

# Comparison of the Feeding Niche of Polyphagous Insectivores (Araneae) in a Texas Cotton Plantation: Estimates of Niche Breadth and Overlap

MARTIN NYFFELER AND WINFIELD L. STERLING

Department of Entomology, Texas A&M University, College Station, TX 77843

Environ. Entomol. 23(5): 1294-1303 (1994)

**ABSTRACT** The feeding niches of 10 spider species that are polyphagous insectivores were compared by computing coefficients of niche breadth and niche overlap. The study is based on predation evidence from an insecticide-free cotton plantation in east Texas. All overlap values were  $<1.00$  (range, 0.08–0.94), which indicates that each spider species has its own feeding niche in the cotton agroecosystem. Diet breadth, that is inversely related to feeding specialization, was computed for each species. The highest value was approximately five times higher than the minimum, which indicates considerable differences between species in feeding specialization. Diet breadth values indicate that large web weavers exhibited a less specialized feeding behavior (relatively broad feeding niche) compared with small web weavers (narrow feeding niche). Prey specialists in this study concentrated on either aphids or fire ants as a primary food source. The nonweb-building spider *Oxyopes salticus* Hentz, which actively searches the cotton plant for prey (up to  $\approx 6$  mm maximum length), showed the highest diet breadth value (broad feeding niche) under the conditions of this experiment. This abundant species, which is considered a highly beneficial biocontrol agent of smaller cotton pests, shows high flexibility in its foraging patterns.

**KEY WORDS** insectivores, feeding niche, cotton

COTTON FIELDS ARE inhabited by rich predator faunas (Whitcomb & Bell 1964, van den Bosch & Hagen 1966, Sterling et al. 1978). Spiders constitute an essential component of this predator-complex (Dean & Sterling 1987, Breene et al. 1989b, Young & Edwards 1990). Although the beneficial role of the spiders as insectivores has been widely recognized for quite some time (e.g., Whitcomb et al. 1963), important aspects of their predation ecology remain unknown (Turnbull 1973, Luczak 1979, Nyffeler 1982, Nyffeler & Benz 1987). In the pest control literature, spiders often have been lumped together as a group. The various species, however, exhibit a very diverse range of life styles and foraging behaviors resulting in species-specific resource utilization patterns (Turnbull 1973, Wise 1993). To understand how the different species complement each other in their insectivorous activities, it must be known to what degree their ecological niches differ (*complementary niches* sensu Whitcomb [1974]). Thus, a comparative niche analysis, providing insight into the community structure (see Petraitis 1979), is a prerequisite to the understanding of the collective predation impact of spiders. Ecologists have developed mathematical methods commonly used in community ecology by which niche dimensions (i.e., food, space,

and time) of coexisting species can be compared quantitatively. Commonly used measures are niche breadth of species and niche overlap between species (Colwell & Futuyama 1971). In feeding behavioral studies, the niche dimension *food* (i.e., *feeding niche* sensu Krebs [1985]) alone is relevant.

During the summer of 1985, an extensive study of spider predation was conducted in an insecticide-free cotton plantation in east Texas. Based on the prey records obtained during that study, the feeding niches of 10 coexisting spider predators were compared quantitatively by means of community ecology indices to evaluate the competitiveness and potential effectiveness of the spiders.

## Materials and Methods

**Study Area.** The study was conducted in a pesticide-free cotton agroecosystem (6.5 ha) in east Texas (Houston County), 8 km west of Austonio. The cotton ('CAMD-E') used in this research was planted on 27 May 1985, with a distance between rows of 1 m and  $\approx 10$  cotton plants per meter of row. The plantation was surrounded by extensive tracts of minimally disturbed meadows composed of various grasses and low grow-

Table 1. Prey records for 10 syntopic spider species in a cotton plantation in east Texas, 85 h of visual observation

Prey group	Spider species <sup>a</sup>										Total
	OS	LM	DS	FP	UG	TL	CT	GH	NA	AS	
	No. predation events										
Homoptera											
Aphids	9	12	16	21	45	32	45	77	10	36	303
Leafhoppers	11	2	0	0	0	3	3	15	1	9	44
Hymenoptera											
Fire ants	14	194	3	0	3	1	1	17	0	1	234
Others	1	1	0	1	0	0	7	6	1	3	20
Diptera	11	0	8	0	2	5	9	23	1	32	91
Coleoptera	0	39	0	0	0	0	1	1	7	15	63
Orthoptera	1	8	1	0	0	0	0	3	0	0	13
Araneae	9	1	0	0	0	0	0	0	0	1	11
Heteroptera	3	0	0	0	0	0	0	2 <sup>b</sup>	1	2	8
Lepidoptera	0	1	0	0	0	0	0	0	1	3 <sup>c</sup>	5
Thysanoptera	0	0	0	0	0	0	2	0	0	0	2
Neuroptera	1	0	0	0	0	0	0	0	0	0	1
Collembola	0	0	0	1	0	0	0	0	0	0	1
Total	60	258	28	23	50	41	68	144	22	102	796
No. webs	— <sup>d</sup>	100	— <sup>e</sup>	— <sup>e</sup>	16	23	— <sup>e</sup>	111	15	44	>300

<sup>a</sup> OS, *Oxyopes salticus*; LM, *Latrodectus mactans*; DS, *Dictyna segregata*; FP, *Frontinella pyramitela*; UG, *Uloborus glomus*; TL, *Tetragnatha laboriosa*; CT, *Cyclosa turbinata*; GH, *Gea heptagon*; NA, *Neoscona arabesca*; AS, *Acanthepeira stellata*.

