SPIDERS AS BIOLOGICAL CONTROL AGENTS IN COTTON PLANTATIONS IN TEXAS

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presented by
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Education • Research • Extension

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To Whom It May Concern:

Dr. Martin J. Nyffeler, formerly associated with the Entomological Institute, Swiss Federal Institute of Technology, Zurich, worked in my laboratory from 1985-86 (as a postdoc on a fellowship of the Swiss National Science Foundation) and from 1988-94 (as a visiting scientist). In association with my laboratory he conducted postdoctoral research on the significance of spiders as biocontrol agents of insect pests. He conducted field work in insecticide-free cotton agroecosystems in Austonio, east Texas (summer 1985) and in Snook, central Texas (summer 1988). Later he conducted extensive literature research for several review papers. More recently he wrote a statistical-mathematical paper that has been accepted by Environmental Entomology (Entomological Society of America). The results of research in which he was involved as a principal investigator or collaborator have been published in over 20 papers in various international and national scientific journals during his stay at my laboratory. Two extensive review papers on the predation ecology of spiders are currently in preparation. - Dr. Nyffeler asked for permission to use the data (from his field and review research) collected during his postdoctoral work at Texas A&M University for a "Thesis of Habilitation" to be submitted to a university in Europe in order to obtain the qualification of the "habilitation." I hereby grant Dr. Nyffeler permission to use these data for a "Thesis of Habilitation" and I am pleased to lend support to his case.

Sincerely,

Winfield Sterling

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TABLE OF CONTENTS:

1 SUMMARY 2

2 GENERAL INTRODUCTION 4

3 PREY SELECTION AND PREDATORY IMPORTANCE OF ORB-WEAVING SPIDERS (ARANEAE: ARANEIDAE, ULOBORIDAE) IN TEXAS COTTON.
(Environmental Entomology 18: 373-380 [1989]) 6

4 PREDATION BY GREEN LYNX SPIDER, *PEUCETIA VIRIDANS* (ARANEAE: OXYOPIDAE), INHABITING COTTON AND WOOLLY CROTON PLANTS IN EAST TEXAS.
(Environmental Entomology 16: 355-359 [1987]) 14

5 EVALUATION OF THE IMPORTANCE OF THE STRIPED LYNX SPIDER, *OXYOPES SALTICUS* (ARANEAE: OXYOPIDAE), AS A PREDATOR IN TEXAS COTTON.
(Environmental Entomology 16: 1114-1123 [1987]) 19

6 DIETS, FEEDING SPECIALIZATION, AND PREDATORY ROLE OF TWO LYNX SPIDERS, *OXYOPES SALTICUS* AND *PEUCETIA VIRIDANS* (ARANEAE: OXYOPIDAE), IN A TEXAS COTTON AGROECOSYSTEM.
(Environmental Entomology 21: 1457-1465 [1992]) 29

7 IMPACT OF THE STRIPED LYNX SPIDER (ARANEAE: OXYOPIDAE) AND OTHER NATURAL ENEMIES ON THE COTTON FLEAHOPPER *PSEUDATOMOSCELIS SERIATUS* (HEMIPTERA: MIRIDAE) IN TEXAS COTTON.
(Environmental Entomology 21: 1178-1188 [1992]) 38

8 COMPARISON OF THE FEEDING NICHE OF POLYPHAGOUS INSECTIVORES (ARANEAE) IN A TEXAS COTTON PLANTATION: ESTIMATES OF NICHE BREADTH AND OVERLAP.
(Environmental Entomology 23: 1294-1303 [1994]) 49

9 HOW SPIDERS MAKE A LIVING (FORUM-article).
(Environmental Entomology 23: 1357-1367 [1994]) 59

10 GENERAL DISCUSSION 70

11 FINAL CONCLUSIONS 77

12 ZUSAMMENFASSUNG 78

SUMMARY

The ecological impact of spider predation on cotton insects in cotton fields in Texas was investigated. In particular, it was assessed how frequently the spiders feed on four 'key pests' of Texas cotton (i.e., cotton fleahopper *Pseudatomoscelis seriatus* [Heteroptera: Miridae], boll weevil *Anthonomus grandis grandis* [Coleoptera: Curculionidae], bollworm *Helicoverpa zea* [= *Heliothis zea*] [Lepidoptera: Noctuidae], and tobacco budworm *Heliothis virescens* [Lepidoptera: Noctuidae]) and to what extent this may impact the mortality of these pests. The data were collected over a period of totally ≈ 200 h of visual observations in the course of two field projects: The first project was conducted during the summer of 1985 in an unsprayed (6.5 ha) cotton plantation near Austonio, Houston County, East Texas. The second project was undertaken during the summer of 1988 in an unsprayed (13.6 ha) cotton plantation located near Snook, Burleson County, Central Texas, approximately 100 km southwest of the previous study site.

The spider assemblages found in cotton in Austonio and Snook were quite similar and represent a species complex typical for extensive cotton growing areas throughout the U.S. cotton belt, with lynx spiders (Oxyopidae) numerically predominating. Lynx spiders consistently constituted > 50% of the spider total throughout the growing season. The second most abundant spider group, the orb-weavers (Araneidae and Tetragnathidae), constituted ≈ 10% of the spider total. Two species of lynx spiders occur in these fields: the 'striped lynx' *Oxyopes salticus* and the 'green lynx' *Peucetia viridans*. The numerically dominant *Oxyopes* occurred in average densities of ≈ 1-1.5/m^2 during mid-season in both plantations. [*Peucetia* is less frequently found in cotton and is therefore expected to be of minor importance as a potential natural enemy of pests in the cotton fields.] The studies focussed primarily on the numerically dominant lynx spiders and orb-weavers.

To evaluate the predatory significance of the lynx spiders relative to the other predaceous arthropods occurring in cotton, the total number of predation events observed attributable to lynx spiders versus other arthropod predators was compared based on the data which had been collected in Snook. A total of 134 arthropod predators with prey in their chelicerae/mandibulae were monitored during the 108 h observation period, which included 94 lynx spiders versus 40 other predators. Thus, 70% of all predation events observed were attributable to lynx spiders which indicates that these spiders were the dominant predators in this cotton plantation. Similar patterns of a predominance of lynx spider predation were observed in Austonio, too.

The predation rate (= no. prey killed/spider/day) was estimated with a visual method based on average feeding frequency (percentage spiders with prey in their chelicerae) observed in the field, average handling time, and hunting (searching) time; it was estimated that a subadult/adult *Oxyopes* (representing a typical agroecosystem spider) may capture ≈ 1 prey organism on an average rainfree day in the field (during the middle of the growing season). The same spiders feed at several times higher rates in laboratory feeding experiments if food is offered *ad libitum* (as is known from literature), which suggests that in the field these spiders often feed below their maximum feeding capacity. Thus, the spiders can be expected to increase their predation rate during severe outbreaks of insect pests (i.e., 'functional response').

The majority of the lynx spiders in cotton were of small size (i.e., *Oxyopes*). *Oxyopes* captures a wide variety of small-sized arthropods ranging from 0.6 to 6 mm length (≈ 2.5 mm optimal prey length). [In contrast to this, the larger *Peucetia* feeds over a broader range of prey size classes and consequently captures a higher proportion of the larger prey organisms, but because this species is much less abundant than *Oxyopes*, its contribution to the overall predation impact is rather low.] Likewise, most orb-weavers occurring in cotton were of small body size. Overall, spider individuals of small size (including large percentages of immatures) numerically dominate the faunas of the investigated cotton fields, and these spiders feed primarily on tiny prey organisms (≤ 3 mm in length).

With a body length range of 1.1-2.9 mm (third instar to adult) cotton fleahoppers ideally fit the optimal prey length of ≈ 2.5 mm for *Oxyopes*. [*Peucetia*, that captures on the average significantly larger-sized prey than *Oxyopes*, seems to be less efficient in capturing fleahoppers.] *Oxyopes* shows considerable flexibility in switching its feeding patterns in response to prey availability. - In the cotton plantation in Austonio, the numbers of cotton fleahoppers were below the economic threshold, and consequently very low predation rates on fleahopper prey by spiders were observed (0% fleahoppers in the diet of *Oxyopes*); instead, *Oxyopes* fed heavily on red imported fire ants (22% of the diet) and other nonfleahopper prey. - A totally different scenario was observed in the cotton plantation in Snook, where cotton fleahoppers occurred in fairly high numbers; in this situation, *Oxyopes* fed heavily on these pests (fleahoppers constituting 24% of the diet). - These data indicate that *Oxyopes* may feed heavily on other predators such as fire ants when pests are rare; however, when pests become abundant this spider can largely switch to pestiferous species such as fleahoppers as a major food source.

The assessment of the killing power of *Oxyopes*, based on the predation rate and the predator-to-prey ratio (i.e., number of *Oxyopes* individuals per fleahopper), suggests that this spider contributes significantly to mortality of the cotton fleahopper (≥ 15% prey mortality per day, in the middle of the growing season) in the plantation in Snook; additional fleahopper mortality is attributable to other spiders and predaceous insects, though they are less effective than *Oxyopes*. - The other key pests (i.e., boll weevil, bollworm, and tobacco budworm) were poorly represented in the spider diets, which apparently reflects that these pests occurred in numbers far below economic injury levels (it is assumed that fire ants are the cause of the low pest levels). - The contribution of the spiders to fleahopper mortality, however, varies between the different fields and within different years, due to the spatial and temporal fluctuations of the numbers of spiders and fleahoppers. An approximately 30 times higher frequency of predation on fleahoppers was recorded in Snook compared to Austonio. Consequently the economic benefit due to these predators varies in different situations.

Based on population density counts in the cotton plantation in Austonio and the assessement of the predation rate, it was estimated that lynx spiders killed perhaps ≈ 0.6% of the potential prey per day in the middle of the growing season; it is assumed in the literature that mortality rates of that magnitude already have a significant positive impact on the community stability; thus, spiders can be considered to serve as 'stabilizing agents' (compare Turnbull, 1973, "Ecology of the true spiders", in: Annu. Rev. Entomol. 18, 305-348).

GENERAL INTRODUCTION

According to a statistics published by the Texas Agricultural Extension Service ≈ 60% of the acrages of cotton in Texas can be grown insecticide-free. Similar statistics are available for other cotton growing areas of the U.S. These statistics suggest that in such areas some type of naturally occurring control mechanisms must operate which maintain insect pests below economic injury levels most of the time. The presence of rich entomophagous arthropod faunas coninciding with absence of economic crop losses observed in cotton growing areas where no or little insecticide is used led to the theory that native entomophages may play a major role in keeping the insect pests in check.

To test this theory, extensive field assessments and laboratory experiments dealing with natural predation on cotton pests were conducted by entomology laboratories across the southern U.S. Detailed studies on the natural enemies of the key pests in cotton were also carried out at Texas A&M University by Prof. Winfield Sterling and his team. Sterling's studies showed that spiders, fire ants, lady beetles, green lacewings, damsel bugs, big-eyed bugs, and minute pirate bugs are the numerically dominant entomophagous arthropods in the cotton fields of Texas; the quantitative impact of spider predation on cotton insects had not been assessed at that time.

After my graduation from ETHZ, I had the opportunity to conduct postdoctoral studies in Texas under the supervision of Prof. Sterling; during this time I studied the quantitative impact of spider predation upon the key pests (i.e., cotton fleahopper *Pseudatomoscelis seriatus* [Heteroptera: Miridae], boll weevil *Anthonomus grandis grandis* [Coleoptera: Curculionidae], bollworm *Helicoverpa zea* [= *Heliothis zea*] [Lepidoptera: Noctuidae], and tobacco budworm *Heliothis virescens* [Lepidoptera: Noctuidae]) in cotton. The data were collected over a period of totally ≈ 200 h of visual observations in the course of two field projects: First a project was conducted during the summer of 1985 in an unsprayed (6.5 ha) cotton plantation in Houston County, East Texas. Later a similar project was undertaken during the summer of 1988 in an unsprayed (13.6 ha) cotton plantation located in Burleson County, Central Texas, ≈ 100 km southwest of the previous study site. In the course of these projects basically the following questions were studied:
- What are the numerically dominant species of spiders in the investigated fields?
- In what numbers per m^2 do these spiders occur?
- In what numbers per m^2 do the cotton pests occur?
- What are the natural diets of these spiders?
- What is the percentage of cotton pests in the spider diets?
- What is the percentage of beneficials in the spider diets?
- How often do the spiders feed?

Based on the data obtained during these studies, it was estimated how frequently the spiders feed on particular cotton pests and in how far this may impact the mortality of the pests. Such estimates allow to quantify the ecological impact of spider predation, providing evidence which supports or contradicts the theory that pests in unsprayed cotton are kept in check by native entomophagous arthropods. The results were published between 1987 and 1994 as seven separate papers in the journal "Environmental Entomology" (Entomological Society of America). The last of these papers is a FORUM-article which summarizes all the information which I had collected on spider predation during my field studies in Texas and elsewhere.

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Finally, I wish to express special appreciation to Prof. Dr. Wolfgang Nentwig (Bern) for his continuous interest and moral support.

Prey Selection and Predatory Importance of Orb-Weaving Spiders (Araneae: Araneidae, Uloboridae) in Texas Cotton

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ABSTRACT In an unsprayed cotton field in east Texas, orb weavers were one of the numerically dominant groups of spiders, constituting 10% of all spiders collected by D-vac during the summer of 1985 (range, 0.04 individuals/m^2 in June to 0.72 individuals/m^2 in August). Direct counts, conducted during peak orb-weaver density in August, showed that 0.86 individuals/m^2 were found. More than two-thirds of all orb weavers collected by D-vac in cotton consisted of the five species *Acanthepeira stellata* (Walckenaer), *Neoscona arabesca* (Walckenaer), *Gea heptagon* (Hentz), *Tetragnatha laboriosa* Hentz, and *Uloborus glomosus* (Walckenaer). Their prey consisted of insects (>99%) and spiders (<1%). Aphids, which occasionally reach pest status in Texas cotton, were the most abundant prey of all five spiders (34.6–90%). Other important prey included small dipterans, cicadellids, and hymenopterans. Furthermore, coleopterans were an important component in the prey of *A. stellata* and *N. arabesca*. Together, these five insect groups made up >90% of the prey of the orb-weaving spiders, which are characterized as generalist predators. Differences among the five spider species indicate that prey selection was occurring; this seems to be determined by web location, web inclination, and web strength. Of the orb weavers occurring in cotton, 99% were small-sized spiders (primarily *G. heptagon*) that intercept small prey with their delicate (about 4 cm diameter) webs. These orb weavers are predators primarily of small-sized pests such as the cotton aphid, *Aphis gossypii* Glover, and the cotton fleahopper, *Pseudatomoscelis seriatus* (Reuter).

KEY WORDS Arachnida, orb-weaving spiders, cotton, predation

MOST SPECIES of Araneidae and Uloboridae spin spiraling orb webs. Although the general biology of orb-weaving spiders is well known (reviews in Witt et al. 1968, Levi 1978), the significance of these predators in the natural control of pest insects is poorly understood, although in some agroecosystems, orb weavers constitute the most abundant spiders. Prey analyses have been conducted in soybean fields in Illinois (LeSar & Unzicker 1978) and Kentucky (Culin & Yeargan 1982), as well as in Polish meadows (Kajak 1965) and Swiss cereal fields (Nyffeler & Benz 1979). The goal of this paper is to give insight into the effect of orb weavers in an east Texas cotton field that can be used to adjust the species-specific indices of efficiency used in the tritrophic cotton insect TEXCIM model (Hartstack & Sterling 1988). Studies on the ecology of other spiders occurring in this agroecosystem are presented elsewhere (Nyffeler et al. 1986, 1987a,b,c, 1988a,b; Dean et al. 1987).

Materials and Methods

Study Area. Investigations were conducted during the summer of 1985 (June to mid-September) in a cotton field that received no pesticide applications. This field was located 8 km west of Austonio, Tex., near Crockett in Houston Co., and was bordered by meadows composed of various grasses and low growing annual Dicotyledonae that were mown once during this study. The cotton field had an area of 6.5 ha with 1 m between rows and about 10 cotton plants per meter of row. Cotton (variety CAMD-E) was planted on 27 May and emerged in the first week of June. Parts of this field were heavily infested with weeds (johnsongrass). The field was cultivated on 10 and 29 June. We finished our investigation on 16 September, at which time the cotton had not been harvested.

Evaluation of Numbers of Orb-Weaving Spiders in Cotton. Numbers of orb weavers per square meter were estimated in two ways: through direct counts in the field, and with a D-vac suction machine (D-vac, Riverside, Calif.).

Direct Count. Numbers of small diurnal orb weavers can easily be assessed by counting webs per square meter during daylight hours. On 7 August, small orb weavers were counted in 50 randomly selected 1-m^2 samples by searching the cotton foliage for webs. Adults of large nocturnal orb-weaving species may be overlooked because many of these spiders remove their webs during the daylight hours and construct retreats under cotton foliage. To accurately estimate their numbers, additional counts were made after dark with a headlamp on 14 and 19 August by walking along

Table 1. Web area versus ground area spun by orb weavers in eastern Texas cotton during their peak numbers, August 1985

Spider group	No. spiders/m² determined by visual counts ($\bar{Z}$)	Estimated cm² web area/m² ground area[a]
	Mean (% total)	Mean (% total)
Small orb-weavers[b]		
Gea heptagon	0.681 (78.9)	9.66 (57.2)
Others[c]	0.176 (20.4)	2.50 (14.8)
Large orb-weavers[d]		
Acanthepeira stellata	0.003 (0.3)	2.07 (12.3)
Neoscona arabesca	0.003 (0.3)	2.66 (15.7)
Total	0.863 (100)	16.89 (100)

[a] Orb-web areas calculated as approximation to a circular area: $(\pi)(\bar{D}^2)(\bar{Z})/4$, where $\bar{D}$ is average web diameter in centimeters.

