972.** Development of a New England salt marsh. *Ecol. Monogr.* 42: 201–237.
- Rey, J. R. & E. D. McCoy. 1983.** Terrestrial arthropods of Northwest Florida salt marshes: Araneae and Pseudoscorpiones (Arachnida). *Fla. Entomol.* 66: 497–503.
- Riechert, S. E. & T. Lockley. 1984.** Spiders as biological control agents. *Annu. Rev. Entomol.* 29: 299–320.
- Robinson, J. V. 1981.** The effect of architectural variation in habitat on a spider community: an experimental field study. *Ecology* 62: 73–80.
- Roderick, G. K. 1987.** Ecology and evolution of dispersal in California populations of a salt marsh insect, *Prokelisia marginata*. Ph.D. dissertation, University of California, Berkeley.
- Rovner, J. S. 1986.** Spider hairiness: air stores and low activity enhance flooding survival in inland terrestrial species, pp. 123–129. In J. A. Barrientos [ed.], *Actas of the 10th International Congress of Arachnology*. Juvenil, Barcelona, Spain.
- 1987.** Nests of terrestrial spiders maintain a physical gill: flooding and the evolution of silk. *J. Arachnol.* 14: 327–337.
- Rypstra, A. L. 1983.** Web spiders in temperate and tropical forests: relative abundance and environmental correlates. *Am. Midl. Nat.* 115: 42–51.
- Schaefer, M. 1974.** Experimentelle Untersuchungen zur Bedeutung der interspezifischen Konkurrenz bei 3 Wolfspinnen-Arten (Araneida: Lycosidae) einer Salzwiese. *Zool. Jahrb. Abt. Syst. Oekol. Geogr. Tiere Syst.* 101: 213–235.
- Shannon, C. E. 1948.** A mathematical theory of communication. *Bell Inst. Tech. J.* 27: 379–423, 623–656.
- Simberloff, D. S. & E. O. Wilson. 1969.** Experimental zoogeography of islands: the colonization of empty islands. *Ecology* 50: 278–295.
- Sokal, R. R. & F. J. Rohlf. 1981.** *Biometry*, 2nd ed. Freeman, New York.
- Sørensen, T. 1948.** A method of establishing groups of equal amplitude in plant society based on similarity of species content. *K. Dan. Vidensk. Selsk. Biol. Skr.* 5: 1–34.
- Specht, H. B. & C. D. Dondale. 1960.** Spider populations in New Jersey apple orchards. *J. Econ. Entomol.* 53: 810–814.
- Spiller, D. A. 1984.** Competition between spider species: experimental field study. *Ecology* 65: 909–919.
- 1986.** Interspecific competition between spiders and its relevance to biological control by general predators. *Environ. Entomol.* 15: 177–181.

- Spiller, D. A. & T. W. Schoener. 1988.** An experimental study of the effect of lizards on web-spider communities. *Ecol. Monogr.* 58: 57-77.
- Sudd, J. H. 1972.** The distribution of spiders at Spurn Head (E. Yorkshire) in relation to flooding. *J. Anim. Ecol.* 41: 63-70.
- Sunderland, K. D., R. J. Chambers, D. L. Stacey & A. F. G. Dixon. 1985.** Distribution of linyphiid spiders in relation to capture of prey in cereal fields. *Bulletin SROP/WPRS VIII/3:* 105-114.
- Tallamy, D. W. & R. F. Denno. 1979.** Responses of sap-feeding insects (Homoptera-Hemiptera) to simplification of host plant structure. *Environ. Entomol.* 8: 1021-1028.
- Turnbull, A. L. 1973.** Ecology of the true spiders (Araneomorphae). *Annu. Rev. Entomol.* 18: 305-348.
- Uetz, G. W. 1975.** Temporal and spatial variation in species diversity of wandering spiders (Araneae) in deciduous forest litter. *Environ. Entomol.* 4: 719-724.
- 1976.** Gradient analysis of spider communities in a streamside forest. *Oecologia* 22: 373-385.
- 1979.** The influence of variation in litter habitats on spider communities. *Oecologia* 40: 29-42.
- In press.** Habitat structure and spider foraging. In E. D. McCoy, S. S. Bell & H. R. Mushinsky [eds.], *Habitat structure and diversity*. Chapman & Hall, London.
- Vioco, S. W., I. Valiela & J. M. Teal. 1981.** An experimental study of the structures of herbivorous insect communities in a salt marsh. *Ecology* 62: 1662-1678.
- Webb, D. P. 1976.** Edge effects on salt marsh arthropod community structures. *J. Ga. Entomol. Soc.* 11: 17-27.
- Whitcomb, W. H., H. Exline & M. Hite. 1963.** Comparison of spider populations of ground stratum in Arkansas pasture and adjacent cultivated field. *Ark. Acad. Sci. Proc.* 17: 1-6.
- Whittaker, R. H. 1975.** *Communities and ecosystems*, 2nd ed. Macmillan, New York.
- Wise, D. H. 1984.** The role of competition in spider communities: insights from field experiments with a model organism, pp. 42-53. In D. R. Strong et al. [eds.], *Ecological communities: conceptual issues and the evidence*. Princeton University Press, Princeton, N.J.

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