<sup>b</sup> Including one adult cotton fleahopper.

<sup>c</sup> Including one bollworm moth.

<sup>d</sup> Active searcher that does not spin webs.

<sup>e</sup> No information available.

ing Dicotyledonae. Parts of the cotton plantation were also heavily infested with johnsongrass. From these reservoir habitats large numbers of predators (primarily fire ants and spiders) migrated into the cotton plantation.

To address the objectives mentioned above, predation events were recorded during 85 h of visual observation at our study site until 16 September 1985 (at which time the cotton had not been harvested). For specific details about the methods used, see Nyffeler et al. (1987b, 1989). The prey records obtained during the study are summarized in Table 1 (see Nyffeler et al. 1986; 1987b; 1988a, b; 1989 for a detailed discussion). As the table indicates, spiders were mostly feeding on nonpest prey; only 0.25% of the total prey were major pests of cotton including one adult cotton fleahopper and one bollworm moth (see Discussion).

**Utilization Curves.** The relative use of resource states (i.e., prey groups) by a species is named its *utilization curve* (Ludwig & Reynolds 1988). However, Petraitis (1979) cautions that resource classes should not be arbitrarily lumped. To prevent arbitrary grouping of resource states, we consistently use *arthropod order* as our prey group classification (c.f., Riechert & Cady 1983). Prey groups were represented by eleven arthropod orders: (Homoptera [aphids and leafhoppers], Hymenoptera [including fire ants], Heteroptera, Diptera, Araneae, Coleoptera, Lepidoptera, Orthoptera, Collembola, Neuroptera, and Thysanoptera).

Utilization curves were computed for each of the following 10 syntopic spider species, based

on our observation data (Table 2): *Oxyopes salticus* Hentz (Oxyopidae), *Latrodectus mactans* (F.) (Theridiidae), *Frontinella pyramitela* (Walckenaer) (Linyphiidae), *Dictyna segregata* Gertsch & Mulaik (Dictynidae), *Uloborus glomus* (Walckenaer) (Uloboridae), *Tetragnatha laboriosa* Hentz (Tetragnathidae), *Cyclosa turbinata* (Walckenaer) (Araneidae), *Gea heptagon* (Hentz) (Araneidae), *Neoscona arabesca* (Walckenaer) (Araneidae), and *Acanthepeira stellata* (Walckenaer) (Araneidae). These 10 species constituted combined  $\approx 80\%$  of total spiders ( $100\% = N = 923$ ) collected with a D-Vac suction machine in this plantation during the summer of 1985 (see Dean et al. [1988] for a detailed species list).

The utilization curves were used to estimate niche overlap and breadth in terms of selection of prey groups by the spiders. For a few species included in this study, the number of observed cases of predation was rather low ( $20 < N < 40$ ) (Table 1). Other species (e.g., jumping spiders and crab spiders) could not even be included because the number of observed cases of predation was too low ( $N < 20$ ) for a meaningful comparison (see Dean et al. 1987). It would certainly be desirable to operate with sample sizes of at least  $N = 100$  prey per spider species. However, for some species it would take an unrealistically long observation time (several hundred man-power hours) to obtain such sample sizes in Texas cotton (see Nyffeler et al. [1987a] for a discussion).

**Estimates of Niche Overlap.** Diet overlap ( $C$ ) of two predator species was computed with the

Table 2. Utilization curves of 10 spider species computed from data in Table 1

Spider species <sup>b</sup>	Relative utilization of prey group (j) <sup>a</sup>										
	(1)	(2)	(3)	(4)	(5)	(6)	(7)	(8)	(9)	(10)	(11)
OS	0.33	0.25	0.18	0.05	0.15	0.00	0.00	0.02	0.00	0.02	0.00
LM	0.05	0.75	0.00	0.00	0.01	0.15	0.01	0.03	0.00	0.00	0.00
DS	0.57	0.11	0.29	0.00	0.00	0.00	0.00	0.03	0.00	0.00	0.00
FP	0.92	0.04	0.00	0.00	0.00	0.00	0.00	0.00	0.04	0.00	0.00
UG	0.90	0.06	0.04	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
TL	0.85	0.03	0.12	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
CT	0.71	0.12	0.13	0.00	0.00	0.01	0.00	0.00	0.00	0.00	0.03
GH	0.64	0.16	0.16	0.01	0.00	0.01	0.00	0.02	0.00	0.00	0.00
NA	0.50	0.05	0.05	0.05	0.00	0.30	0.05	0.00	0.00	0.00	0.00
AS	0.44	0.04	0.31	0.02	0.01	0.15	0.03	0.00	0.00	0.00	0.00

A few values slightly altered in order that the eleven states in each line sum up to 1.00.