[b] Immatures and adults of small-sized species and immatures of large-sized species.

[c] *T. laboriosa*, *U. glomosus*, and others.

[d] Adults of large-sized species.

cotton rows and recording the numbers of large orb webs hanging across the free space between adjacent rows or in gaps within a row. Each night, spiders were counted along a distance of 500 m (walking speed about 250 m/h), and data were later converted into average number of spiders per square meter. Numbers per square meter of small orb weavers (assessed by day) and of large orb weavers (assessed by night) were combined (Table 1) to provide an estimate of the total number of orb weavers in this cotton field in August.

D-vac Method. Twenty-five D-vac suction samples (Dietrick 1961), each of 1 m of row, were taken weekly over a 14-wk period during the summer of 1985 to obtain estimates of numbers of spiders and of potential prey composition. Details are described in Nyffeler et al. (1987b). Number of spiders per meter of row represents the number per square meter, because the lateral distance between rows was 1 m.

Assessment of Web Size and Catching Area. Because most orb-weaving spiders spin slightly asymmetrical orb webs (Nentwig 1985), it follows that often horizontal diameter is not equal to vertical diameter. In this study, we measured horizontal diameter and vertical diameter of an orb web with a meter stick, and from these two values we calculated the arithmetic mean used as an estimate of parameter $\bar{D}$ (see below). The catching area per spider was calculated as an approximately circular area; the average square centimeters of web area per square meter of ground area was estimated as follows (see Table 1):

$$\text{cm}^2 \text{ web area/m}^2 \text{ ground area} = \frac{(\pi)(\bar{D}^2)(\bar{Z})}{4},$$

where $\bar{D}$ is the average web diameter in centimeters and $\bar{Z}$ is the average number of spiders per square meter (see above).

Evaluation of the Spiders' Prey. Evidence of predation by orb weavers in cotton was obtained by removing arthropod remains from webs. All arthropods found dead in spider webs were considered as prey. Webs were searched for prey during the day and night, and prey items were removed from webs with forceps and preserved in 70% ethyl alcohol. They were later identified and counted under the microscope. Some of the insect carcasses are discarded by the spiders from the web after the meal (Turnbull 1973); these dropped carcasses are usually removed by the scavenging activities of *Solenopsis invicta* Buren worker ants. Because of different handling times exhibited by the spiders for differing prey taxa, our data may be biased.

Statistical Procedures for Testing Interspecific Differences of Prey Selection. Interspecific differences in the selection of "type" of prey by the investigated orb weavers were tested by computing the proportion of prey items in the four "types" of prey categories—"flying insects;" "jumping insects;" "wingless, mobile arthropods;" and "wingless, immobile arthropods"—for each orb-weaver species. Interspecific differences of proportions within a type of prey category were tested by comparing the 0.95 confidence intervals (CI) for proportions using tables in Documenta Geigy (1968); nonoverlapping 0.95 CIs indicate significant differences at the 5% level. However, because confidence intervals do not constitute a rigorous statistical test, those significant differences of proportions discussed in the text were doublechecked using the χ^2 test for the comparison of proportions.

Results

In this study, orb-weaving spiders were a numerically dominant spider group constituting 10% of all spiders collected during the summer by D-vac (total $n = 923$; monthly means: June, 15.6%; July, 14.6%; August, 9.3%; September, 3.5%). The taxonomic composition of orb weavers in Texas cotton fields is presented in Dean et al. (1982) and Dean & Sterling (1987). Five species, *Acanthepeira stellata* (Walckenaer), *Neoscona arabesca* (Walckenaer), *Gea heptagon* (Hentz), *Tetragnatha laboriosa* Hentz, and *Uloborus glomosus* (Walckenaer), constituted more than 80% of the 88 orb weavers sampled by D-vac in 1985. In early June, when the cotton plants emerged, very few orb-weaving spiders were in the field (0.04 ± 0.04 individuals/m² [$\bar{x}$ ± SE] in D-vac samples), but a large number already existed in the adjacent meadows (assessed by direct observations and sweep sampling; D.A.D., unpublished data). The same species were found in the meadow as in cotton, with *G. heptagon* constituting 75% of all orb weavers sampled in the meadow by D-vac (D.A.D., unpublished data). Those found in cotton and the adjacent meadow move readily through the air by ballooning (Dean & Sterling 1985), and it is likely that meadows function as reservoirs for the colonization of cotton fields by orb weavers. Numbers in cotton increased to a maximum in August (0.72 ± 0.18 individuals/m^2 [$\bar{x}$ ± SE] in D-vac samples). The 0.86 individuals/m^2 (Table 1) that were visually counted is about 20% more than the average numbers assessed by D-vac sampling. In August, these spiders spun an estimated average web area of about 17 cm^2/m^2 ground area (Table 1).

Of these orb weavers, about 99% were small-sized spiders <5 mm long, with *G. heptagon* clearly dominating (Table 1). Large orb weavers, such as adults of *A. stellata* and *N. arabesca* >7 mm long, constituted <1%.

Locations and relative size of the webs on cotton plants of the five orb-weaver species mentioned above are illustrated in Fig. 1. Considerable differences in habitat use by these spiders were found. The small webs (mean diameter, 4.25 ± 0.30 [$\bar{x}$ ± SE]; range, 2.5–7.5 cm; $n = 21$) of *G. heptagon* are hung almost vertically in plants close to the ground; this species was found in the cotton field in summer as immatures and is reported in the literature to mature in autumn (Sabath 1969). In contrast, *U. glomosus* constructs delicate, horizontally oriented nets (about 10 cm diameter) in the middle part of the plants, and *T. laboriosa* spins small to medium-sized webs (about 11 cm diameter) oriented at various angles in the top half of the plant. The large, almost vertically oriented webs (about 30 cm diameter) of adult *A. stellata* and *N. arabesca* are normally hung across the free space between adjacent cotton rows and sometimes in gaps within a row. A statistically significant difference was found between average web diameter of large orb weavers (*A. stellata, N. arabesca*) and smaller orb weavers (*G. heptagon, T. laboriosa*) ($P < 0.001$, Mann-Whitney U test, two-tailed).

Gea heptagon and *U. glomosus* remain on the hub of their webs day and night, whereas the adults of *A. stellata* and *N. arabesca* are nocturnal foragers. *T. laboriosa* were found on the hub of their webs during the night and sometimes during the daylight hours. *A. stellata, N. arabesca,* and *T. laboriosa* were observed constructing webs shortly before sundown. *G. heptagon* was observed spinning webs in the laboratory in the evening or early morning (Sabath 1969). No observations were made on the time of day of web spinning of *U. glomosus,* but another species of *Uloborus* was observed building its web 1 or 2 h before dawn (Eberhard 1971). Feeding spiders were found in only 7% of the webs of *G. heptagon* as assessed in the first half of August during daylight hours.

The prey of the five orb-weaving spiders in cotton consisted of insects (>99%) and spiders (<1%) (Table 2). Aphids were the most abundant prey of all five species (34.6–90%), which is not surprising because these insects also prevailed in D-vac samples (Table 2), indicating that they were a very abundant potential prey on the cotton foliage. Other important prey were small dipterans, cicadellids, and hymenopterans. Furthermore, coleopterans were an important component in the prey of *A. stellata* and *N. arabesca.* These five insect groups combined made up >90% of the orb weavers' prey. One cotton fleahopper, *Pseudatomoscelis seriatus* (Reuter), and one adult bollworm moth, *Heliothis zea* (Boddie), were observed as prey of orb weavers (Table 2), indicating that orb weavers occasionally capture these cotton pests. In the cotton field, evidence of prey selection between the five orb-weaver species was found.

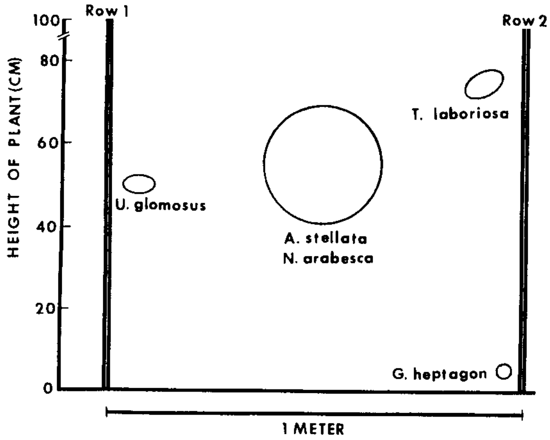

Fig. 1. Relative size and location of the webs (mean values) of five orb-weaving spider species on cotton plants in eastern Texas (web positions of feeding active spiders between mid-July and August 1985).

A high proportion (>80%) of flying insects was captured by the two large orb weavers *A. stellata* and *N. arabesca,* which spin their strong webs across the free spaces between adjacent cotton rows. The percentages of flying insects in the prey of these two species did not differ significantly ($P > 0.05$, χ^2). The three smaller orb-weaver species, which spin their orbs within and on the cotton plants, captured a significantly ($P < 0.05$, χ^2) lower proportion (<50%) of flying insects (Table 3).

Jumping insects and wingless, mobile arthropods each constituted <13% in all five orb weavers' prey (Table 3). Seventeen workers of the red imported fire ant, *S. invicta,* were trapped in webs of *G. heptagon.* Because this spider builds its small orbs attached to cotton leaves close to the ground, ant workers occasionally get stuck in the sticky threads and are wrapped into silk by the spider. In orbs of other spider species positioned on higher levels above ground, *S. invicta* workers were rarely captured; on one occasion a *T. laboriosa* was observed consuming an *S. invicta* worker.

Wingless, relatively immobile insects such as brachypterous aphids constituted a low proportion (<3%) of the prey of the large orb weavers, *A. stellata* and *N. arabesca,* but made up a high proportion (>25%) in the smaller orb weavers' prey (Table 3); this difference is statistically significant ($P < 0.05$, χ^2).

Table 2. Prey (% by number) of five orb-weaving species and their estimated potential prey in a cotton agroecosystem in eastern Texas, summer 1985

Prey	Spider					
	A. stellata $n = 104$, $z = 44$	*N. arabesca* $n = 22$, $z = 15$	*G. heptagon* $n = 147$, $z = 111$	*T. laboriosa* $n = 41$, $z = 23$	*U. glomosus* $n = 50$, $z = 16$	Estimate % potential prey[a] $n = 58{,}528$
Homoptera						
Aphididae, wingless	2.9	0	25.2	43.9	68.0	72.2
Aphididae, winged	31.7	45.5	27.2	34.1	22.0	3.2
Cicadellidae	8.7	4.5	10.2	7.3	0	4.8
Diptera, small	30.8	4.5	15.6	12.2	4.0	2.1
Hymenoptera						
S. invicta, worker	1.0	0	11.6	2.4	6.0	12.6
Other, small	2.9	4.5	4.1	0	0	1.9
Coleoptera						
Curculionidae	2.9	0	0	0	0	0.1
Scarabaeidae	4.8	22.7	0	0	0	0
Other	6.7	9.1	0.7	0	0	0.3
Heteroptera	1.9	4.5	1.4[b]	0	0	1.2
Lepidoptera, adults	2.9[c]	4.5	0	0	0	—[d]
Orthoptera	0	0	2.1	0	0	—[d]
Araneae, orb weavers	1.0	0	0	0	0	1.6
Other	1.9	0	1.4	0	0	0
Total	100	100	100	100	100	100

n = no. prey items; z = no. spider webs.

[a] Based on D-vac sample data; those samples have bias toward some prey types (Pieters & Sterling 1973) but are at least an estimate of potential prey composition.

[b] Includes one cotton fleahopper.

[c] Includes one *H. zea* adult.

[d] Missing in samples because D-vac method not suitable for collecting Lepidoptera or Orthoptera.

Within the cotton foliage, wingless aphids constituted a significantly ($P < 0.05$, χ^2) higher proportion in the prey spectrum of *U. glomosus* (>60%), which builds horizontal webs, than in that of *G. heptagon* (<30%), which builds vertical webs. The percentage of wingless, relatively immobile insects in the prey of *T. laboriosa* (44%, Table 3), whose webs are oriented at various angles, was between the values of *G. heptagon* (25%) and *U. glomosus* (68%) and differed from them significantly ($P < 0.05$, χ^2).

Discussion

The investigated orb weavers captured a variety of prey taxa characterizing them as generalist predators (Table 2), which is in agreement with previous prey analyses of orb-weaving spiders (LeSar & Unzicker 1978; Nyffeler & Benz 1978; Culin & Yeargan 1982; Nyffeler 1982; Nyffeler et al. 1986, 1987c). One could question if the carcasses of arthropods found in spider webs actually represent the diet or if some of them may have been caught in the webs accidentally. From the point of view of natural pest control, it matters little whether the spider actually feeds on insects caught in webs if the "prey" dies anyway. However, the insect groups which are considered in this paper as prey of orb weavers (such as aphids, cicadellids, dipterans, ants, coleopterans, heteropterans, lepidopterans, and others) have been observed in the field being eaten by orb-weaving spiders (LeSar & Unzicker 1978; Culin & Yeargan 1982; M.N., unpublished data). Thus, we assume that most species of insects found in webs in this study were used as food. According to a field study by Turnbull (1960), a web-building spider accepted 98% of 153 species of insects trapped in the web, demonstrating the low rejection rate of such spiders. Intuitively, many defenses of prey may be largely immobilized by capture in a web.

If we compare the five spiders of this study and their selection of type of prey in relation to the different web positions, web inclinations, and other web characteristics (Fig. 1; Table 3), the following pattern emerges.

Web position was found to be a determinant of prey selection by comparing small orb webs on cotton foliage with the large orb webs spun between cotton rows. We found that orb webs between the rows captured a higher proportion of flying and a lower proportion of wingless, immobile prey.

Orb webs may function as protective barriers (sensu Turnbull 1973) against *S. invicta*, which are aggressive predaceous ants occasionally biting into the legs of spiders (M.N., unpublished data). Web position also was found to be a determinant of prey selection in other studies (Nyffeler & Benz 1978, Olive 1980, Pasquet 1984).

Web orientation may be another factor determining prey selection, evidenced by the observa-

Table 3. Selection of "type" of prey (in %, with 0.95 CI), in relation to web characteristics by five orb-weaving spiders in a cotton agroecosystem in eastern Texas (based on data in Table 2)

	Large, nocturnal orb weavers[a]		Small, diurnal orb weavers[b]		
	A. stellata	*N. arabesca*	*G. heptagon*	*T. laboriosa*	*U. glomosus*
Spider web characteristics					
Placement	Between cotton rows	Between cotton rows	Within plant	Within or on plant	Within plant
Inclination	Vertical	Vertical	Vertical	At various angles	Horizontal
Size and strength	Large, strong	Large, strong	Small, delicate	Small, delicate	Small, delicate
Mesh size	Wide meshed	Wide meshed	Close meshed	Close meshed	Close meshed
Thread type	Warps and droplets of gum[c]	Warps and droplets of gum[c]	Warps and droplets of gum[c]	Warps and droplets of gum[c]	Warps and cribellum wool[d]
Type of prey, % (0.95 CI)					
Flying insects[e]	84.7 (76–91)	95.3 (77–100)	50.0 (41–58)	46.3 (31–63)	26.0 (15–40)
Jumping insects[f]	8.7 (4–12)	4.5 (0.1–23)	12.5 (8–19)	7.3 (1–20)	0 (0–7)
Wingless, mobile[g]	2.0 (0.2–7)	0 (0–15)	11.8 (7–18)	2.4 (0.1–13)	6.0 (1–17)
Wingless, immobile[h]	2.9 (0.6–8)	0 (0–15)	25.7 (19–34)	43.9 (28–60)	68.0 (53–80)
Total	100	100	100	100	100

0.95 confidence intervals for proportions computed using tables in Documenta Geigy (1968); if CIs do not overlap within a line, two compared percentages differ significantly at 5% level.

[a] Nocturnal as adults; early instars diurnal.

[b] May be active day and night.

[c] Ecribellate spiders with venom glands, wrap and bite prey.

[d] Cribellate spiders wrap prey but do not bite because venom glands are lacking.

[e] Winged Aphididae, Diptera, winged Hymenoptera, Coleoptera, Heteroptera, and Lepidoptera.

[f] Cicadellidae and Orthoptera.

[g] *S. invicta* workers and spiders.

[h] Wingless Aphididae.

tions that within the cotton plants a significantly ($P < 0.05$, χ^2) higher percentage of flying insects were trapped in the vertical *G. heptagon* webs than in the horizontal *U. glomosus* webs (50% versus 26%, Table 3). Experiments with artificial traps by Chacon & Eberhard (1980) suggest that insects tend to fly more horizontally than vertically and therefore would be more effectively intercepted in vertical webs. In contrast, horizontal orb webs may be more effective in intercepting wingless, relatively immobile insects (Table 2). How do such wingless, relatively immobile insects fall prey to orb weavers which are "sit-and-wait foragers"? Many wingless aphids located on the undersides of leaves are regularly detached from cotton foliage by wind (M.N., unpublished data). Hunting predators also may disturb them. Sunderland et al. (1986) observed in winter wheat fields that wingless aphid morphs fell from foliage to the ground at a rate of up to >100 individuals/m^2/d. Many of these falling aphids were intercepted in horizontally oriented spider webs. Chacon & Eberhard (1980) suggested that horizontal orb webs may be designed for the capture of prey falling from above.

Mesh size was suggested in the literature to be a determinant of prey selection (Risch 1977, Uetz et al. 1978). In this study, we found that orb weavers spinning close-meshed orbs as well as those spinning wide-meshed orbs (Table 3) caught many small insects of aphid size (>50% in total prey of all five orb-weaver species). No correlation between mesh size and prey size was found by Nentwig (1983) in experiments with artificial webs.