<sup>a</sup> (1) Homoptera (aphids and leafhoppers); (2) Hymenoptera (including fire ants); (3) Diptera; (4) Heteroptera; (5) Araneae; (6) Coleoptera; (7) Lepidoptera; (8) Orthoptera; (9) Collembola; (10) Neuroptera; (11) Thysanoptera.

<sup>b</sup> OS, *O. salticus*; LM, *L. mactans*; DS, *D. segregata*; FP, *F. pyramitela*; UG, *U. glomosus*; TL, *T. laboriosa*; CT, *C. turbinata*; GH, *G. heptagon*; NA, *N. arabesca*; AS, *A. stellata*.

method presented by Colwell & Futuyma (1971):

$$C_{1,2} = 1 - \frac{1}{2} \sum |(p_{1j} - p_{2j})|, \quad (1)$$

where  $p_{1j}$  and  $p_{2j}$  is the frequency of utilization of prey group  $j$  by predator species 1 and 2, respectively ( $j = 1$  to  $R$  prey groups; data taken from the utilization curves in Table 2). An overlap value was computed for each of the 45 species pairs. Values can range between 0 (no overlap) and +1 (complete overlap). For each spider species a mean overlap (= mean value of nine overlaps)  $\pm$  SEM was computed.

**Test for Complete Overlap.** Petraitis (1979) developed an additional overlap measure ('specific overlap'  $SO$ , ranging from 0 to +1), which is based on the likelihood that the utilization curve of predator species 1 could have been drawn from that of species 2 (see review by Ludwig & Reynolds [1988]). Note, the amount of specific overlap of species 1 onto species 2 is not necessarily that of species 2 onto species 1 because the utilization curve of a species may completely overlap that of a second species, whereas the utilization curve of that second species may overlap only part of that of the first species (see Ludwig & Reynolds 1988). Thus, specific overlap must be computed for species 1 onto 2 and also vice versa. The null hypothesis can be tested that two species completely overlap (i.e., identical utilization curves); the alternatives are *none* or *some* overlap (see Ludwig & Reynolds [1988], pp. 115–116). Specific niche overlap of species 1 onto species 2 (and vice versa) across all prey groups is computed as follows:

$$SO_{1,2} = e^{E_{1,2}}, \quad (2)$$

$$SO_{2,1} = e^{E_{2,1}}, \quad (3)$$

where

$$E_{1,2} = \sum (p_{1j} \ln p_{2j}) - \sum (p_{1j} \ln p_{1j}), \quad (4)$$

$$E_{2,1} = \sum (p_{2j} \ln p_{1j}) - \sum (p_{2j} \ln p_{2j}), \quad (5)$$

where  $p_{1j}$  is the frequency of utilization of prey group  $j$  by predator species 1, and  $p_{2j}$  is the same as before for species 2 ( $j = 1$  to  $R$ ; data taken from the utilization curves in Table 2). To test the null hypothesis that the specific overlap of species 1 onto 2 (and vice versa) is complete, we compute (Ludwig & Reynolds 1988):

$$Z_{1,2} = -2 * N_1 * \ln(SO_{1,2}), \quad (6)$$

$$Z_{2,1} = -2 * N_2 * \ln(SO_{2,1}). \quad (7)$$

The test statistics has a  $\chi^2$  distribution with  $R-1$  degrees of freedom (see Petraitis 1988, Ludwig & Reynolds 1988). (In equations 6 and 7, we chose  $Z$  instead of the  $U$  proposed by Ludwig & Reynolds [1988], because by convention letter  $U$  is reserved for the Mann-Whitney  $U$  test). If  $Z$  exceeds the critical value for  $\chi^2$  at  $P = 0.05$ , then the null hypothesis of complete overlap is rejected. The equations operate with logarithms and because  $\ln 0$  is undefined, zero values ( $p_{ij} = 0.00$  in Table 2) were arbitrarily set to  $1 \times 10^{-7}$  (Ludwig & Reynolds [1988], p. 122). The null hypothesis that the specific overlap of two species is complete was tested for each of the 45 species pairs.

**Estimates of Niche Breadth.** Diet breadth ( $H'$ ) was computed with the Shannon-Weaver equation (Colwell & Futuyma 1971):

$$H' = - \sum p_{ij} \ln p_{ij}, \quad (8)$$

where  $p_{ij}$  is the frequency of utilization of prey group  $j$  by predator species  $i$  ( $j = 1$  to  $R$ ; data taken from the utilization curves in Table 2).