Web strength, which is a function of web size (according to Craig [1987], high-energy-absorbing webs tend to be large), was found to be another determinant of prey selection by orb weavers. Small, delicate orb webs (e.g., those of *G. heptagon*, *U. glomosus*, and *T. laboriosa*) are designed for the interception of small insects and are not suited to capture larger prey such as Lepidoptera and Coleoptera (LeSar & Unzicker 1978, Culin & Yeargan 1982). On the contrary, the large, strong orb webs of adult *A. stellata* and *N. arabesca* are designed for the interception of small and large prey. This is consistent with observations of Castillo & Eberhard (1983), who reported that larger orb weavers captured larger prey and a greater variety of prey sizes than smaller spiders.

Coleoptera are excluded as prey of small orb weavers, as observed in *T. laboriosa*, which was seen eliminating entangled beetles from the web by violently shaking the web until the beetle fell, by ignoring the beetles until they worked themselves free and could escape, and by cutting the web around an adult beetle and allowing it to drop from the web (LeSar & Unzicker 1978, Culin & Yeargan 1982).

Adult Coleoptera constituted >10% of the prey of the large orb weavers in this study and almost 50% of the prey of *N. arabesca* in Kentucky soybean fields (Culin & Yeargan 1982). These authors assume that the high proportion of Coleoptera in the prey of *N. arabesca* reflects web location and locomotory activity patterns of potential prey.

Noctuid moths also are trapped in these large orb webs (this study, Whitcomb et al. 1963). Large orb weavers were observed in this study feeding on the captured beetles and moths, indicating that those insects actually are used as food. These spiders' efficiency as predators of injurious moths is uncertain because of the ability of those insects to escape from spider webs. Eisner et al. (1964) stated: "Moths, by virtue of the loose scales that cover their wings and bodies, are admirably adapted to elude capture by orb-weaving spiders. Rather than sticking to the web, they may simply lose some of their scales to the viscid threads, and fly on." Robinson & Robinson (1970) estimated from field data that >50% of the moths encountering the webs of a large orb weaver were able to escape; on the other hand, Whitcomb et al. (1963) found many noctuid moths captured in large orb webs in Arkansas cotton fields.

Feeding spiders were found in <10% of the webs of *G. heptagon*. In comparison, spiders were found feeding in about 12% of the webs of *T. laboriosa* in soybeans (LeSar & Unzicker 1978). According to LeSar & Unzicker (1978), those low feeding frequency values suggest that such small orb weavers have low prey capture rates. An immature *G. heptagon* building orbs of only about 4 cm in diameter in August has on the average a 50 times smaller catching area than an adult large-sized orb weaver (e.g., *A. stellata*). However, *G. heptagon*, having reached maturity in fall, build webs of 10–12 cm diameter (Sabath 1969).

In east Texas where small orb weavers predominate, these spiders are primarily predators of small-sized pests such as the cotton aphid, *Aphis gossypii* Glover, and the cotton fleahopper. Orb-weaver predation on these two insects was reported by Kagan (1943) in Texas cotton. Predation of the boll weevil and *Heliothis* spp. by orb-weaving spiders appears to be insignificant because of the apparent inability of small orb weavers to overcome larger pests and because of the low numbers of large-sized orb weavers in the cotton fields (see above).

In 1985, all key pests (sensu Bohmfalk et al. 1983) combined constituted only about 1% of the prey of *G. heptagon* and *A. stellata* and were missing in the prey spectra of the other orb-weaver species (Table 2). The low frequency of key cotton pests is in part because of the low densities of those key pests in that area during the summer of 1985 (D.A.D., unpublished data). Conversely, occasional pests (sensu Bohmfalk et al. 1983) such as aphids constituted >30% of the spiders' prey. Predaceous arthropods were rarer (<7%) in the prey of orb weavers except for occasional capturing of *S. invicta* by *G. heptagon*.

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Predation by Green Lynx Spider, *Peucetia viridans* (Araneae: Oxyopidae), Inhabiting Cotton and Woolly Croton Plants in East Texas

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ABSTRACT Predation by green lynx spider, *Peucetia viridans* (Hentz), was studied on cotton and woolly croton plants in East Texas. This species feeds both diurnally and nocturnally. *P. viridans* was observed feeding on insects of orders Diptera, Hymenoptera, Heteroptera, Homoptera, Coleoptera, Lepidoptera, Neuroptera, and Odonata, as well as on several spider species. Predaceous arthropods (e.g., *Hippodamia convergens* Guérin-Méneville, Coccinellidae; *Chrysoperla rufilabris* [Burmeister], Chrysopidae) constituted more than half of the spiders' diet. In cotton, *P. viridans* was found to be a predator of the pests *Heliothis zea* (Boddie) and *Alabama argillacea* (Hübner) (together 8% of the spiders' prey). Size of killed prey in cotton ranged between 0.14- and 1.3-fold the spiders' size (average prey length, 5.90 ± 0.99 mm). On woolly croton plants, *P. viridans* was often seen feeding on cotton fleahopper, *Pseudatomoscelis seriatus* (Reuter) (numerically almost 30% of the spiders' prey), which is a key pest in cotton. It was estimated that on cotton and croton plants in East Texas, one *P. viridans* captured an average of less than one prey daily. Our results are compared with data in the literature on the diet of *P. viridans*.

KEY WORDS *Peucetia, Pseudatomoscelis,* cotton, croton, predation, diet

ONE OF THE most conspicuous American spiders is the green lynx, *Peucetia viridans* (Hentz). This vivid green species is armed with many black spines on its legs. Average length of adult females is 16 mm and that of adult males is 12 mm, making it the largest lynx spider north of Mexico (Brady 1964). *P. viridans* is a hunting spider that remains motionless on leaves in a characteristic prey-catching posture. This spider inhabits foliage of tall grass, weeds, and shrubs throughout the southern United States from coast to coast. *P. viridans* has been found in cotton fields in Arkansas (Whitcomb et al. 1963) and Texas (Dean et al. 1982), soybean fields in Arkansas (Whitcomb et al. 1966) and North Carolina (Deitz et al. 1980), and grasslands in Texas (Brady 1964).

Whitcomb et al. (1963) reported that *P. viridans* feeds on bollworm, *Heliothis zea* (Boddie), moths; cotton leafworm, *Alabama argillacea* (Hübner), moths; and cabbage looper, *Trichoplusia ni* (Hübner), moths. All are considered to be pests in cotton. Thus, a better understanding of the feeding ecology of this spider species is important to entomologists and ecologists interested in natural and biological control of cotton pests. Data on the feeding ecology of *P. viridans* on cotton and croton plants in East Texas are presented to add to the list of known prey species of this spider.

Materials and Methods

Part of this investigation was conducted in an unsprayed cotton field located 8 km west of Austonio, Tex., near Crockett in Houston County, during the summer of 1985 (June–mid-September). The cotton field bordered on extensive meadows (composed of various grasses and low-growing annual Dicotyledonae), which are considered to be predator reservoirs for colonization of the cotton fields by spiders (unpublished data). The cotton was planted on 27 May and emerged in the 1st wk of June. Observations were also made in an unsprayed cotton field near Huntsville, Tex., from 1978 to 1981.

Other studies were conducted in a plant community (ca. 0.1 ha) dominated by woolly croton, *Croton capitatus* Michaux, in late summer 1984 (August–September). Woolly croton is the primary host of the cotton fleahopper, *Pseudatomoscelis seriatus* (Reuter). The site was located next to a residential area.

Feeding by *P. viridans* was observed along cotton rows or across the croton field at different times of the day and year, and the numbers of spiders with and without prey were recorded. To test if the frequency of feeding in *P. viridans* depends on time of day or season, we applied the χ^2-test for contingency tables to our data. A total of 85 h was spent observing *P. viridans* in cotton and 25.5 h in croton. Additional data were gathered while we observed the feeding habits of other spider species. Between 1978 and 1984 the observed cases of predation were recorded directly in a field book. In 1985, spiders with prey were captured by hand in a plastic cup (7 cm diameter), killed, and preserved in 70% ethyl alcohol. Later, the prey were

Table 1. Striped and green lynx spiders as a percentage of all hunting spiders[a] on cotton foliage

Date	Total no. foliage-hunting spiders observed[a]	Striped lynx (%)	Green lynx (%)	Both lynx species (%)
22–28 July	170	74.7	19.4	94.1
29 July–4 Aug.	400	68.8	20.5	89.3
5–11 Aug.	479	79.1	12.3	91.4
12–18 Aug.	548	70.8	19.7	90.5
19–25 Aug.	305	75.7	11.5	87.2
26 Aug.–3 Sept.	395	84.3	11.1	95.4
4–8 Sept.	124	83.1	12.1	95.2
$\bar{x}$	—	76.6	15.2	91.8

[a] All spiders found on cotton plants that capture prey without a web.

identified in the laboratory under a microscope. Night observations were carried out with a head lamp.

An important parameter in the evaluation of the spiders' potential as biological control agents is the prey capture rate (no. of prey/spider/day), because the impact of spiders on prey populations is, among others, a function of this value. The prey capture rate (b) of *P. viridans* was calculated according to Edgar's (1970) method developed for wolf spiders, modified by us as follows:

$$b = (T_f \cdot 60 \cdot w)/(1 \cdot T_h \cdot 100),$$

where T_f is the time (hours per day) available for prey capture and feeding in the field, w is the percentage of spiders with prey in a sample, and T_h is the average handling time (in minutes). The handling time is the period between the initiation of an attack and the cessation of feeding. To assess T_f and w, collections were made in the field at different times of the day, and the numbers of spiders with and without prey were recorded (see above). T_h was evaluated in feeding experiments.

Results

During the summer of 1985, the green lynx constituted 11–20% of the hunting-spider fauna observed on the foliage in an East Texas cotton agroecosystem (Table 1). In the same agroecosystem, the striped lynx, *Oxyopes salticus* Hentz, constituted 70–84% of the observed hunting spiders on foliage (Table 1). Studies on the feeding ecology of *O. salticus* are described in Nyffeler et al. (1987). Together, these oxyopids constituted >85% of the entire hunting-spider fauna on foliage, suggesting that based on abundance they are the dominant spiders in East Texas cotton fields.

P. viridans is univoltine in East Texas (Killebrew & Ford 1985), and according to a study by Whitcomb et al. (1966) in Arkansas cotton fields, late instars of *P. viridans* occur in late May and early June, and adults are present in late June and thereafter. A similar seasonal trend was observed in East Texas. In the cotton agroecosystem at Austonio, the green lynx spiders observed feeding had an average body length of 10.96 ± 0.41 mm ($\bar{x}$ ± SE; range, 8.2–12.7 mm). The early instars of this spider were not found in this cotton agroecosystem. Thus, all *P. viridans* observed in cotton were late instars or adults. In cotton, *P. viridans* killed prey of a size between 0.14- and 1.3-fold its own size. Prey had an average body length of 5.90 ± 0.99 mm ($\bar{x}$ ± SE; range, 1.6–16.5 mm).

Twenty-five predation events by *P. viridans* on

Table 2. Prey of *P. viridans* in unsprayed cotton fields

Prey			No. prey	Location[a]	Stage[b]	% prey
Diptera			2	A	a	8.0
Hymenoptera	Apidae	*Apis mellifera* L.	1	H	a	4.0
	Wasps		1	H	a	4.0
	Unidentified		1	A	a	4.0
Heteroptera	Reduviidae	*Zelus cervicalus* Stål	1	A	a	4.0
	Miridae	*Spanagonicus albofasciatus* (Reuter)	1	A	a	4.0
	Nabidae	*Tropiconabis capsiformis* (Germar)	1	A	a	4.0
Coleoptera	Coccinellidae	*H. convergens*	1	A	a	4.0
Lepidoptera	Noctuidae	*A. argillacea*	1	H	i	4.0
	Noctuidae	*H. zea*	1	H	a	4.0
Neuroptera	Chrysopidae	*C. rufilabris* (Burmeister)	2	A	a	8.0
Araneae	Araneidae	*A. stellata*	2	A	a, i	8.0
	Linyphiidae	*Eperigone* sp.	1	A	a	4.0
	Oxyopidae	*O. salticus*	2	A	a	8.0
	Oxyopidae	*P. viridans*	1	A	a	4.0
	Clubionidae	*C. inclusum*	2	A	a	8.0
	Lycosidae		1	A	i	4.0
	Salticidae		1	H	i	4.0
Unidentified arthropods			2	A		8.0
Total			25			100

[a] A, Austonio (1985); H, Huntsville (1978–81).

[b] a, adult; i, immature.

Table 3. Diel change of percentage of feeding spiders in a *P. viridans* population in a cotton agroecosystem

Time (hours; CST)	No. h spent observing (x)	No. spiders observed (y)	No. spiders observed/h (y/x)	No. spiders with prey[a] (z)	% spiders with prey ($100z/y$)
0800–1155	25	140	5.6	7	5.0
1200–1555	17	69	4.1	4	5.8
1600–1955	19	94	4.9	4	4.3
2000–2355	13	53	4.1	0	0
2400–0355	3.5	12	3.4	1	8.3
0400–0755	7.5	29	3.9	4	13.8

[a] $P > 0.05$; χ^2-test for contingency tables.

Table 5. Prey of *P. viridans* on croton plants

Prey		No. prey	% prey
Diptera	Muscidae	1	1.5
	Asilidae	1	1.5
Hymenoptera	Ants	1	1.5
	Wasps (medium-sized)	8	11.8
	Apis mellifera	9	13.2
	Bumble bees	1	1.5
Heteroptera	Cotton fleahoppers[a]	20	29.4
Homoptera	Leafhoppers	1	1.5
Coleoptera		5	7.3
Neuroptera	Chrysopidae	3	4.4
Lepidoptera	Moths	6	8.8
Odonata		1	1.5
Araneae			
Araneidae	*Neoscona arabesca* (Walckenaer)	1	1.5
Oxyopidae	*O. salticus*	3	4.4
Oxyopidae	*P. viridans*	2	2.9
Lycosidae	*Pardosa* sp.	1	1.5
Thomisidae	*Misumenops* sp.	2	2.9
Salticidae	*Hentzia palmarum* (Hentz)	1	1.5
Salticidae	*P. audax*	1	1.5
Total		68	100

[a] All adults except one.

cotton arthropods were recorded (Table 2). Food of *P. viridans* consisted exclusively of arthropods (Insecta or Arachnida). Forty percent of the prey items were spiders. Events of inter- and intraspecific predation were observed. Among the insects captured by *P. viridans* were species of the orders Hymenoptera, Heteroptera, Coleoptera, Diptera, Lepidoptera, and Neuroptera. More than half of these 25 prey were predaceous arthropods (e.g., *Chrysoperla rufilabris* [Burmeister] and *Hippodamia convergens* Guérin-Méneville); and two cotton pests, *H. zea* and *A. argillacea*, were observed as prey. One reason for the low incidence of predation by spiders on pests in the cotton fields near Austonio is that the pests were relatively rare during the period of this study; however, pests were more abundant at Huntsville (D.A.D., unpublished data).

The proportion of *P. viridans* with prey at different times of the day (Table 3) suggests that this species feeds both day (0800–2000 hours CST) and night (2400–0800 hours). The number of spiders with prey did not depend on the time of day ($P > 0.05$; χ^2-test for contingency tables). The percentage of feeding spiders was <10% throughout the 1985 season (Table 4); no dependence of the number of spiders with prey upon the time of the year was found ($P > 0.05$; χ^2-test for contingency tables).

Edgar's (1970) formula for calculation of b of *P. viridans* was used as previously described. Values used were as follows: $T_f = 20$ (see Table 3), $w = 5.35$ (mean from Table 4), and $T_h = 270$ (based on our observations). On this basis it was estimated that one spider captured about one prey every 4 d.

A total of 68 instances of prey capture was observed on woolly croton during late summer in 1984 near College Station (Table 5). As in cotton, the food of *P. viridans* consisted exclusively of Insecta and Arachnida. Sixteen percent of the prey were spiders (inter- and intraspecific predation). Among the insects killed by *P. viridans* on croton plants were species of the orders Diptera, Hymenoptera, Heteroptera, Homoptera, Coleoptera, Neuroptera, Lepidoptera, and Odonata. Half of the prey were entomophagous arthropods or pollinators. Twenty-nine percent of the prey of *P. viridans* were cotton fleahoppers, considered to be key pests in cotton in East Texas.

A total of 668 *P. viridans* was encountered on woolly croton with 68 observed cases of predation

Table 4. Seasonal change of percentage of feeding spiders in a *P. viridans* population and estimated prey capture rates

Date	No. h spent observing (x)	No. spiders observed (y)	No. spiders observed/h (y/x)	No. spiders with prey[a] (z)	% spiders with prey ($w = 100z/y$)	No. prey/spider/d ($b = 0.0444w$)
22–28 July	4.5	33	7.33	2	6.1	0.22
29 July–4 Aug.	14	76	5.43	5	6.6	0.29
5–11 Aug.	17	65	3.82	3	4.6	0.20
12–18 Aug.	18.5	108	5.84	3	2.8	0.12
19–25 Aug.	9	35	3.89	1	2.9	0.13
26 Aug.–3 Sept.	10	44	4.40	4	9.1	0.40
4–8 Sept.	4.5	15	3.33	0	[b]	[b]
$\bar{x}$	—	—	4.86	—	5.35	0.23

[a] $P > 0.05$; χ^2-test for contingency tables.

[b] Sample size too small for calculation of w and b.