**Table 3.** Coefficient of diet overlap (*C*) (Colwell-Futuyma niche overlap measure) for 10 spider species in a cotton plantation in east Texas, computed from the utilization curves (Table 2)

	Spider species <sup>a</sup>									
	LM	OS	NA	AS	FP	UG	TL	DS	CT	GH
LM	—	0.33	0.26	0.26	0.09	0.11	0.08	0.19	0.18	0.24
OS	0.33	—	0.48	0.58	0.37	0.43	0.48	0.64	0.58	0.68
NA	0.26	0.48	—	0.73	0.54	0.59	0.58	0.60	0.61	0.62
AS	0.26	0.58	0.73	—	0.48	0.52	0.59	0.77	0.62	0.66
FP	0.09	0.37	0.54	0.48	—	0.94	0.88	0.61	0.75	0.68
UG	0.11	0.43	0.59	0.52	0.94	—	0.92	0.67	0.81	0.74
TL	0.08	0.48	0.58	0.59	0.88	0.92	—	0.72	0.86	0.79
DS	0.19	0.64	0.60	0.77	0.61	0.67	0.72	—	0.81	0.86
CT	0.18	0.58	0.61	0.62	0.75	0.81	0.86	0.81	—	0.90
GH	0.24	0.68	0.62	0.66	0.68	0.74	0.79	0.86	0.90	—
Mean	0.19	0.51	0.56	0.58	0.59	0.64	0.65	0.65	0.68	0.69
±SEM	0.03	0.04	0.04	0.05	0.09	0.09	0.09	0.07	0.07	0.06

<sup>a</sup> LM, *L. mactans*; OS, *O. salticus*; NA, *N. arabesca*; AS, *A. stellata*; FP, *F. pyramitela*; UG, *U. glomosus*; TL, *T. laboriosa*; DS, *D. segregata*; CT, *C. turbinata*; GH, *G. heptagon*.

The evenness ( $H'/H'_{max}$ ) is used as a supplementary measure to characterize the breadth of the feeding niche (Hurtubia 1973). The evenness was computed as follows (Pielou 1966):

$$H'/H'_{max} = H'/\ln R. \tag{9}$$

[The  $S$  (= number of species) in Pielou's formula, as used in biodiversity studies, is here substituted by  $R$  (= number of prey groups)]. This measure takes on the value of one when all prey groups are used evenly and a value of zero when only one prey group is used.

**Statistical Comparison of Niche Breadths.** According to Poole (1974), the variance of the estimate of  $H'$  is:

$$\text{var}(H') = \frac{\sum p_{ij} \ln^2 p_{ij} - (\sum p_{ij} \ln p_{ij})^2}{N} + \frac{R - 1}{2N^2} + \dots \tag{10}$$

[The  $S$  (= number of species) in the second term of Poole's formula is here substituted by  $R$  (= number of prey groups);  $p_i$  is replaced by  $p_{ij}$  ( $j = 1$  to  $R$ )].  $N$  is the number of individuals in the sample (representing predator species  $i$ ). In large samples the first term is usually sufficient (Poole 1974). Two  $H'$  values can be compared, with a  $t$ -test, to see if they are significantly different (Hutcheson 1970, Poole 1974):

$$t = \frac{H'_1 - H'_2}{[\text{var}(H'_1) + \text{var}(H'_2)]^{1/2}}. \tag{11}$$

The null hypothesis is  $H_0 : H'_1 = H'_2$ . The degrees of freedom of the test is (Poole 1974):

$$\text{df} = \frac{[\text{var}(H'_1) + \text{var}(H'_2)]^2}{[\text{var}(H'_1)^2/N_1 + \text{var}(H'_2)^2/N_2]}, \tag{12}$$

where  $N_1$  is the number of individuals in the first sample (species 1), and  $N_2$  is the number of individuals in the second (species 2).

**Prey Electivity versus Diet Breadth.** To evaluate whether some prey types were captured selectively, Ivlev's index of electivity ( $IE$ ) was computed. The index (ranging between  $-1$  and  $+1$ ) gives an indication of the extent to which a predator selects its prey from the pool of potential prey (Ivlev 1961, Nyffeler et al. 1987b) and is computed using the equation:

$$IE = (p_j - q_j) * (p_j + q_j)^{-1}, \tag{13}$$

where  $p_j$  is the percentage of a food component  $j$  in the spider's actual prey (Table 1), and  $q_j$  is the percentage of this component in the potential prey assessed at the same location during the same period of time. In this experiment seven prey types ( $j = 1$  to  $7$ ) were tested: (1) aphids, (2) fire ants, (3) leafhoppers, (4) dipterans, (5) spiders, (6) bugs, and (7) beetles. A D-Vac suction machine (D-Vac, Riverside, CA) (Dietrick 1961) was used to assess the percentage composition of potential prey (100% =  $N = 58,528$ ) on cotton. Based on those samples the following  $q_j$  estimates were obtained:  $q_1 = 75$ ,  $q_2 = 13$ ,  $q_3 = 6$ ,  $q_4 = 2$ ,  $q_5 = 2$ ,  $q_6 = 1$ , and  $q_7 = <1$ . See Nyffeler et al. (1987b) for methods details. A regression analysis (linear model) of prey preference versus diet breadth was performed (Draper & Smith 1981).

**Results**

**Estimates of Diet Overlap.** Table 3 shows that each spider species has its own feeding niche within the cotton agroecosystem, evidenced by deviation of the  $C$  values (Colwell-Futuyma niche overlap measure) from a theoretical maximum value 1.00 (complete overlap). Diet overlaps ( $C$ ) ranged from very low to very high values

**Table 4. Response of 10 spider predators to availability of seven different prey types measured with Ivlev's index of food electivity ( $E$ ) in a cotton plantation in east Texas**

Spider species	Prey type						
	Aphids <sup>a</sup>	Leafhoppers <sup>a</sup>	Fire ants <sup>b</sup>	Diptera	Coleoptera	Araneae	Heteroptera
<i>F. pyramitela</i>	+0.10	-1.00	-1.00	-1.00	-1.00	-1.00	-1.00
<i>U. glomosus</i>	+0.09	-1.00	-0.37	+0.33	-1.00	-1.00	-1.00
<i>T. laboriosa</i>	+0.02	+0.08	-0.62	+0.71	-1.00	-1.00	-1.00
<i>L. mactans</i>	-0.90	-0.71	+0.70	-1.00	+0.95	-0.67	-1.00
<i>C. turbinata</i>	-0.06	-0.09	-0.73	+0.73	+0.43	-1.00	-1.00
<i>D. segregata</i>	-0.14	-1.00	-0.08	+0.87	-1.00	-1.00	-1.00
<i>G. heptagon</i>	-0.16	+0.25	-0.04	+0.78	+0.43	-1.00	0.00
<i>N. arabesca</i>	-0.25	-0.09	-1.00	+0.43	+0.97	-1.00	+0.67
<i>A. stellata</i>	-0.36	+0.20	-0.86	+0.88	+0.95	-0.33	+0.33
<i>O. salticus</i>	-0.67	+0.50	+0.28	+0.80	-1.00	+0.76	+0.67

$E < 0$ , negative food selection;  $E = 0$ , random feeding;  $E > 0$ , positive food selection.  $E$  values are based on a comparison of the proportion of a given prey type in the actual prey (Table 1) with the proportion of this type in the potential prey (D-Vac samples) assessed at the same location during the same period of time (see Nyffeler et al. 1987b).

<sup>a</sup> Homoptera.

<sup>b</sup> Hymenoptera.

(0.08–0.94, overall mean =  $0.57 \pm 0.04$  SEM) (Table 3), which suggests that under the conditions of this experiment some spider species had very similar feeding niches, whereas others showed large differences. The null hypothesis of complete overlap (= identical utilization curves) was examined with Petratis' (1979) test statistics (see Ludwig & Reynolds 1988). For forty-three of the forty-five examined species pairs computed  $\chi^2$ s exceeded the critical value at  $P = 0.05$  and, thus, the null hypothesis of complete overlap can be rejected. For two species pairs (*U. glomosus* versus *T. laboriosa* and vice versa; *D. segregata* versus *G. heptagon*), the null hypothesis of complete overlap must be accepted at  $P = 0.05$ , although computed  $\chi^2$ s were not much below the critical value.

Each species differs in its response to prey availability (i.e., prey preference) (Table 4). Prey preferences are largely determined by the spi-

der's specific foraging mode (see Table 5 for comparison of foraging modes). Webs that function in a similar manner as insect traps catch similar prey. Three species (*F. pyramitela*, *U. glomosus*, and *T. laboriosa*), that all spin approximately horizontally oriented, small webs on plant foliage (Table 5), had very similar feeding niches ( $C = 0.88$ – $0.94$ ) (Table 3). Two species (*C. turbinata* and *G. heptagon*), that both spin approximately vertically oriented, small orb webs on plant foliage (Table 5), had also very similar feeding niches ( $C = 0.90$ ) (Table 3).

Eight species that spin webs on the cotton plant exhibited fairly high mean diet overlaps (*N. arabesca* [ $0.56 \pm 0.04$  SEM], *A. stellata* [ $0.58 \pm 0.05$ ], *F. pyramitela* [ $0.59 \pm 0.09$ ], *U. glomosus* [ $0.64 \pm 0.09$ ], *T. laboriosa* [ $0.65 \pm 0.09$ ], *D. segregata* [ $0.65 \pm 0.07$ ], *C. turbinata* [ $0.68 \pm 0.07$ ], *G. heptagon* [ $0.69 \pm 0.06$ ]) (each mean overlap represents the mean value of nine overlaps; Ta-

**Table 5. Foraging modes and relative abundance of 10 spider species in a cotton plantation in east Texas**

Spider family and species	Foraging mode	Relative abundance <sup>a</sup>
Oxyopidae		
<i>Oxyopes salticus</i>	Small active searcher on plants and near the ground	67.2
Linyphiidae		
<i>Frontinella pyramitela</i>	≈Horizontal, small space webs (not sticky), on plants	<1.0
Uloboridae		
<i>Uloborus glomosus</i>	≈Horizontal, small orb webs (cribellate silk), on plants	<1.0
Theridiidae		
<i>Latrodectus mactans</i> (small- to medium-sized immatures)	Small to medium-sized space webs (partly sticky), near and on the ground	1.0
Dictynidae		
<i>Dictyna segregata</i>	Small space webs (cribellate silk), on plants	3.3
Tetragnathidae		
<i>Tetragnatha laboriosa</i>	Small (sticky) orb webs, on plants	2.2
Araneidae		
<i>Cyclosa turbinata</i>	Small (sticky) orb webs, on plants	<1.0
<i>Gea heptagon</i>	Small (sticky) orb webs, on plants	1.1
<i>Neoscona arabesca</i>	≈Vertical, large (sticky) orb webs, between and on plants	<1.0
<i>Acanthepeira stellata</i>	≈Vertical, large (sticky) orb webs, between and on plants	3.5

<sup>a</sup> Percentage of total spiders (100% =  $N = 923$ ) collected with a D-Vac suction machine during summer 1985 (Dean et al. 1988).