(10.2%). Using this w value, and under the assumption that the T_h is about the same in cotton and croton, we calculated $b = 0.5$, indicating that on woolly croton plants a spider captures an average of one prey every 2nd d.

Discussion

On shrubs in California, Turner (1979) collected 189 prey of *P. viridans* and reported this spider feeding on Hymenoptera (41%), Diptera (15%), Lepidoptera (15%), Heteroptera (9%), Orthoptera (8%), Araneae (7%), and Coleoptera (4%).

In Florida, Randall (1982) collected 66 prey of *P. viridans,* which belonged to the insect orders Hymenoptera (41%), Diptera (27%), Heteroptera (21%), Lepidoptera (8%), and Coleoptera (3%). In Arkansas, Whitcomb et al. (1963, 1966) reported *P. viridans* feeding on moths of the families Noctuidae, Geometridae, and Pyralidae, as well as on dipterans (syrphid and tachinid flies), and hymenopterans (honey bees, sphecid and vespid wasps).

In our study, a considerable proportion of the prey of *P. viridans* was spiders. Eighteen cases of interspecific predation and three cases of cannibalism were observed. This result is contrary to the observations of Whitcomb et al. (1963), Turner (1979), and Randall (1982), who reported either no or few cases of interspecific predation between *P. viridans* and other spiders. Among those spiders captured by the green lynx, *O. salticus, Phidippus audax* (Hentz), *Misumenops* sp., *Chiracanthium inclusum* (Hentz), and *Acanthepeira stellata* (Walckenaer) are abundant spiders in East Texas cotton fields (Dean et al. 1982). *P. viridans* killed orb-weavers and irregular-web-building spiders, as well as hunting spiders. It is interesting that *P. viridans* even preyed on a large orb-weaver (adult *A. stellata*). During interspecific encounters, the green lynx probably has an advantage over most other spiders in cotton because of its large size. In the field we never found another species of spider feeding on a green lynx. Because birds are fairly minor predators in these cotton fields (W.L.S., unpublished data), the green lynx may be considered a top predator in cotton fields.

Our data concerning the prey of *P. viridans* confirm the findings of Turner (1979) and Randall (1982) that this spider has a diverse diet and, therefore, must be characterized as a food generalist. Another oxyopid spider occurring in this East Texas cotton agroecosystem, which was also observed to be a generalist predator, is *O. salticus* (Nyffeler et al., 1987).The striped lynx has a body length of <50% of that of *P. viridans*. The average prey length of the striped lynx was only 44% of that of the green lynx. This means that the striped lynx and the green lynx complement each other in their predatory activities; the striped lynx kills mainly small prey and the green lynx kills in addition medium- and larger-sized prey.

Previous reports described *P. viridans* as a diurnal species (e.g., Weems & Whitcomb 1977). But as our study revealed, this species is active diurnally and nocturnally. Nocturnal feeding in this species probably was overlooked because few investigators conducted night observations.

During the summer of 1985, only 20 instances of feeding in *P. viridans* were observed. This number of observed cases of predation seems to be very low. We found in cotton 4.86 green lynx spiders per hour on the average (Table 4), but in a California shrub habitat 15–25 green lynx spiders per hour were observed from July to September (Turner & Polis 1979), indicating that in California the population density was ca. 4-fold higher. In our study, the proportion of feeding spiders was ca. 3–9% (Table 4), but in the California shrub habitat 4-fold as many green lynx spiders (21.4%) were observed feeding (Turner 1979). Thus, in the California study the probability of encountering a feeding green lynx spider was ca. 16-fold higher than in our study. If the density of feeding spiders had been as high in the Texas agroecosystem as in the California shrub habitat, then we would have expected to find ca. 320 prey items during the summer of 1985.

Whitcomb et al. (1966) in Arkansas based their prey analysis on the collection of the dry carcasses of insects that were found below green lynx spiders and were considered to have been prey dropped by the spiders after the meal. This method of prey analysis is much less time-consuming than our method of direct observation. But in parts of the southern United States (e.g., in East Texas), the method of Whitcomb et al. can no longer be applied because these areas are now colonized by red imported fire ants, *Solenopsis invicta* Buren, scavengers that remove the carcasses.

It was estimated that on cotton and croton plants in East Texas less than one prey per green lynx spider per day was killed. If we put Turner's value of $w = 21.4$ into Edgar's (1970) formula and if we assume that on shrubs in California the T_h was the same as in our study in Texas, then we calculate $b = 0.95$, which indicates that on shrubs in California about one prey per spider per day was killed by *P. viridans* females. Also, in other hunting spiders it was found that not more than one prey per spider was killed daily (Edgar 1970, Schaefer 1974, Nyffeler & Benz 1981). In Europe, Edgar (1970) found that frequency of feeding in the wolf spider *Pardosa amentata* (Clerck) was affected by the time of day and by weather conditions. In our study we tested to see if frequency of feeding of *P. viridans* depended on the time of day or season, but no such dependence was found.

The previous work on *P. viridans* in Arkansas, California, and Florida led to the conclusion that this spider species captures numerous beneficial arthropods (predators or pollinators, or both). Weems & Whitcomb (1977, 1) stated that these spiders' "... usefulness in control of insect pests is counteracted by their willingness to prey also upon beneficial insects." The same authors wrote that *P. viridans* killed large numbers of honey bees and sphecid and vespid wasps, as well as syrphid and tachinid flies. In Turner's (1979) study, honey bees constituted the single most important prey taxon in the diet of *P. viridans* in California. Also, Randall (1982, 20) came to the conclusion that *P. viridans* "is counterproductive as a predator of economically important insects since it takes beneficial insects as prey more often than it takes harmful insects." According to Randall the ratio of "beneficial prey : harmful prey" in Florida was 44:12.

Our work confirms the observations of these previous workers that the diet of larger *P. viridans* may consist of a high percentage of beneficial arthropods (in our study more than half of *P. viridans*'s prey were beneficial). However, more data about the prey of these spiders and the mortality of the prey in cotton and other crops are needed before we can draw conclusions about the overall positive, neutral, or negative effect of the green lynx as a biological control agent. On the basis of our experience, we estimated that 425 h would have to be spent in cotton fields comparable with those in Austonio to be able to collect just 100 specimens of *P. viridans* with prey. On croton plants, 50% of the green lynx's diet consisted of predaceous arthropods and 10% of pollinators, but at the same time numerous economic pests (ca. 30% cotton fleahoppers) were killed by the green lynx. It would be of interest to conduct a similar study on green lynx spider predation in cotton in a year when the injurious pests are common.

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Evaluation of the Importance of the Striped Lynx Spider, *Oxyopes salticus* (Araneae: Oxyopidae), as a Predator in Texas Cotton

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ABSTRACT Predation by the striped lynx spider, *Oxyopes salticus* Hentz, on cotton arthropods was studied in an unsprayed field in east Texas. *O. salticus* was the most abundant spider species in cotton (68% of all spiders collected by D-Vac), with population densities of <0.1 spiders per m^2 in June gradually increasing to 7.2 per m^2 in September. This diurnally and nocturnally feeding spider captured prey ranging between 0.1 and 1.1 of its own size. Most prey were small (average body length = 2.61 ± 0.16 mm [SEM]). The natural diet of *O. salticus*, a generalist predator, was diverse, and consisted (by number) mainly of *Solenopsis invicta* Buren (21.9%), leafhoppers (17.2%), dipterans (15.6%), aphids (14.1%), and spiders (14.1%). Predaceous arthropods, including *Geocoris* bugs, and larvae of *Chrysopa* and Syrphidae, composed 42% of the spiders' diet. The proportion of *O. salticus* feeding at any one time was <5% throughout the 1985 season. A subadult/adult spider captured about one prey daily in the middle of the growing season. Based on population density counts and the assessment of the prey capture rate we estimated that in the middle of the growing season ca. 0.12 million prey may have been killed by *O. salticus* per ha cotton land per wk (weekly kill ca. 4.5% of the average arthropod density).

KEY WORDS *Oxyopes salticus*, cotton, prey capture rate, prey preference, phenology

INTEREST IN the role of spiders as natural control agents in agroecosystems is increasing world-wide (review in Nyffeler [1982], Riechert & Lockley [1984]). One of the most common foliage-dwelling spiders in the United States is the striped lynx spider, *Oxyopes salticus* Hentz (Young & Lockley 1985). This vagrant spider hunts among the foliage of various plant species, and has an average adult length of about 6 mm (females) and 5 mm (males) (Brady 1964). *O. salticus* forages throughout the entire plant, at times sitting motionless awaiting prey, at times running over leaves and stems of plants, and occurs in many different types of habitats throughout the United States (Brady 1964). *O. salticus* was found to be the most abundant spider in cotton fields in Arkansas (Whitcomb et al. 1963), Mississippi (Laster & Brazzel 1968), and Texas (Dean et al. 1982), as well as in soybean fields in North Carolina (Deitz et al. 1976) and Missouri (Blickenstaff & Huggans 1962). Because of its abundance, *O. salticus* was suspected of being a major predator of insects in these habitats (Brady 1964, Weems & Whitcomb 1977).

Very little research has been conducted on the feeding ecology of this species, perhaps due to the difficulty of observing predation by these vagrant spiders in the field (Brady 1964). The goal of this paper is to give some insight into the predatory activities of *O. salticus* in a Texas cotton agroecosystem. Studies on the feeding ecology of other spider species occurring in this agroecosystem are presented elsewhere (Nyffeler et al. 1986, 1987a, b,c).

Materials and Methods

During the summer of 1985 (June to mid-September) we evaluated the feeding biology and ecological importance of *O. salticus* by observing certain predatory activities at different times of the day and night in cotton. The investigations were conducted in a cotton field that received no insecticides or other chemicals and was located 8 km west of Austonio, Tex., near Crockett in Houston County. These fields border on meadows (composed of various grasses and low-growing annual Dicotyledoneae) that were mown once during this study. Most of our investigations were carried out in a 6.5-ha cotton field. Half of this field was heavily infested with weeds (Johnson grass); in the other half weeds had been removed mechanically. The lateral distance between rows was 1 m, with a mean of 10.1 cotton plants per m of row. The cotton (var. CAMD-E) was planted on 27 May, and emerged in the first week of June. The fields were cultivated twice. We finished our investigation on 16 September. At that time the fields had not yet been harvested.

Twenty-five semirandom D-Vac suction samples (Dietrick 1961), each of 1 m of row, were taken weekly for 14 wk during the summer of 1985 to assess spider and potential prey densities. Number

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Table 1. Proportion of *O. salticus* and other predaceous arthropods in the entire arthropod/predator complex of an east Texas cotton agroecosystem (14 June–4 September 1985)

Date	N^a	% different predators				
		O. salticus	Other spiders	Ants^b	Other predaceous insects^c	Total
14 June	935	0.11	0.86	94.55	4.49	100
21 June	318	0	1.57	91.82	6.62	100
26 June	1,887	0.11	0.85	97.40	1.64	100
3 July	1,212	0.33	1.49	91.58	6.60	100
10 July	729	2.33	2.47	69.00	26.20	100
19 July	921	2.28	4.89	77.20	15.64	100
24 July	371	7.01	7.01	46.36	39.62	100
31 July	219	7.31	12.79	20.55	59.36	100
7 Aug.	529	5.67	8.32	56.00	29.11	100
14 Aug.	758	6.86	4.35	58.84	29.95	100
21 Aug.	702	14.10	7.69	49.86	28.35	100
28 Aug.	734	16.76	5.31	61.58	16.35	100
4 Sept.	529	32.51	4.91	49.53	13.04	100
Mean	—	7.34	4.81	66.48	21.30	100

[a] N = total number of predaceous arthropods collected by D-Vac (for each date, 25 D-Vac samples each of 1 m of row).

[b] Primarily *S. invicta.*

[c] *Geocoris, Orius,* Coccinellidae, Chrysopidae, Syrphidae, and others.

of spiders per meter of row were converted into number of spiders per square meter. Number of spiders per meter of row equals number of spiders per square meter, since the lateral distance between rows was 1 m. Samples were begun away from the edge of the field and taken in a circular pattern throughout the season. The collected arthropods were returned to the laboratory and later identified and counted under the microscope. In addition, 10 D-Vac samples were taken in an adjacent meadow on five different dates to determine the population density of *O. salticus* in meadows compared with cotton fields.

For evaluation of the diet, during both day and night, the vegetation of cotton fields was thoroughly searched for feeding specimens of *O. salticus*. Such spiders were captured by hand with a transparent plastic cup (7.5-cm upper diameter). Spiders with prey between the chelicerae were killed and preserved in alcohol, and the prey later identified in the laboratory under a microscope.

For evaluation of prey selection, to determine whether *O. salticus* captured its prey randomly or selectively from the range of potential prey, we compared the diet of *O. salticus* with the spectrum of potential prey based upon D-Vac samples. Prey selection was evaluated by Ivlev's electivity index (E), a measure previously used for the estimation of food preference in fish and spiders, which gives a relative value between −1 and +1 (Ivlev 1961, Kajak 1965):

$$E = (r_i - p_i)(r_i + p_i)^{-1}, \qquad (1)$$

where r_i is the proportion of a certain prey type i in the diet of *O. salticus,* and p_i is the proportion of prey type i in the range of potential prey. Electivity values of $E < 0$ indicate negative selection, $E = 0$ random feeding, and $E > 0$ positive selection.

The prey capture rate (b, number of prey per spider per day) of *O. salticus* can be assessed according to Edgar's (1970) method developed for wolf spiders. We used a formula we modified as follows:

$$b = \frac{(t_f)(60)(w)}{(1)(t_h)(100)}, \qquad (2)$$

where t_f is the time (hours per day) available for prey capture and feeding in the field, w is the percentage of spiders with prey in a sample, and t_h is the average handling time (sensu Krebs [1985], in minutes). The handling time was taken as being the period between the initiation of an attack and the cessation of feeding.

In this study we used exclusively the handling time measured for subadult/adult *O. salticus* without differentiating between sexes; the handling time for very small spiders (1–1.9 mm total body length) was not measured. We calculated the prey capture rate for the middle of the cotton-growing season only, because at that time there was a size/age structure in the field, with >90% of the spiders coinciding largely with the size range of adults (adult *O. salticus* ranged from 2–2.9 mm to a maximum size of 8 mm). At other times of the growing season, immatures of 1–1.9 mm in size constituted up to 90% of the *O. salticus* population and without the knowledge of these very small spiders' handling time their prey capture rate could not be calculated.

Feeding frequency (w) and the time available for prey capture and feeding in the field (t_f) were assessed by walking along cotton rows at different times of the day and season and recording the numbers of spiders with and without prey. Night observations were carried out using a head-lamp with white light. The spiders remained motionless when blinded by a beam of white light and could then easily be captured along with prey. These data were also used for the evaluation of changes in the diel and seasonal feeding activity of the spiders. To show if the frequency of feeding in *O. salticus* is dependent on the time of day or season, we used the χ^2 test of association.

To measure the handling time (t_h), 10 specimens of *O. salticus* (subadults/adults) were captured in the field on 8 August, introduced into plastic cages, and fed with leafhoppers of adequate size as the average natural prey.

Results

Numbers, Phenology, and Age Structure. *O. salticus* was the numerically dominant spider species in the cotton field (Fig. 1A). This species composed 68% of the total spiders collected by

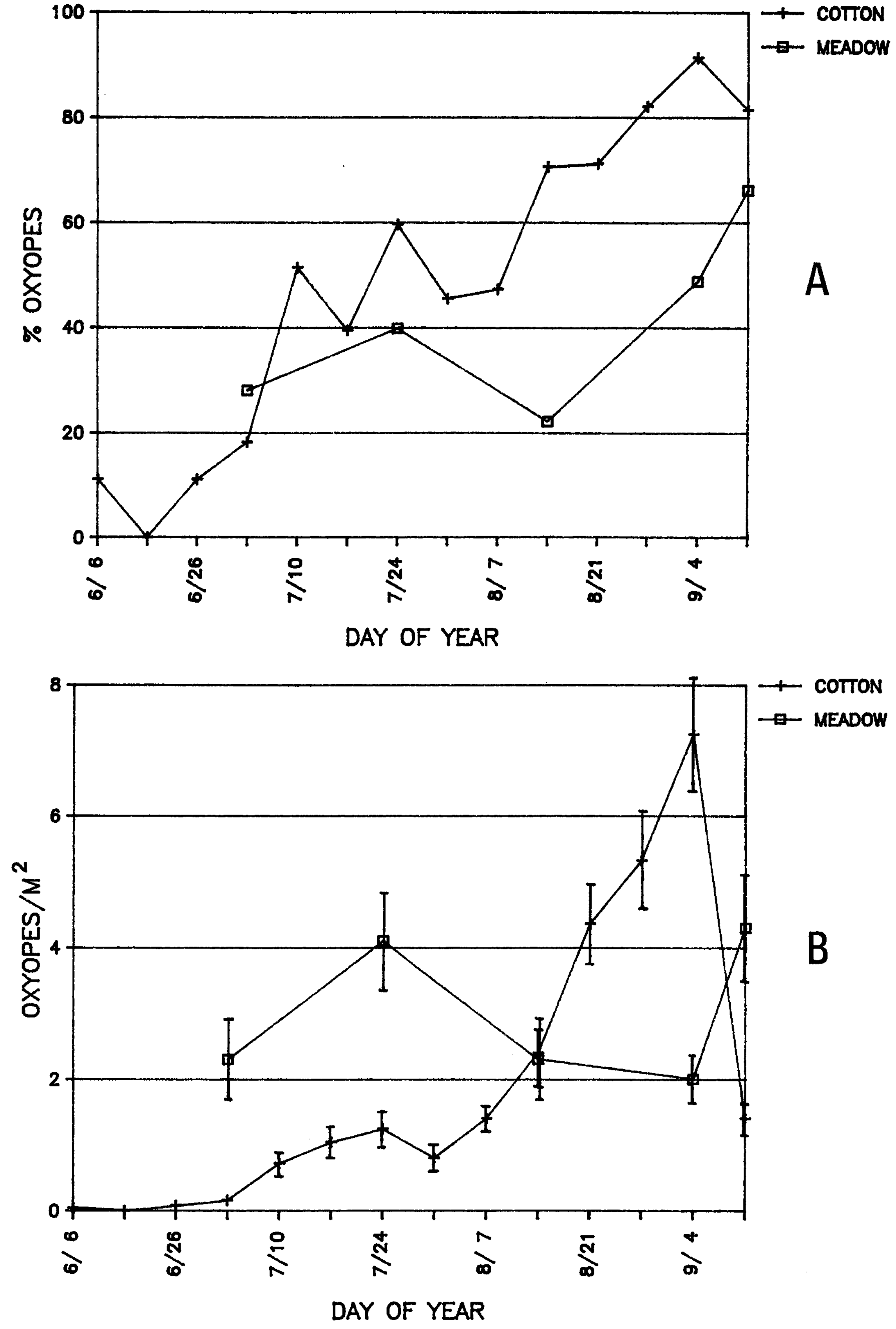
100
80
60
40
20
0
% OXYOPES
COTTON
MEADOW
A
6/ 6
6/26
7/10
7/24
8/ 7
8/21
9/ 4
DAY OF YEAR
8
6
4
2
0
OXYOPES/M²
COTTON
MEADOW
B
6/ 6
6/26
7/10
7/24
8/ 7
8/21
9/ 4
DAY OF YEAR