Table 6. Comparison of diet breadth  $H' \pm$  variance (Colwell–Futuyma niche breadth measure) of 10 spider species in a cotton plantation in east Texas, computed from the utilization curves (Table 2)

Spider species	R	$H' \pm$ variance	$H'/H'_{max}$ <sup>a</sup>
<i>F. pyramitela</i>	3	0.3343 $\pm$ 0.03334a	0.3043
<i>U. glomosus</i>	3	0.3924 $\pm$ 0.01531a	0.3572
<i>T. laboriosa</i>	3	0.4977 $\pm$ 0.01726a	0.4530
<i>L. mactans</i>	6	0.8474 $\pm$ 0.00440b	0.4729
<i>C. turbinata</i>	5	0.9140 $\pm$ 0.01381bc	0.5679
<i>D. segregata</i>	4	1.0274 $\pm$ 0.01883bc	0.7411
<i>G. heptagon</i>	6	1.0422 $\pm$ 0.00600bc	0.5817
<i>N. arabesca</i>	6	1.3100 $\pm$ 0.03979cde	0.7311
<i>A. stellata</i>	7	1.3671 $\pm$ 0.00709d	0.7025
<i>O. salticus</i>	7	1.6120 $\pm$ 0.00779e	0.8284

$H'$  values followed by the same letters are not significantly different ( $P > 0.05$ ) compared with pairwise  $t$ -tests.

<sup>a</sup> Evenness,  $H'/H'_{max} = H'/\ln R$ , where  $R$  = number of prey groups (arthropod orders) (Table 2).

ble 3). The striped lynx spider, *O. salticus*, that actively searches the cotton plant for prey, exhibited a lower mean overlap ( $0.51 \pm 0.04$ ) than the other foliage-dwellers (Table 3). The black widow spider, *L. mactans*, a ground level web weaver (consisting in this plantation exclusively of small to medium sized immatures), showed minimum diet overlap with each of the foliage-dwellers, ranging from 0.08 to 0.33 (mean overlap =  $0.19 \pm 0.03$ ) (Table 3). This indicates that *L. mactans* was a unique forager in the investigated cotton ecosystem (see Tables 1 and 4).

**Estimates of Diet Breadth.** Diet breadth values ( $H'$ ) (Colwell–Futuyma niche breadth measure) of the ten species are presented in Table 6. A trend of increasing evenness ( $H'/H'_{max}$ ) with increasing diet breadth ( $H'$ ) was observed (Table 6). The significance of the difference of the  $H'$  values was further examined pairwise with  $t$ -test statistics (Table 6). Based on statistical differences (Table 6), the following four groups were distinguished: (1) the lowest diet breadth values ( $H' = 0.33$ – $0.50$ ) are attributable to three small web weavers, *F. pyramitela*, *T. laboriosa*, and *U. glomosus* (total number of webs =  $>40$ ). (2) Four other small web weavers, *C. turbinata*, *D. segregata*, *G. heptagon*, and immature *L. mactans*, showed moderate values ( $H' = 0.85$ – $1.04$ ) (total number of webs =  $>200$ ). (3) Fairly high diet breadth values were found for the large orb weavers *N. arabesca* ( $H' = 1.31$ ) and *A. stellata* ( $H' = 1.37$ ) (total number of webs =  $>50$ ). (4) The highest value is attributable to the nonweb-building spider *O. salticus* ( $H' = 1.61$ ) (total number of records =  $>50$ ), which indicates a broad feeding niche relative to the other species. The highest value was approximately five times higher than the minimum ( $H' = 1.61$  versus 0.33), which indicates considerable between-species differences in diet breadth.

## Discussion

Limitations of this project are that jumping spiders (Salticidae) and crab spiders (Thomisidae) were not included; the study was conducted for only one year and variability in the numbers of predators and pests can be expected from year to year (see Breene et al. 1989a, Sterling et al. 1992); and the data were collected during a low incidence of major pests, thus, spiders fed mostly on nonpest prey. Nevertheless, the study gives valuable insight into the general feeding behavior of cotton spiders that is significant from a biocontrol point of view and that can be translated to field situations where major pests occur in higher numbers.