Table 2. Size and age structure of *O. salticus* population in an east Texas cotton agroecosystem (mid-June to mid-September 1985)

Date	Range of body length (mm)/carapace width (mm)[a]						Total (all sizes)			
	1–1.9/ 0.4–0.8	2–2.9/ 0.5–1.2	3–3.9/ 0.9–1.9	4–4.9/ 1.0–2.1	5–5.9/ 1.3–2.3	6–6.9/ 1.7–2.3	Imma-ture	♂	♀	Σ
14 June	1						1			1
21 June										0
26 June				2			2			2
3 July	2	1		1			4			4
10 July	3	1	5	6 (1♂)	3		17	1		18
19 July	1	8 (1♀)	10 (1♂)	6 (2♂)	1 (1♀)		21	3	2	26
24 July	2	5	8	10 (3♂)	6 (2♂)		26	5		31
31 July	5	2	2	6 (1♂)	3 (1♂)	2 (2♀)	16	2	2	20
7 Aug.	10	7	7	10 (5♂)	1		30	5		35
14 Aug.	41	3	2	6 (3♂)	7 (3♂) (1♀)	1 (1♀)	52	6	2	60
21 Aug.	86	3	10 (2♂)	7 (5♂)	3 (1♂) (2♀)		99	8	2	109
28 Aug.	116	3	7 (3♂)	4 (3♂) (1♀)	2 (2♀)	1 (1♀)	123	6	4	133
4 Sept.	164	6	2	6 (1♂) (5♀)	2 (1♂) (1♀)	1 (1♀)	172	2	7	181
16 Sept.	25	5	3 (3♂)	1 (1♂)	1 (1♀)		30	4	1	35
Total	456	44 (1♀)	56 (9♂)	65 (25♂) (6♀)	29 (8♂) (8♀)	5 (5♀)	593	42	20	655

Numbers of each date are based on 25 D-Vac samples each of 1 m of row. Numbers in columns give total spiders (immatures plus adults) with number of adults in parenthesis.

[a] Mean carapace width: 0.50, 0.91, 1.27, 1.63, 1.79, 2.05.

D-Vac from June to September. *O. salticus* was also the most abundant spider in meadows bordering on these cotton fields (Fig. 1A).

The proportion of *O. salticus* in the entire arthropod predator complex sampled by D-Vac constituted <1% by the beginning of July, and increased in the course of the growing season up to >10% in the second half of August and later (Table 1).

In June the densities of *O. salticus* in cotton were very low (<0.1 per m^2). From then to mid-July the population density gradually increased to ca. 1 per m^2, and increased to 7.2 per m^2 in early September (Fig. 1B).

In July <40% of all *O. salticus* collected by D-Vac were <3 mm total body length. At the beginning of August about half of the collected spiders were <3 mm total length. After mid-August >70% of the collected spiders reached a total length of <3 mm (Table 2).

Until 3 July only immature *O. salticus* were collected. The proportion of adults increased from 6% on 10 July to ca. 16–20% in the second half of July (adults of both sexes were found since 19 July). In the first half of August, ca. 14% of the spiders were adults and, after 21 August, the proportion of adults was <10% (Table 2).

Potential Prey. The seasonal trend of the potential prey (available arthropods) of *O. salticus* in cotton is shown in Fig. 2. The numbers of potential prey in the cotton field steadily increased from mid-June (46.44 per m^2) with the progressing season up to a peak (348.24 per m^2) on 7 August. After that date, the numbers of potential prey decreased to 92.84 per m^2 in September. At all times predaceous arthropods and aphids were the most abundant potential prey of *O. salticus* in cotton (by numbers together >85%).

Natural Diet. In the cotton field, *O. salticus* killed prey between 0.1 and 1.1 of its own size. Most prey were small (average prey length = 2.61 ± 0.16 mm [$\bar{x}$ ± SEM]; range, 0.6–5.6 mm) relative to the size range of potential prey. We found a low positive correlation ($r^2 = 0.27$) between spider size and prey size.

A total of 64 prey items was collected in 85 h of searching (Table 3). Only one spider (1.6%) was found holding two prey items simultaneously between the chelicerae (multiple prey). Of the observed predation events, 35% were due to immature spiders, 18% due to penultimate/adult males, and 47% due to adult females. The spiders found feeding belonged to the following size classes (total body length): 1–1.9 mm (0% of the spiders), 2–2.9 mm (2% of the spiders), and ≥3 mm (98% of the spiders). The food of *O. salticus* consisted of phytophagous (e.g., leafhoppers and aphids) and predaceous arthropods. Workers of the red imported fire ant, *Solenopsis invicta* Buren, were the most frequent prey of *O. salticus*, constituting 22% of the spiders' diet. Both immature and adult spiders were observed feeding on *S. invicta*. Predaceous arthropods, including spiders; *S. invicta*; the big-eyed bug, *Geocoris punctipes* (Say); and the larvae of *Chrysopa* sp. and Syrphidae, accounted for 42% of the diet of *O. salticus*.

←

Fig. 1. (A) Proportion of *O. salticus* of all spiders in a cotton field and comparative values from an adjacent meadow in 1985 (D-Vac samples). (B) Numbers of *O. salticus* per square meter in a cotton field and comparative values from an adjacent meadow in 1985 (D-Vac samples). Vertical bars indicate SEM.

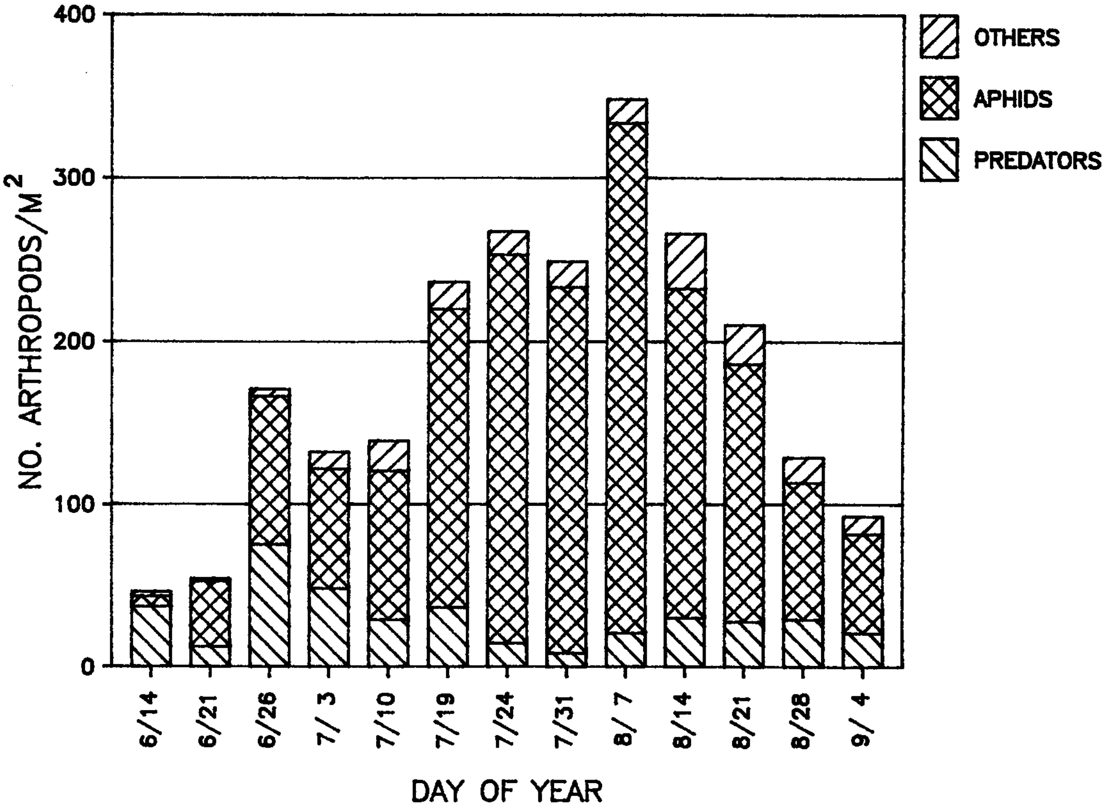

Fig. 2. Seasonal trend of the potential prey of *O. salticus* in an east Texas cotton agroecosystem in 1985 (numbers of arthropods per square meter sampled by D-Vac). Predators include ants, spiders, Heteroptera, Coccinellidae, Chrysopidae, Syrphidae, etc. Others include leafhoppers, Diptera, etc.

Prey Selection. Five major arthropod groups—*S. invicta*, leafhoppers, dipterans, aphids, and spiders—dominated in both the actual and potential prey (Fig. 3) constituting together 84% of the actual prey and 93% of the potential prey. *O. salticus* appeared to prefer spiders ($E = 0.82$) followed by Diptera ($E = 0.77$) and leafhoppers ($E = 0.43$), whereas aphids ($E < 0$) were underrepresented in the striped lynx spiders' natural diet relative to the proportion of these insects in the pool of potential prey.

Diel and Seasonal Changes in Feeding Activity. The proportion of *O. salticus* with prey at different times of the day (Table 4), suggests that this species feeds both day and night. The number of spiders with prey did not depend on the time of day. The percentage of feeding spiders was <5% throughout the 1985 season (Table 5); no dependence of the number of spiders with prey upon the time of the year was found.

Prey Capture Rate. For the estimation of the prey capture rate (b) of *O. salticus* we used formula 2. The following values were put into the formula: $t_f = 24$ (based on Table 4), $t_h = 49.00$ (mean value of 10 measurements on subadults/adults), and $w = 4.72$ (value for 22–28 July from Table 5). On this basis we estimated that a subadult/adult spider captured, in the middle of the cotton-growing season, on the average of a little more than one prey daily. This is, however, a rough estimate that needs to be verified by food-consumption studies under laboratory conditions.

The number of prey killed by *O. salticus* per square meter per week was estimated for the time from 22 to 28 July 1985 (in the middle of the growing season) by multiplying the estimated number of prey captured daily times 7 d times number of spiders per square meter. We estimated that from 22 to 28 July ca. 12 prey per m^2 may have been killed by *O. salticus*. An extrapolation of this value over an entire field leads to the conclusion that approximately 0.12 million prey may have been killed by *O. salticus* per ha cotton land during that week. At that time of the season the number of arthropods per square meter available as potential prey for *O. salticus* was 267.12 (Fig. 2). Thus, in the middle of the growing season the weekly prey kill by *O. salticus* may have been ca. 4.5% of the average arthropod density.

Discussion

During early June, very few spiders were found on the small cotton plants but high densities were already present in the adjacent meadows (based on

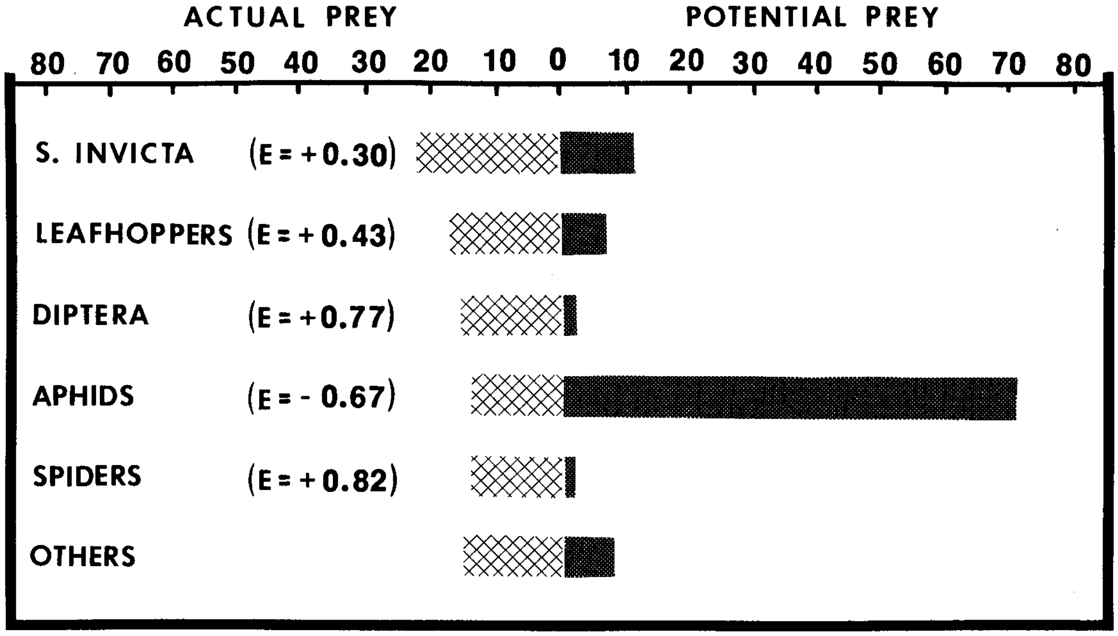

Fig. 3. Comparison of actual and potential prey (percentage by number) of *O. salticus* in a cotton agroecosystem, with calculated electivity indices (*E*).

direct observations and sweep-net samples). Thus, the cotton fields were surrounded by high densities of *O. salticus* and it is likely that those meadows functioned as reservoirs for the colonization of the cotton fields by *O. salticus*. As Dean & Sterling (1985) demonstrated in a study conducted in eastern Texas, this spider is very vagile. The marked increase of the population density of *O. salticus* from mid-August to the beginning of September is likely due to reproduction in the cotton field, because many females guarding egg sacs as well as recently hatched spiderlings were observed in the field during August.

According to the literature, *O. salticus* is a diur-

Table 3. Natural diet of *O. salticus* in an east Texas cotton agroecosystem (summer 1985)

Prey	July		Aug.		Sept. 1–15	Total		Prey size range (mm)	Predator size range (mm)	Stage and sex of predator[a]
	1–15	16–31	1–15	16–31		*N*	%			
Solenopsis invicta Buren worker	0	1	5	7	1	14	21.9	2.1–2.9	3.7–6.8	i, p♂, ♀
Leafhopper sp.	0	2	6	3	0	11	17.2	2.2–3.4	2.6–8.0	i, ♀
Diptera sp.	1	1	7	1	0	10	15.6	1.5–4.1	4.6–5.6	i, p♂, ♂, ♀
Aphid sp.	0	6	3	0	0	9	14.1	0.6–1.3	3.7–7.3	i, p♂, ♂, ♀
Hymenoptera	0	0	1	0	0	1	1.6	2.1	7.4	♀
Grasshoppers	0	0	0	1	0	1	1.6	4.4	5.6	♀
Lygaeidae	0	0	0	1	0	1	1.6	3.9	[b]	[b]
Geocoris punctipes (Say)	0	0	2	0	0	2	3.1	3.6–3.9	5.9–6.8	♀
Chrysopa sp. larvae	0	0	0	1	0	1	1.6	5.6	6.9	♀
Syrphidae larvae	0	1	0	0	0	1	1.6	4.5	[b]	[b]
Oxyopes salticus Hentz	0	0	2	1	2	5	7.8	1.1–5.0	3.9–7.1	i, ♀
Acanthepeira stellata (Walckenaer)[c]	0	0	2	0	0	2	3.1	1.3–1.5	3.6–4.4	i, ♂
Tetragnatha laboriosa Hentz	0	0	1	0	0	1	1.6	3.4	6.4	♀
Pardosa atlantica Emerton	0	0	0	1	0	1	1.6	2.8	6.6	♀
Unidentified[d]	0	1	3	0	0	4	6.3	—	—	—
Total	1	12	32	16	3	64	100	—	—	—

[a] i, immatures; p♂, penultimate males; ♂, adult males; ♀, adult females.

[b] Spider size and stage not identified.

[c] The two *Acanthepeira* found as prey were immatures. In Texas both *Acanthepeira stellata* and *Acanthepeira cherokee* Levi occur, which cannot be separated as immatures. However, because numerous adults captured in east Texas cotton fields all were *A. stellata*, we suppose that the two specimens listed in the table belong to this latter species.

[d] Could not be identified due to spider mastication.