**Complementary Feeding Niches.** In ecological theory, niche overlap is considered a determinant of species diversity and community structure (e.g., Pielou 1966, Petraitis 1979). The data presented here confirm Whitcomb's (1974) concept of the complementary niches. Feeding niche separation reduces interspecific competition for food and evidently allows a great diversity of spider species to coexist in cotton fields (Whitcomb & Bell 1964, Dean & Sterling 1987). In the cotton plantation described in this study,  $>40$  spider species were collected with a D-Vac suction machine during the summer of 1985, with *O. salticus* being the numerically dominant species (Table 5 and Dean et al. 1988). *O. salticus* is the most abundant spider predator in cotton fields throughout wide parts of Texas (Dean & Sterling 1987). This species has several attributes that characterize it as an excellent survivor and colonizer of field crops (Dean & Sterling 1987, Mack et al. 1988, Young & Edwards 1990). It is noteworthy that *O. salticus* had the lowest mean diet overlap among the foliage-dwellers (0.51 versus 0.56–0.69) (Table 3), enhancing its competitiveness among the cotton spiders by reducing interspecific competition for food.

**Feeding Specialization.** Diet breadth is inversely related to feeding specialization (Colwell & Futuyma 1971). Although all 10 spiders compared in our study are generalist predators (number of prey species per spider species  $>1.00$ ) (Table 1), they exhibit differing degrees of feeding specialization. The values presented in Table 6 suggest that the small web weavers (groups 1 and 2) exhibited a more specialized feeding behavior compared with large web weavers (group 3) and *O. salticus* (group 4). A less specialized feeding behavior (groups 3 and 4) may be advantageous from a nutritional point of view by optimizing a balanced essential amino acid composition in the diet (Greenstone 1979). However, generalist predators must invest energy into overcoming the diverse defensive mechanisms of multiple prey species.

The high diet breadth of *O. salticus* (group 4) relative to other species evidently reflects the

wide variety of prey types encountered during search movements of this predator on the plant surface (Whitcomb et al. 1963). *O. salticus* is an *active searcher* that forages throughout the cotton plant and even on the ground (Whitcomb et al. 1963, Nyffeler et al. 1992b). This diurnally and nocturnally active spider is a generalist that feeds upon practically any available prey not too large ( $\approx 6$  mm or smaller) (Nyffeler et al. 1987b, 1992a). Even small immobile prey such as insect eggs are included in the diet of this spider (i.e., oophagy) (McDaniel & Sterling 1982). The optimal prey length of *O. salticus* in Texas cotton is  $\approx 2.5$  mm (Nyffeler et al. 1987b, 1992a). In a review published in 1985, *O. salticus* was reported to attack 28 identified species of insects from eight orders (Young & Lockley 1985), and additional records of insect prey were published in more recent studies (Lockley & Young 1987; Agnew & Smith 1989; Nyffeler et al. 1987b, 1992a). Agnew & Smith (1989), Guillebeau & All (1989), and Nyffeler et al. (1987b, 1992a) observed that *O. salticus* frequently feeds on other spiders. Thus, this spider exhibits a mixed strategy of insectivorous and araneophagous foraging patterns (Table 4). The high diet breadth value ( $H' = 1.61$ ) for *O. salticus* reported in Table 6 was confirmed during a recent 108-h observational study in an insecticide-free cotton agroecosystem ( $\approx 14$  ha) in central Texas where a value of  $H' = 1.66$  was computed based on prey orders (M.N., unpublished data).

Web spiders frequently intrude into the webs of other spiders resulting in intensive territorial fights; these aggressive displays, however, rarely result in the death of the inferior individual (Wise 1993) and araneophagy is insignificant in the energy budget of web weavers (Nyffeler 1982, Nentwig 1985). In contrast to the active searchers, web weavers are almost strictly insectivore (insects constituting  $>99\%$  of the total prey) (Tables 1 and 4). Large web weavers retain a wider diversity of insect groups with their strong nets (broader feeding niche) (group 3) compared with small webs (Castillo & Eberhard 1983). The large web weavers are able to overcome the defenses of insects with strong chitinization (e.g., beetles), chemical protection (e.g., bugs and beetles), and aggressive behavior (e.g., large stinging bees) (Nentwig 1987, Nyffeler & Breene 1991). In our study, large web weavers show high electivity for beetle prey ( $+0.95 \leq IE \leq +0.97$ ; Table 4) (compare Culin & Yeargan 1982). Among the smaller web weavers only *L. mactans* demonstrated high electivity for beetle prey ( $IE = +0.95$ ; Table 4) (c.f. Whitcomb 1974). Those web spiders, that exhibit high electivity for beetle prey, show potential as predators of the boll weevil (see Whitcomb et al. 1963). Fragile, small nets are suitable for interception of small insects only which narrows their feeding

niche (groups 1 and 2) (LeSar & Unzicker 1978, Culin & Yeargan 1982).

Prey specialists among the spiders tend to specialize on abundant prey species (Nentwig 1986). [Here a specialist feeder is defined as one that exhibits a narrow feeding niche in a particular environment.] In the investigated cotton field, aphids were the most abundant arthropods (75% of the total potential prey-complex), followed by fire ants (13% of total); these two groups of small insects combined constituted almost 90% of the potential prey total (see section *Prey Electivity versus Diet Breadth in Materials and Methods*). Applying Nentwig's theory to our study, one would expect that specialists among the cotton spiders concentrated on either aphids or ants, or both, as a primary food source.