Table 4. Diel change of the percentage of feeding spiders in an *O. salticus* population in an east Texas cotton agroecosystem (summer 1985)

Time of day	Time spent observing (h)	No. spiders observed	No. spiders with prey^a	% spiders with prey
0800–1155	25	445	16	3.6
1200–1555	17	229	7	3.1
1600–1955	19	480	14	2.9
2000–2355	13	385	15	3.9
0000–0355	3.5	144	7	4.9
0400–0755	7.5	207	7	3.4

^{a} $P > 0.05$; χ^2.

Table 5. Seasonal variation of the percentage of feeding spiders in an *O. salticus* population in an east Texas cotton agroecosystem (summer 1985)

Time of year	Time spent observing (h)	No. spiders observed	No. spiders with prey^a	% spiders with prey
22–28 July	4.5	127	6	4.72
29 July–4 Aug.	14	275	10	3.64
5–11 Aug.	17	379	12	3.17
12–18 Aug.	18.5	388	15	3.87
19–25 Aug.	9	231	4	1.73
26 Aug.–3 Sept.	10	333	9	2.70
4–8 Sept.	4.5	103	2	1.94

^{a} $P > 0.05$; χ^2.

nal species (Whitcomb et al. 1963, Brady 1964, Leigh & Hunter 1969), whereas we found that this species feeds day and night. We consider feeding (likewise locomotion, mating, hunting, etc.) as an activity and, thus, define animals that are feeding during the daylight hours as diurnal and those feeding during the period of darkness as nocturnal. The fact that *O. salticus* was observed feeding during the night is not proof for nocturnal foraging, because these spiders may feed during the night on prey that they captured before sunset or during dusk. However, because adult females of *O. salticus* have an average handling time of <1 h (range of 10 measurements for average-sized prey, 8–86 min), one can assume that some of the spiders that were found several hours after sunset feeding on prey of rather small size had foraged nocturnally. This hypothesis of nocturnal foraging in *O. salticus* is verified by an incidental observation from 5 August, when in the cotton field a spider of this species was observed capturing a small fly during the period of darkness (at 2210 hours CST, ca. 1.5 h after sunset).

Our data indicate that *O. salticus* is a generalist. Other oxyopid species also were found to be generalist predators (Furuta 1977, Turner 1979, Nyffeler et al. 1987a). The major food component of *O. salticus* in this Texas cotton agroecosystem was *S. invicta*. Red imported fire ants are themselves aggressive predators and, thus, it is quite interesting that lynx spiders are able to use these insects as a primary food source. We assume that ants at times try to defend themselves against the attacks of spiders, because we observed workers of *S. invicta* biting the legs of *O. salticus*. Spiders of the genus *Oxyopes* have also been observed capturing ants in Asia (Furuta 1977). Other important prey of *O. salticus* in Texas cotton were Diptera, aphids, and leafhoppers. According to Altieri & Whitcomb (1979), *O. salticus* inhabiting Mexican tea (*Chenopodium ambrosioides* L.) in north Florida have also been observed feeding on aphids and leafhoppers. A considerable proportion of the prey of *O. salticus* was spiders (cannibalism and interspecific predation). Other lynx spider species have also been observed to capture spiders. The green lynx spider, *Peucetia viridans* (Hentz), was frequently observed feeding on spiders on cotton and croton plants in east Texas (Nyffeler et al. 1987a), and in the laboratory prey taken by the gray lynx, *Oxyopes scalaris* Hentz, included spiders of the families Clubionidae, Oxyopidae, Salticidae, Thomisidae, and Theridiidae (Cutler et al. 1977).

The key pests in Texas cotton fields are the boll weevil, *Anthonomus grandis* Boheman; the cotton fleahopper, *Pseudatomoscelis seriatus* (Reuter); and *Heliothis* spp. In our study no cases of predation by *O. salticus* on one of these pests were observed, possibly due to the low numbers of the pests. However, during the summer we collected only 64 prey items. Studies of the diets of *Oxyopes scalaris* (Cutler et al. 1977, Carroll 1980) and *Oxyopes sertatus* L. Koch (Furuta 1977) provide evidence that spiders of this genus are able to kill various prey, including different kinds of beetles and moths. As our study in east Texas shows, *O. salticus* captured prey with a total length of up to 5.6 mm (Table 3). Thus, small adults of the boll weevil as well as eggs and larvae of *Heliothis* spp. are in *O. salticus*'s prey range. Also, the cotton fleahopper falls into this prey-size range, and *O. salticus* has been observed feeding on this insect by Kagan (1943), Whitcomb et al. (1963), and D.A.D. and W.L.S. (unpublished data). In previous observational studies on lynx spiders, no insect eggs are recorded as prey of these spiders. However, McDaniel & Sterling (1982) placed radioactive *Heliothis virescens* (F.) eggs in a cotton field and captured radioactive specimens of *O. salticus*, indicating that lynx spiders may be egg predators.

In *O. salticus*, as in other hunting spiders, the average proportion of feeding individuals in a population was <10% (Table 6). The low proportion of feeding spiders seems to be a pattern typical for several species of hunting spiders, whereas in some species of web-building spiders a large proportion of a spider population (>40%) is simultaneously feeding at certain times of the day (see Nyffeler [1982]).

Using Edgar's (1970) method, we estimated for subadult/adult *O. salticus* a prey capture rate of approximately one prey per spider per day (in the middle of the cotton growing season). We com-

Table 6. Percentage of feeding spiders observed in populations of hunting spiders (literature review)

Spider species	Location	Habitat	Authors	% spiders feeding
Oxyopes salticus Hentz[a]	Texas	Cotton field	This paper	3.2
Peucetia viridans (Hentz)[a]	Texas	Cotton field	Nyffeler et al. (1987a)	5.0
Pardosa agrestis (Westring)[b]	Switzerland	Wheat field	Nyffeler (1982)	3.9
Pardosa amentata (Clerck)[b]	Holland	[e]	Edgar (1970)	7.8
Pardosa lugubris (Walckenaer)[b]	Switzerland	Forest	Nyffeler & Benz (1981)	6.0
Pardosa pauxilla Montgomery[b]	Texas	Cotton field	D.A.D. (unpublished data)	8.2
Pardosa spp.[b]	Switzerland	Meadow	Nyffeler (1982)	5.0
Pirata piraticus (Clerck)[b]	Germany	Salt marsh	Schaefer (1974)	8.0
Xysticus cristatus (Clerck)[c]	Switzerland	Meadow	Nyffeler (1982)	8.3
Misumenops celer (Hentz)[c]	Texas	Cotton field	D.A.D. (unpublished data)	1.4
Phidippus audax (Hentz)[d]	Texas	Cotton field	D.A.D. (unpublished data)	3.1

[a] Lynx spiders (Oxyopidae).
[b] Wolf spiders (Lycosidae).
[c] Crab spiders (Thomisidae).
[d] Jumping spider (Salticidae).
[e] Habitat not mentioned.

pared this value with data from the literature. In laboratory experiments confined to small (237 ml) containers, Lingren et al. (1968) showed that adult females of *O. salticus* consumed an average of 93.6 first-instar *Heliothis* sp. per spider per d, but adult spider males consumed fewer larvae (56.7 larvae per spider per d). This experiment by Lingren et al. (1968) indicates that adult *O. salticus* have a high prey-killing capacity, especially if prey are abundant. However, this is a very "unnatural" experiment that may not extrapolate to the much more complex field conditions. Being aware of that, Lingren et al. (1968) conducted a second experiment that provided the larval prey with refugia. Adult *O. salticus* were confined with *Heliothis* sp. larvae on 25.4-cm cotton terminals for 4 d; here the average prey capture rate for adult *O. salticus* was 0.5 larvae per spider per d, which is a much lower value than in the first experiment in small containers. A different approach was chosen by Richman et al. (1980), who assessed the prey capture rate of *O. salticus* by field cage experiments in a Florida soybean field; here *O. salticus* consumed an average of 1.14 soybean looper larvae per spider per d. The results of these experiments do not differ much from our estimate with Edgar's (1970) method. It is probably realistic to assume for subadult/adult *O. salticus* an average prey capture rate of approximately one average sized prey per spider per day. The prey capture rates of adult European wolf spiders, which have approximately the same average adult length as *O. salticus*, were estimated to be of the same magnitude (Edgar 1970, Schaefer 1974, Nyffeler 1982).

From June to the beginning of July the proportion of *O. salticus* in the entire arthropod/predator complex was <1% (Table 1), suggesting that the spiders' impact on cotton insects was very small during that period of the growing season; during the same period, red imported fire ants were very abundant predators in cotton, constituting >90% of the predaceous arthropods (Table 1). After 10 July, the proportion of *O. salticus* in the predator complex increased to ca. 7% in the middle of the growing season and reached >10% in the second half of August and later (Table 1). However, from the significantly increased numbers of *O. salticus* after 14 August one cannot necessarily deduce that the spiders' impact as predators was higher then, because >80% of all *O. salticus* occurring in the cotton field in the second half of August and later had a total body length of <2 mm (Table 2); the food intake capacity and success rates of the very small *O. salticus* stages in capturing certain cotton pests may be limited by the small size of these early instars.

In future research the handling time (t_h) of the various development stages for both sexes of *O. salticus* should be measured, so that the spiders' prey capture rates in the different periods of the cotton growing season can be calculated with Edgar's (1970) method. Due to limitation of time we have chosen a simplistic approach without a differentiation of the foraging parameters between the sexes of *O. salticus*, but we are fully aware that the foraging parameters of males and females may differ (Lingren et al. [1968] and Furuta [1977] found that in adult *Oxyopes* spp. males captured fewer prey than females). Prey capture rates of the various *O. salticus* stages should also be assessed with feeding tests in the laboratory. In addition, the instars of various pest species that can be overcome by very small *O. salticus* should be evaluated to determine the prey-size range of these very small spiders. Currently little is known about the natural diet and prey capture rates of the very small *O. salticus* stages; we assume that they capture small insects, because Whitcomb & Eason (1965) were able to feed second-instar *O. salticus* with the flower thrips, *Frankliniella tritici* (Fitch). The assessment of prey-size range and prey capture rates of these very small *O. salticus* stages is of special importance, because they predominated in the spider fauna in cotton in August and September (Table 2). To understand their impact, one needs to know more about their feeding biology. Another future step in the assessment of the impact of *O. salticus* as a predator of cotton pests should be to evaluate through field experiments the values of mortality of economically important cotton arthropods caused by this spider. A field experiment in that direction was carried out in Arkansas cotton fields by Whitcomb & Eason (1967), who came to the conclusion that in 2 different yr, 11 and 14% of all arthropod predation on second-instar bollworms was due to *O. salticus*.

O. salticus is a predator of cotton pests (Kagan 1943, Whitcomb et al. 1963) and natural enemies (this study). Thus, the positive effect of this spider species as a predator of pests may be counteracted to some extent by its activity in killing natural enemies. The green lynx was also found to be a predator of both pests and beneficial insects (Turner 1979, Randall 1982, Nyffeler et al. 1987a). As the data presented in this paper show, we found low incidence of predation by *O. salticus* on cotton pests, probably because the pests (with the exception of aphids) were relatively rare in the area of Austonio during the period of this study (D.A.D., unpublished data). It would be important to conduct a similar observational study on striped lynx spider predation in a cotton season, when injurious pests (such as cotton fleahoppers, *Heliothis* spp., and boll weevils) are common. Because spiders of the genus *Oxyopes* are abundant in agroecosystems in different parts of the world (review in Young & Lockley [1985]), the evaluation of their role as natural control agents of insect pests is of importance.

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BIOLOGICAL CONTROL

Diets, Feeding Specialization, and Predatory Role of Two Lynx Spiders, *Oxyopes salticus* and *Peucetia viridans* (Araneae: Oxyopidae), in a Texas Cotton Agroecosystem

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ABSTRACT The predation ecology of the striped lynx spider, *Oxyopes salticus* Hentz, and green lynx spider, *Peucetia viridans* (Hentz), was studied during 108 h of visual observation in an insecticide-free cotton field in central Texas. Evidence obtained during this study indicates that lynx spiders were the dominant arthropod predators (among 134 cases of arthropod predation observed, 94 were attributable to lynx spiders). *P. viridans* is a powerful species (10.08 ± 0.52 mm [mean ± SEM] body length) compared with the significantly smaller *O. salticus* (4.24 ± 0.16 mm). The *O. salticus* individuals fed on small-sized prey (2.41 ± 0.17 mm average prey length). In contrast, the *P. viridans* individuals fed over a broader range of prey size classes and captured a higher proportion of the larger prey organisms (7.04 ± 0.73 mm average prey length). However, the smallest *P. viridans* (≤8 mm spider length) and the largest *O. salticus* (≥4.5 mm spider length) selected prey of similar average length (≈3 mm). The lynx spiders are polyphagous insectivores that feed on a variety of prey species predominantly in the insect orders Heteroptera, Hymenoptera, and Diptera. They also frequently eat other spiders. The most frequently captured prey of *O. salticus* were small Heteroptera (predominantly cotton fleahopper, *Pseudatomoscelis seriatus* [Reuter]), whereas *P. viridans* most frequently seized large stinging Hymenoptera (e.g., honey bee, *Apis mellifera* L.). The degree of the feeding specialization of the two spider species was mathematically assessed (niche breadth coefficients) and statistically compared; computed coefficients indicate that *P. viridans* is a significantly more polyphagous predator than the smaller-sized *O. salticus*. *O. salticus*, therefore, shows a better fit to the "model predator" of classical biological control because of its relative specialization.

KEY WORDS Lynx spiders, biological control, cotton

LYNX SPIDERS ARE cursorial hunters (i.e., foraging without a web) that have become specialized for a life on plants (Gertsch 1949). They are characterized by a hexagonal eye arrangement, erect spines on their legs, and their habit of running and jumping rapidly and erratically over plants when disturbed (Bohmfalk et al. 1983, Young & Lockley 1985). The lynx spiders are generally considered to be diurnal predators with keen eyesight (e.g., Gertsch 1949, Whitcomb et al. 1963, Young & Lockley 1985), but in more recent studies these spiders were observed feeding both day and night (nocturnalism described by Nyffeler et al. [1987a,b]). The striped lynx spider, *Oxyopes salticus* Hentz, and the green lynx spider, *Peucetia viridans* (Hentz), are two of the most common lynx spiders throughout most of the southern United States (Weems & Whitcomb 1977, Young & Lockley 1985); the geographic distribution of *O. salticus* reaches into the northern states. Based on an analysis of 29 faunal surveys of spiders found in nine field crops in the United States, Young & Edwards (1990) found *O. salticus* to be one of the three most frequently occurring spider species in field crops. In contrast, *P. viridans* is less abundant in field crops (e.g., Johnson et al. 1986, Dean & Sterling 1987), but it was sometimes found to be one of the most common spiders on wild flowers, weeds (Altieri & Whitcomb 1980; M. N., unpublished data), and on low shrubs (Turner & Polis 1979). Lynx spiders (i.e., *O. salticus*) were found to be the most abundant spider predators in cotton fields in South Carolina, Mississippi, Alabama, Arkansas, and Texas (Young & Lockley 1985, Dean & Sterling 1987). In some cotton fields, *O. salticus* constitutes up to 90% of the spiders sampled (Laster & Brazzel 1968). On cotton, the light-colored *O. salticus* forages throughout the plant strata and even on the ground, whereas the bright green-colored *P. viridans* awaits prey on leaves in the plant terminal (Whitcomb et al. 1963, Nyffeler et al. 1992).

The two species of lynx spiders have been reported to feed on various economically important crop pests (Whitcomb et al. 1963; Young &

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Lockley 1985; Nyffeler et al. 1987a,b). Young & Lockley (1985) published a list of known prey species of *O. salticus* documented in literature up to 1984. Most of these records of lynx spider predation resulted either from cage experiments in the laboratory or from nonquantitative incidental observations in the field. Quantitative data on the natural diets of these spiders are scarce because thorough observational field assessments are very time consuming (Young & Lockley 1986; Nyffeler et al. 1987a,b).

A quantitative dietary analysis of the two species of lynx spiders was conducted during the summer of 1985 by means of 85 h of visual observation in an insecticide-free cotton agroecosystem located in Houston County, in east Texas (Nyffeler et al. 1987a,b). The cotton bordered on extensive tracts of minimally disturbed noncrop land composed of various grasses and wild plants, areas that are considered to be predator reservoirs (Nyffeler et al. 1987b). A multitude of predators (preponderantly fire ants, lynx spiders, and other spiders) occurred on the cotton plants and on the neighboring wild plants (Nyffeler et al. 1987b). A low proportion of major pests in the spiders' diet was observed (Nyffeler et al. 1987a,b,c; 1989), which partly reflects low numbers of such pests (far below threshold level) monitored in that area (D.A.D., unpublished data). Pest insects were apparently kept in check by the predatory activities exhibited by the extensive predator complex present on the cotton plants and on the neighboring wild plants. Nyffeler et al. (1987a,b) stressed the need to repeat a similar visual observation project in another cotton agroecosystem under conditions where higher numbers of major pests were present.

A new visual observation project was undertaken during the summer of 1988 in an insecticide-free cotton agroecosystem located in Burleson County (central Texas), ≈100 km southwest of the previous study site. This time higher numbers of major pests were present in the field (Nyffeler et al. 1992). The natural diets of *O. salticus* and *P. viridans* were evaluated comparatively, and their feeding specialization and predatory role were discussed.

Materials and Methods

Study Area. The study site refers to an unsprayed, weed-free cotton agroecosystem (13.6 ha) in central Texas (Burleson County), ≈20 km southwest of College Station. Wild plants (source of lynx spiders for colonization of crop fields) grew on the field borders and in neighboring grasslands. Cotton, sorghum, and corn were grown in the surrounding fields. The cotton ('Paymaster 145') was planted on 8 April 1988, started blooming on 22 June, and produced 950 kg/ha (1.7 bales/acre).

Dietary Analysis. Field observations were conducted for 9 consecutive wk, from mid-June to mid-August 1988, during daylight hours (the majority between 1200 and 1800 hours CST). In total, 108 h of visual observation were spent in the field; 34 h in June, 50 h in July, and 24 h in August, with an average of 3 h/d. The numbers of predators were monitored by counting them along the field rows during 1-h periods (walking speed ≈0.8 km/h). During each observation period, the following data were recorded: date, time of day, numbers of lynx spiders with prey, numbers of lynx spiders without prey, and numbers of other predators with or without prey.

Lynx spiders with prey in their chelicerae were captured by hand with a transparent cup (7.5 cm upper diameter, 10 cm depth). They were killed, preserved (along with their prey) in 70% ethyl alcohol, and later identified in the laboratory under a dissecting microscope. See Nyffeler et al. (1987a,b) for methodological details. Because the age-size structure of predaceous arthropods and their prey are important variables in determining which species fits the definition of a "key predator" (Sterling et al. 1989), the body lengths (mm) of spiders and prey were measured from the anterior margin of the cephalothorax or cephalon to the apex of the abdomen (excluding the spinnerets in the case of the spiders). Whitcomb & Eason (1967), Turner (1979), and others suggest that carapace width is preferable as an indicator of spider size; the measurement of total spider body length, however, is inevitable in studies where the "subduing potential" of the spiders relative to their prey is analyzed (Nentwig & Wissel 1986, Hayes & Lockley 1990). The subduing potential (in percentage) was calculated as prey length divided by predator length multiplied by 100. For each lynx spider species, the mean, minimum, and maximum subduing potential were determined.

Comparison of Diets by Niche Overlap and Niche Breadth Coefficients. The extent of species overlap in resource exploitation can be assessed mathematically by computing a niche overlap coefficient for each resource dimension (i.e., food, time, and space) (Turner & Polis 1979). The resource dimension "food" alone was relevant to this investigation. Dietary overlap among the two species was computed in terms of the utilization of "prey type" and "prey size" (sensu Turner & Polis 1979). The overlap coefficient (α) was computed with the following equation presented by Pianka (1974):

$$\alpha_{jk} = \frac{\sum_{i=1}^{n} p_{ij}\, p_{ik}}{\sqrt{\sum_{i=1}^{n} p_{ij}^2 \sum_{i=1}^{n} p_{ik}^2}}, \qquad (1)$$

Table 1. Proportion of lynx spiders, *O. salticus* and *P. viridans*, and other species within the spider community of a cotton agroecosystem near College Station in central Texas (June–August 1988)

Week	Time spent observing, h	n[a]	% Different spider taxa						
			O. salticus	*P. viridans*	Crab spiders[b]	Jumping spiders[c]	Orb weavers[d]	Other spiders[e]	Total
13–19 June	6.9	105	19.9	26.0	3.9	5.6	21.6	22.9	100
20–26 June	11.2	172	53.1	12.4	6.2	5.3	15.3	7.6	100
27 June–3 July	15.8	616	55.7	15.6	5.9	3.7	15.3	3.9	100
4–10 July	11.2	538	58.5	17.3	5.2	6.0	10.7	2.3	100
11–17 July	9.4	401	57.6	17.9	7.5	4.5	10.9	1.5	100
18–24 July	15.9	611	60.6	15.7	9.6	7.1	5.3	1.8	100
25–31 July	13.0	444	62.1	12.4	7.4	5.7	8.7	3.7	100
1–7 August	15.1	819	71.0	13.8	2.8	5.0	5.1	2.2	100
8–14 August	9.3	275	64.0	19.2	1.5	5.4	8.7	1.1	100
Mean	—	—	55.8	16.7	5.5	5.4	11.3	5.2	100
± SEM			± 4.8	± 1.4	± 0.8	± 0.3	± 1.8	± 2.3	

[a] Total number of spiders observed during a week.

[b] *Misumenops* spp.

[c] *Phidippus audax, Metaphidippus galathea, Hentzia palmarum.*

[d] *Tetragnatha laboriosa* and others.

[e] Various species including *Pardosa* sp.

where p_{ij} and p_{ik} represent the proportions of the i^{th} food category (i.e., prey of a particular "type" or "size class," respectively) used by the j^{th} species (*O. salticus*) and k^{th} species (*P. viridans*). Values range between 0 (no overlap) and +1 (complete overlap).

To determine relative feeding specialization, a niche breadth coefficient (β) was computed with the Shannon-Weaver equation based on information theory (Turner & Polis 1979):

$$\beta = -\Sigma p_i \log p_i, \qquad (2)$$

where p_i is the proportion of the i^{th} food category (i.e., prey of a particular "type" or "size class," respectively) used. Natural logarithms are used in the Shannon-Weaver equation (Poole 1974). High β-values are characteristic for exceedingly polyphagous predators, whereas low β-values indicate a specialized feeding behavior (Turner & Polis 1979). Two Shannon-Weaver diversities (β) can be compared, with a t test, to see if they are significantly different (Poole 1974).

Because the numbers of prey records obtained during this project were fairly low ($n = 63$ versus $n = 31$ for *O. salticus* and *P. viridans*, respectively) for a meaningful between-species comparison, they were combined with those from another insecticide-free Texas cotton field (see Nyffeler et al. 1987a,b) and pooled data (total $n = 127$ [*O. salticus*] versus $n = 51$ [*P. viridans*]) were used for the computation of the α- and β-values.

Means (± SEM) were computed for body lengths of spiders and prey and were further compared by t tests (where sample size was small, the Mann-Whitney U test was chosen) (Sokal & Rohlf 1969). Proportions of prey-carrying spiders were compared with a χ^2-test of independence without Yates' correction (Sokal & Rohlf 1969). A regression analysis (linear model) of prey length versus spider length was performed for *O. salticus* and *P. viridans*, respectively (Draper & Smith 1981).

Results

Numerically Dominant Spiders. The lynx spiders numerically dominated the spider assemblage in the investigated cotton field throughout the growing season; the dominance of the lynx spiders increased with time, reaching a maximum in August (Table 1). Among the 3,981 spider individuals encountered during the growing season in the field were 2,402 *O. salticus* (60% of total) and 626 *P. viridans* (16%). A predominance of lynx spiders among the arthropod predators is characteristic for many cotton fields in central and east Texas (Dean & Sterling 1987; Nyffeler et al. 1987a,b; Breene et al. 1989).

Feeding Frequency. Of the 2,402 *O. salticus* encountered in the field (Table 1), 63 individuals (2.6%) held prey between their chelicerae (Table 2). At the same time, among the 626 *P. viridans* observed (Table 1), 31 individuals (4.9%) were in possession of prey (Table 3). Thus, the larger *P. viridans* exhibited a proportion of feeding spiders almost double that of *O. salticus*, the interspecific difference being statistically significant ($\chi^2 = 8.96$; df = 1; $P < 0.01$).

Predator Length Versus Prey Length. The 63 *O. salticus* (Table 2) had an average body length of 4.24 ± 0.16 mm (mean ± SEM; range, 1.9–8.0 mm), while the 31 *P. viridans* (Table 3) had an average length of 10.08 ± 0.52 mm (range, 4.5–16.5 mm); the difference between the two species was statistically significant ($t = 10.70$; df = 29; $P < 0.001$). *O. salticus* captured rather small prey with an average length of 2.41 ± 0.17 mm (range, 0.5–5.8 mm). In contrast, *P. viridans* captured prey organisms with an average length of

Table 2. Prey of *O. salticus* in a cotton agroecosystem near College Station in central Texas (summer 1988)

	Prey type	Total		Prey size range, mm	Predator size range, mm
		No. prey	% Prey		
Heteroptera	*P. seriatus*[a]	15	23.8	1.1–2.9	2.6–5.7
	Orius sp.	3	4.8	1.5–1.6	3.1–4.5
	Geocoris punctipes	1	1.6	3.6	5.0
	Lygus lineolaris	1	1.6	5.0	4.9
	Keltonia sp.	1	1.6	2.6	3.6
	Pentatomidae (nymph)	1	1.6	0.5	6.1
Diptera		10	15.9	1.2–2.1	1.9–4.9
Homoptera	Aphididae	8	12.7	0.7–1.8	2.4–4.7
Hymenoptera	*Solenopsis invicta*[b]	6	9.5	1.8–5.8	4.4–4.7
	Solenopsis sp.	1	1.6	2.4	4.3
	Others (winged)	1	1.6	2.1	3.5
Coleoptera	Nitidulidae (?)	1	1.6	2.3	5.0
Orthoptera		1	1.6	4.0	5.5
Araneae	*Oxyopes salticus*	4	6.3	3.0–4.8	4.3–8.0
	Phidippus audax	2	3.2	1.7–2.4	4.2–4.4
	Hentzia palmarum	3	4.8	2.6–5.5	5.1–7.1
	Pardosa sp.	1	1.6	3.0	4.8
Unidentified		3	4.8	—	3.3–4.1
Total		63	100	0.5–5.8	1.9–8.0

Total no. spiders observed = 2402.

[a] Third instar (1), fifth instar (2), unidentified instar (1), adult (11).

[b] Worker (4), males (2).

7.04 ± 0.73 mm (range, 1.3–13.6 mm). The difference in the average prey size between the two spider species was statistically significant ($t = 6.12$; df = 29; $P < 0.001$). A highly significant correlation between predator length (X) and prey length (Y) was found for *O. salticus* ($r = 0.487$, $P < 0.001$) and *P. viridans* ($r = 0.628$, $P < 0.001$) (i.e., larger spiders seize larger prey). A regression analysis (linear model) produced the equations $Y = -0.13 + 0.59X$ and $Y = -2.17 + 0.92X$ for the regression lines of *O. salticus* and *P. viridans*, respectively.

The lynx spiders killed preponderantly prey organisms that were smaller than themselves. The subduing potential of the spiders relative to their prey ranged between 8 and 129% of the spider's size in *O. salticus*, and between 26 and 136% of the spider's size in *P. viridans*. The mean subduing potential was 56 ± 3% [mean ± SEM] for *O. salticus*, and 68 ± 6% for *P. viridans*. These data suggest that the most profitable prey to the predator are slightly more than half the size of the spiders.

Natural Diets. The lynx spiders were found feeding on a variety of prey species predominantly from the class Insecta (i.e., polyphagous insectivores; Tables 2 and 3). Both lynx spiders were repeatedly observed feeding on dipterans (Tables 2 and 3), and *O. salticus* also fed on aphids (Table 2). These two insect groups constitute a key food source for spiders (Nyffeler & Benz 1987).

Table 3. Prey of *P. viridans* in a cotton agroecosystem near College Station in central Texas (summer 1988)

	Prey type	Total		Prey size range, mm	Predator size range, mm
		No. prey	% Prey		
Diptera		3	9.7	1.3– 7.1	4.5–12.5
Hymenoptera	Apidae	6	19.4	9.1–13.6	9.9–14.5
	Halictidae	1	3.2	6.8	12.5
	Vespidae	1	3.2	13.0	11.5
	Colletidae	1	3.2	11.2	12.0
	Forelius pruinosus	1	3.2	5.4	7.4
	Solenopsis invicta	3	9.7	2.5– 6.5	8.5
Heteroptera	*P. seriatus*	4	12.9	2.2– 2.9	6.4– 7.4
Coleoptera	*Hippodamia convergens*	1	3.2	6.6	9.0
	D. undecimpunctata howardi	2	6.4	5.8– 6.6	9.2
	Anthonomus grandis grandis	1	3.2	5.5	8.8
Homoptera	Cicadellidae	1	3.2	2.5	9.6
Araneae	*Peucetia viridans*	1	3.2	9.0	16.5
	Oxyopes salticus	3	9.7	3.6– 5.3	8.1–13.2
	Metaphidippus galathea	1	3.2	2.8	9.1
	Tetragnatha laboriosa	1	3.2	4.8	7.8
Total		31	100	1.3–13.6	4.5–16.5

Total no. spiders observed = 626.

The prey group most often captured by *O. salticus* were Heteroptera (35% of total observations in Table 2) representing six genera including the minute pirate bug, *Orius insidiosus* (Say); the big-eyed bug, *Geocoris punctipes* (Say); the tarnished plant bug, *Lygus lineolaris* (Palisot de Beauvois); and the cotton fleahopper, *Pseudatomoscelis seriatus* (Reuter). The cotton fleahopper constituted the single most important prey taxon in the diet of *O. salticus* (Table 2) and was also found in the diet of *P. viridans* (Table 3).

Hymenoptera represented by several ants, wasps, and bees (e.g., halictid and honey bees) made up the majority of the prey records for *P. viridans* (42% of total observations in Table 3). Honey bees (*Apis mellifera* L.) and other bees were caught by *P. viridans* during bloom (July; Table 3), when large numbers of pollinating insects were attracted into the field. Bees and wasps were the largest prey items (6.8–13.6 mm in length; Table 3) taken by these spiders. *P. viridans* (10–14.5 mm in length) overpowered stinging Hymenoptera with a length of 86–136% the spider's size. Thus, *P. viridans* is an aggressive predator that attacks and kills large and dangerous prey. The smaller, less powerful *O. salticus* was never observed eating bees or wasps. Both lynx spider species repeatedly were observed eating fire ants, *Solenopsis invicta* (Buren) (Tables 2 and 3).

Four adult beetles including two spotted cucumber beetles, *Diabrotica undecimpunctata howardi* Barber; one lady beetle, *Hippodamia convergens* Guerin-Meneville; and one boll weevil, *Anthonomus grandis grandis* Boheman, are also listed (Table 3) in the prey spectrum of *P. viridans*. *O. salticus* proved to be poor predators of coleopterans (see also Nyffeler et al. 1987b). Only one incidence of predation by *O. salticus* on a coleopteran prey, a tiny beetle of <2.5 mm length, was recorded (Table 2). No cases of predation by lynx spiders on lepidopteran prey were documented in this study (Tables 2 and 3).

Both species of lynx spiders were observed repeatedly eating spiders, including members of their own species (Tables 2 and 3). *P. viridans* was observed eating *O. salticus*, but the reverse was not observed (Tables 2 and 3). The asymmetry (term sensu Polis et al. 1989) of the predation relationship between the two species can be explained by the significantly larger average size of *P. viridans* (see above), giving this more powerful species an advantage over *O. salticus* during interspecific aggressive encounters.

Comparison of Diets by Niche Overlap and Niche Breadth Coefficients. The resource exploitation patterns of *O. salticus* and *P. viridans* were compared in terms of the common use of prey of a certain type (or size). An overlap index computed with equation 1 equalled $\alpha = 0.60$ (prey type) and $\alpha = 0.67$ (prey size).

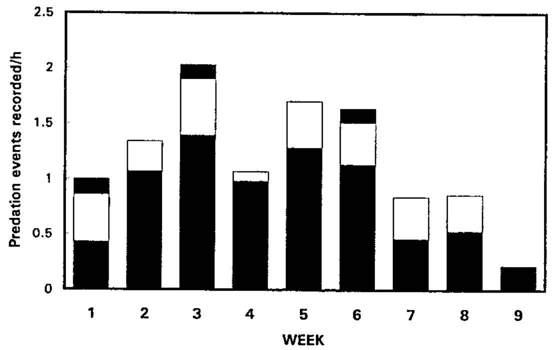

Fig. 1. Number of prey-carrying predators found per hour in a cotton agroecosystem near College Station in central Texas (9 wk during summer 1988). See Table 1 for dates of weeks. Total no. predation events observed = 134. Solid, lynx spiders; empty, other spiders; shaded, insects.

A coefficient (β) as a measure of feeding specialization was computed for each spider species with equation 2. In terms of prey types eaten in the field, the computed values ($\beta = 2.61$ versus 3.05 for *O. salticus* and *P. viridans*, respectively) were significantly different ($t = 3.11$; df = 114; $P < 0.01$). For the prey sizes selected by the two spider species, the computed values ($\beta = 1.51$ versus 2.41 for *O. salticus* and *P. viridans*, respectively) differed highly significantly ($t = 7.50$; df = 92; $P < 0.001$). Because β-values are inversely related to feeding specialization (Turner 1979), these data suggest that *P. viridans* is a less specialized predator than the smaller-sized *O. salticus* in terms of prey types and prey sizes eaten in the field. In a field study in California, Turner & Polis (1979) likewise found that *P. viridans* was exceedingly polyphagous ($\beta = 3.58$ in terms of prey type) relative to four smaller-sized species of hunting spiders ($\beta = 0.20$–2.86).

Relative Importance of Lynx Spiders Compared with Other Arthropod Predators. To evaluate the predatory significance of the lynx spiders relative to other predaceous arthropods occurring in this cotton field, we compared the total number of predation events observed attributable to lynx spiders versus other arthropod predators. During the 108-h observation time, we monitored a total of 134 arthropod predators with prey in their chelicerae or mandibulae, including 94 lynx spiders (Tables 2 and 3). Thus, 70% of all predation events observed were attributable to lynx spiders, which indicates that these spiders were the dominant predators in the investigated cotton agroecosystem (Fig. 1). However, often the most abundant prey in cotton fields is small, such as aphids, thrips, spider mites, and arthropod eggs. Our study may underestimate the frequency of predation on small arthropods because it is difficult to observe these acts of predation.

Discussion

Feeding Frequency. In this study, 0.9 prey-carrying lynx spiders per hour were collected (94 records in 108 h, *O. salticus* plus *P. viridans* combined) (Tables 2 and 3), which is of the same magnitude as the 1.0 prey-carrying lynx spiders per hour collected in a cotton field in east Texas (84 records in 85 h; Nyffeler et al. 1987a,b). A low proportion (≤5%) of the lynx spiders sampled during the present study held prey in their chelicerae. In the previous study conducted by Nyffeler et al. (1987a,b) in east Texas, likewise a low proportion of the sampled lynx spiders were in possession of prey (≈3% versus 5% for *O. salticus* and *P. viridans*, respectively). Two to four times higher feeding frequencies of *P. viridans* were observed on noncrop vegetation (Turner 1979, Nyffeler et al. 1987a).