Small- to medium-sized immatures of *L. mactans* (group 2) built irregular mesh type webs in holes in the ground, in large depressions between dirt clods on the ground surface, or in the lowest branches of the cotton plant and specialized primarily on fire ants (Table 1), i.e., ants were captured preferentially ( $IE = +0.70$ ; Table 4). None of the other spiders showed such high electivity for ant prey (Table 4). Evidently ants are optimal diet for black widow spiders (*Latrodectus* spp.) (MacKay 1982, Nyffeler et al. 1988a).

Of the other species from groups 1 and 2, that spun their webs on the cotton foliage (*F. pyramitela*, *U. glomosus*, *T. laboriosa*, *G. heptagon*, *C. turbinata*), aphids were captured most frequently (Table 1). Winged and wingless aphids are intercepted in spider webs (see Nyffeler et al. 1989). Low negative and low positive electivity values ( $IE$ , ranging from  $-0.16$  to  $+0.10$ ; Table 4) for these five small web spiders suggest that aphids were captured almost randomly from the pool of potential prey. Thus, the high percentage of aphids in the prey of small web spiders reflects the availability of aphid prey in the environment (*passive prey selection* sensu Riechert & Luczak [1982]).

A highly significant negative correlation between preference for aphid prey  $IE$  ( $= X$  axis; data from Table 4) and diet breadth  $H'$  ( $= Y$  axis; data from Table 6) of foliage-dwelling spiders (*L. mactans* not included) was found ( $r = 0.938$ ,  $P < 0.001$ ). A regression analysis (linear model) produced the equation  $Y = 0.66 - 1.71X$  for the regression line. The large web weavers (group 3) which had fairly high diet breadth, demonstrated negative electivity for aphid prey ( $IE = -0.25$  and  $-0.36$ , respectively; Table 4); this differs from other studies on large web weavers where distinct positive electivity for aphid prey was reported (see Nentwig [1985] for a detailed discussion). *O. salticus*, the species with the highest diet breadth (group 4), demonstrated a distinct negative electivity for aphids ( $IE = -0.67$ ), but positive electivity for other prey groups ( $+0.28 \leq IE \leq +0.80$ ; Table 4). This implies that during

the buildup of large numbers of aphids in cotton, *O. salticus* may preferentially feed on a less abundant, but more profitable prey group. Freed (1984) provided experimental evidence that active searchers among the spiders spend significantly less time feeding on *lower ranked prey groups* in the presence of alternative prey as predicted by the optimal foraging theory. Because aphids seldom reach pest status in cotton (Bohmalk et al. 1983), preference for other insects as a food source by *O. salticus* may be favorable from a biocontrol point of view, especially in situations where a major pest such as the cotton fleahopper reaches damaging levels.

Feeding studies in the field and laboratory indicate that various small bugs (Heteroptera), including the cotton fleahopper (body length range 1.1–2.9 mm), are optimal diet (optimal prey length  $\approx 2.5$  mm) for *O. salticus* (see Whitcomb et al. 1963, Ragsdale et al. 1981, Lockley & Young 1987, Agnew & Smith 1989, Breene et al. 1989b, Guillebeau & All 1989). In the current study, numbers of harmful bugs and other pests were far below the economic threshold recommended by the Texas Agricultural Extension Service (W.L.S., unpublished data) and consequently spider predation on these pests was insignificant (<1% of the total spider prey [100% =  $N = 796$ ]) (Table 1). However, in other field studies with higher incidence of economically harmful bugs, *O. salticus* was observed feeding heavily on these pests (Lockley & Young 1987; Breene et al. 1989a, b; Nyffeler et al. 1992a, b); thus, this spider can largely switch its dietary habits from nonpest prey to pestiferous species. Breene et al. (1990) demonstrated with field cage confinement tests that *O. salticus* exhibits a sigmoid functional response to availability of fleahopper prey (i.e., increased predation rate at elevated pest levels). High diet breadth combined with high flexibility in switching to pestiferous species when those become abundant, is a very significant characteristic for *O. salticus* (c.f. Agnew & Smith 1989). This is of importance from a biocontrol point of view because *O. salticus* is considered a highly beneficial biocontrol agent of small-sized insect pests in cotton (see Whitcomb & Eason 1967; McDaniel & Sterling 1982; Lockley & Young 1987; Breene et al. 1989a, b; Sterling et al. 1989, 1992; Nyffeler et al. 1992a, b).

#### Acknowledgments

Bob Breene, Allen Dean, Wolfgang Nentwig, Will Whitcomb, and an anonymous reviewer offered valuable criticisms. We also thank L. N. Brown, farmer in Austonio, for permission to carry out this project in his cotton plantation and T. L. Payne for the use of his trailer as a field lab. This research was partially supported by a postdoctoral fellowship of the Swiss National Science Foundation granted to one of us (M. N.) and by the Expanded Research Project H-2591–2100 of

the Texas Agricultural Experiment Station. Approved for publication as TA 31199 by the director, Texas Agricultural Experiment Station.

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*Received for publication 10 June 1993; accepted 13 April 1994.*

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