With a visual method based on average feeding frequency (percentage spiders with prey) observed in the field, average handling time, and hunting (searching) time, we estimated that the larger stages of *O. salticus* may have captured an average of about one small-sized prey daily in Texas cotton (Nyffeler et al. 1987b, 1992). Significantly higher numbers of small-sized prey were captured by medium to large *O. salticus* in laboratory feeding experiments (Lingren et al. 1968, Young & Lockley 1986, Bumroongsook et al. 1992). This suggests that the *O. salticus* individuals observed in Texas cotton fields (Nyffeler et al. 1987b, 1992) fed below their maximum feeding capacity and could increase their feeding rates during severe outbreaks of cotton insect pests (i.e., under conditions of increased potential prey density; see Breene et al. 1990).

Predator Length Versus Prey Length. The predator-prey size ratios of the two lynx spiders assessed in this article resemble those described by Nyffeler et al. (1987a,b) for lynx spiders in east Texas. The majority of the captured prey organisms of the lynx spiders were smaller than the length of the predator (mean subduing potential 56 versus 68% for *O. salticus* and *P. viridans*, respectively), which fits the general theory of prey size selection in nonweb-building spiders (see Nentwig & Wissel 1986, Nentwig 1987). Both lynx spider species never were observed with prey organisms larger than 140% of their own size (Tables 2 and 3). These data agree with the laboratory feeding experiments of Nentwig & Wissel (1986), who showed that most nonweb-building spiders overpowered prey organisms not larger than 150% of the spider's size, with an optimal range of the subduing potential of 50–80% of their own size. A similar mean subduing potential (mean = 59%) was found in wolf spiders (Hayes & Lockley 1990).

Comparison of Diets by Niche Overlap-Coefficients. If we compare the prey utilization patterns of *O. salticus* versus *P. viridans*, the following relationship appears. The values of dietary overlap (0.5 < α < 0.7, see above) of the species pair computed in this study indicate that *O. salticus* and *P. viridans* partially differ in their prey selection. The *O. salticus* population feeds on the lower end of the potential prey size distribution (maximum prey length <6 mm; Fig. 2B). In contrast, *P. viridans* individuals feed over a broader range of prey size classes and capture a higher proportion of the larger prey organisms (Fig. 2B). The interspecific difference of the average prey length (Fig. 2B) reflects the statistically significant body size differential between the two predators (Fig. 2A). More than 80% of the *O. salticus* predators were <6 mm in body length, while 87% of the *P. viridans* predators were >8 mm in length (Fig. 2A). The body size frequency distributions of the two species overlap in the size range between 4.5 and 8 mm to

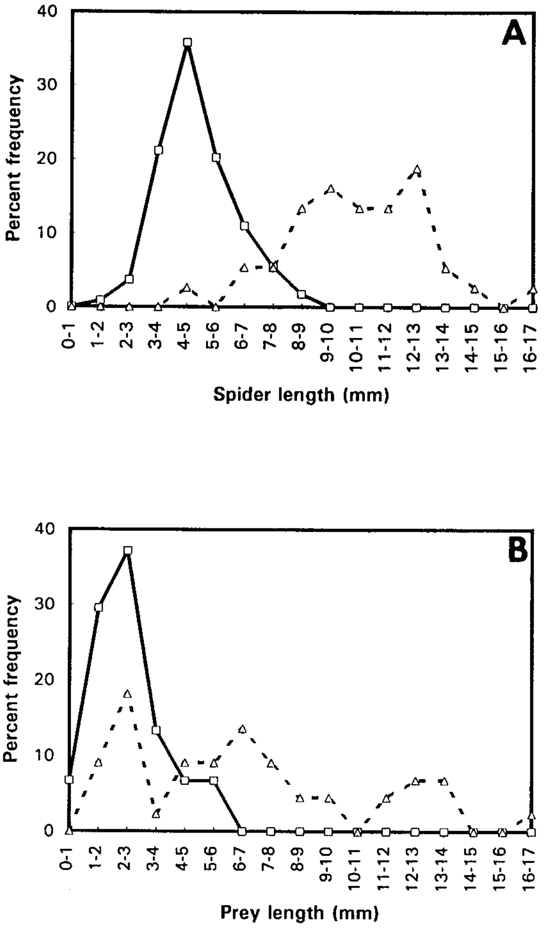

Fig. 2. (A) Body length frequency distribution of *Oxyopes salticus* (squares) versus *P. viridans* (triangles), among 17 size classes. Pooled data for prey-carrying spiders sampled between June and August in two cotton fields in Texas. (B) Prey length frequency distribution for *Oxyopes salticus* (squares) versus *P. viridans* (triangles). Same samples as in (A).

which the 13% smallest *P. viridans* (all immature) and the 20% largest *O. salticus* belong (Fig. 2A). A comparison of the average prey length of the smallest individuals of *P. viridans* (≤ 8 mm length) versus the largest individuals of *O. salticus* (≥ 4.5 mm) gave no statistically significant difference (Mann-Whitney U test; $U_s = 117.5$; df = 25, 10; $P > 0.05$), suggesting that the smallest *P. viridans* and the largest *O. salticus* (in the 4.5–8 mm size classes) select prey of similar average length (≈ 3 mm).

Similarities in the foraging patterns of *O. salticus* and immature *P. viridans* were observed by Whitcomb (1974). This author noted that *O. salticus* and immature *P. viridans* both actively search for prey on foliage (i.e., "active foragers"), whereas the large adult *P. viridans* exhibit a distinctly different foraging strategy (i.e., "sit-and-wait foragers"). Thus, Whitcomb's and our observations (Fig. 2) suggest that *O. salticus* and the small immature *P. viridans* function as predators in a similar manner.

Spider Predation on Cotton Insect Pests. Sterling et al. (1989) note that most predators of the small stages of insect pests are themselves predators of small size (i.e., small spiders), while it takes larger predators (i.e., large spiders) to overcome the defenses of the larger stages of these pests. *O. salticus* as a small-sized spider (Fig. 2A) qualifies as a predator of small insect pests (small species or small stages of the larger insect species; Fig. 2B), whereas the large more powerful *P. viridans* (Fig. 2A) can overpower large pest insects (Fig. 2B). The two lynx spider species therefore complement each other in their predatory activities (Fig. 2B; Nyffeler et al. 1987b), reducing the niche overlap.

The following four insect species are considered "key pests" in Texas cotton (Bohmfalk et al. 1983): cotton fleahopper; boll weevil; bollworm, *Helicoverpa zea* (Boddie); and tobacco budworm, *Heliothis virescens* (F). In the current study, the cotton fleahopper was the most important prey species in the diet of *O. salticus* (24% of total prey; Table 2). Fleahoppers were also eaten by *P. viridans* (Table 3).

In one instance, *P. viridans* was observed feeding on an adult boll weevil (Table 3), which is a new prey record for this spider species. Beetles are poorly represented in the diet of *O. salticus* (Table 2), and the boll weevil is not listed so far among the known prey species of this spider (Young & Lockley 1985, Lockley & Young 1987, Nyffeler et al. 1987b). The hard-chitinized beetles apparently are not optimal diet for most spiders, because the chelicerae cannot penetrate the thick cuticle of these insects (Turner 1979, Nentwig 1987).

Spider Predation on Bees. Besides pestiferous insects, the lynx spiders capture large numbers of beneficial pollinators and entomophages (Randall 1982; Nyffeler et al. 1987a,b; Agnew & Smith 1989). Bees attracted to the cotton plants during bloom often are encountered and overpowered by the aggressive *P. viridans* that lie in ambush on the upper surface of leaves in the plant terminal well camouflaged by their bright green color and cryptic posture (Whitcomb et al. 1966). Bees constituted 23% (by numbers) of the diet of *P. viridans* in the investigated Texas cotton field (Table 3). *P. viridans* is generally known to seize bees frequently (Whitcomb et al. 1966, Turner 1979, Goodenough et al. 1986, Nyffeler et al. 1987a). In their capacity to overpower and eat large stinging Hymenoptera, the *P. viridans* behave similarly to aggressive large orb-weaving spiders such as *Argiope aurantia* Lucas (Nyffeler et al. 1987c). Large stinging Hymenoptera are a primary food source for some aggressive large spiders hunting on or near flowering plants (Nyffeler et al. 1987c, Nyffeler & Breene 1991). Although it has been documented that some aggressive large spider species can affect honey bee colonies in small localized areas during short time periods (Nyffeler & Breene 1991), there is no evidence that *P. viridans* should be considered more economically harmful than beneficial. By means of a cost-benefit analysis, Louda (1982) examined the net effect of predation by *P. viridans* on seed production by a native plant (family Asteraceae) and found that "pollination success was lower on branches with *P. viridans* (versus branches without spiders), but insect damage to seeds was also reduced on those branches; the net result was an increase in the number of viable seeds where *P. viridans* was present." Large bees (9–14 mm in length; Table 3) evidently are beyond the maximum subduing potential of *O. salticus* (Fig. 2B), which seems to explain why bees are missing in the prey spectrum of this spider (Table 2; Young & Lockley 1985, Lockley & Young 1987, Nyffeler et al. 1987b).

Spider Predation on Other Predators. Both lynx spiders frequently eat spiders (Tables 2 and 3), which agrees with data from other crop fields and wild plants in Texas (Nyffeler et al. 1987a,b; Agnew & Smith 1989). The list of spiders eaten by both lynx spiders includes jumping spiders (*Phidippus audax* [Hentz]), crab spiders (*Misumenops* spp.), striped lynx spiders (*O. salticus*), star-bellied orb-weavers (*Acanthepeira stellata* [Walckenaer]), and long jawed orb-weavers (*Tetragnatha laboriosa* Hentz) (Tables 2 and 3; Nyffeler et al. 1987a,b; Agnew & Smith 1989). Furthermore, *P. viridans* will eat winter spiders (*Cheiracanthium inclusum* [Hentz]) (Nyffeler et al. 1987a). Predaceous insects eaten by lynx spiders include *S. invicta, H. convergens, Chrysoperla rufilabris* (Burmeister), *O. insidiosus*, and *G. punctipes* (Nyffeler et al. 1987a,b; Agnew & Smith 1989; Guillebeau & All 1989). These six spider species and five insect species killed by spiders are themselves "key predators" that contribute significantly to mortality of bollworm-budworm eggs and larvae in Texas cotton (Bohmfalk et al. 1983, Goodenough et al. 1986, Sterling et al. 1989). The question arises whether spiders eating other predators (i.e., "intraguild predation" sensu Polis et al. 1989) eventually have negative economic implications by disrupting natural control of bollworm–budworm numbers. Although there may be some negative effect of intraguild predation where high predator numbers and simultaneously high levels of intraguild predation were monitored (Nyffeler et al. 1987a,b; M. N., unpublished data), bollworm–budworm numbers in these cotton fields remained below the threshold level (D.A.D., unpublished data). Bollworm–budworm infestations rarely reach economic levels in insecticide-free cotton fields where an extensive natural enemy complex has been preserved (e.g., Laster & Brazzel 1968, McDaniel et al. 1981). Cannibalism and interspecific predation within the predator complex may even have positive ecological implications by providing food for predators during time periods of low herbivore numbers, which helps to create sustainable predator communities. We therefore feel that predator mortality from intraguild predation is not of great overall economic importance. Costs and benefits of each of these predators can be estimated in each cotton field using the TEXCIM50 computer model (Sterling et al. 1992b). Agnew & Smith (1989) discussed the same problem in the case of insecticide-free peanut fields in central Texas and stated, "Predation by predators on each other should not be viewed as disadvantageous as long as the predators largely switch to pestiferous species when they become abundant (i.e., functional response)." A sigmoid functional response of *O. salticus* and of two other spider species to fleahopper density has been demonstrated in field cage experiments in a cotton field in central Texas (Breene et al. 1990).

Biocontrol Implications. The "model predator" of classical biological control should show high prey specificity to a particular pest (Riechert & Lockley 1984). *P. viridans* is exceedingly polyphagous (Turner & Polis 1979, Randall 1982), whereas *O. salticus* is a significantly more specialized feeder (see β-values in *Results* section). *O. salticus* thus exhibits a better fit to the model predator. *O. salticus* is an excellent agroecosystem colonizer (Dean & Sterling 1987) with the capacity to build up fairly large population numbers (up to 7 individuals per square meter in Texas cotton; Nyffeler et al. 1987b). Because *O. salticus* preferentially feeds on prey organisms in the 1–2.9 mm size classes (Fig. 2B), the cotton fleahopper with a body length range of 1.1–2.9 mm (third instar to adult; Table 2) evidently is an optimal diet for this spider. *O. salticus* has proven to be a significant mortality factor of fleahoppers in cotton fields in central Texas (Breene et al. 1989, Nyffeler et al. 1992). Because of their activity in killing numerous insect pests, the lynx spiders are of economic value, which also was demonstrated with computer modelling techniques (Sterling et al. 1992a).

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BIOLOGICAL CONTROL

Impact of the Striped Lynx Spider (Araneae: Oxyopidae) and Other Natural Enemies on the Cotton Fleahopper (Hemiptera: Miridae) in Texas Cotton

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ABSTRACT Natural predation on nymphs and adults of the cotton fleahopper, *Pseudatomoscelis seriatus* (Reuter), was assessed during 108 h of visual observation in an insecticide-free cotton field in central Texas. Predaceous arthropods of 13 species (from nine families) were observed to forage on the fleahopper. More than 80% of the predation events observed were attributable to spiders. The striped lynx spider, *Oxyopes salticus* Hentz, was dominant among the predators observed eating fleahoppers (15 records of feeding in action). Cotton fleahoppers composed ≈25% of the total prey of *O. salticus* during June and July. It was estimated during midseason that once every 4 d, one *O. salticus* would kill one cotton fleahopper. The assessment of the killing power of *O. salticus*, based on the predation rate and the predator-to-prey ratio (i.e., number of *O. salticus* individuals per fleahopper), suggests that these spiders are important mortality agents of the cotton fleahopper (≥15% prey mortality per day in the middle of the growing season). Additional fleahopper mortality is attributable to other predaceous arthropods such as *Peucetia viridans* (Hentz) (Oxyopidae), jumping spiders (Salticidae), crab spiders (Thomisidae), web-building spiders (Araneidae, Dictynidae, Theridiidae), damsel bugs (Nabidae), and ants (Formicidae).

KEY WORDS *Pseudatomoscelis*, *Oxyopes*, cotton

THE COTTON FLEAHOPPER, *Pseudatomoscelis seriatus* (Reuter), is a major pest of cotton in Texas (Adkisson 1973, Sterling et al. 1992b). Fleahoppers are eaten by various polyphagous arthropod predators as has been detected by visual observation (Whitcomb et al. 1963, Dean et al. 1987, Lockley & Young 1987) and by ^{32}P-labeling (Breene & Sterling 1988). These polyphagous predators are numerous in some cotton fields (Whitcomb & Bell 1964, van den Bosch & Hagen 1966, Johnson et al. 1986, Dean & Sterling 1987), suggesting that they may contribute to the natural mortality of the cotton fleahopper.

An observational study (>85 h) was conducted in an east Texas cotton agroecosystem during the summer of 1985 to evaluate quantitatively the effect of arthropod predation on the population dynamics of the cotton fleahopper (Nyffeler et al. 1986; 1987a, b, c; 1988a, b; 1989; Dean et al. 1987). The study site was an insecticide-free cotton agroecosystem surrounded by extensive tracts of minimally disturbed noncrop habitats composed of various wild plants and grasses. From these "reservoir habitats," large numbers of predators (primarily spiders and fire ants) migrated into the cotton agroecosystem. Large numbers of predators were observed on cotton, but a very low frequency of predation on the fleahopper was monitored (three prey records over an 85-h observation period, or 0.03 record per hour) (Table 6). Numbers of cotton fleahoppers counted in that cotton field in 1985 was 0.04–1.3 individuals per meter of row (early season until bloom). This is below the economic threshold of 15–35 fleahoppers per 100 plants (≈1.5–3.5 individuals per meter of row in the Austonio field) recommended by the Texas Agricultural Extension Service. The low predation rates on fleahopper prey apparently reflected the reduced fleahopper numbers on cotton (Nyffeler et al. 1987a). Possibly the fleahoppers were kept in check by the numerous predators on the wild host plants in the "reservoir habitats" before they migrated into cotton (unpublished data). Nyffeler et al. (1987a, b) stressed the need to repeat a similar visual observation project in another cotton agroecosystem where cotton fleahoppers were more abundant.

During the summer of 1988, the effect of arthropod predators on fleahopper numbers was evaluated quantitatively in a cotton field in central Texas, where cotton fleahoppers occurred in fairly high numbers (two per meter of row in midseason). Predation activities of insectivores on the various instars of the cotton fleahopper were observed, and the killing power of the nu-

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merically dominant predator species was estimated.

Materials and Methods

Study Area. The study site was a weed-free cotton agroecosystem untreated with insecticides in central Texas (Burleson County), ≈20 km southwest of College Station. This cotton field (13.6 ha) was surrounded by grassland (grazed pastures), with wild plants growing on the field borders and in adjacent grasslands. Cotton, sorghum, and corn were grown in nearby fields. The cotton ('Paymaster 145') was planted on 8 April 1988 with a distance between rows of 1 m. The cotton yield was 950 kg/ha (1.7 bales/acre).

Evidence of Predation. Field observations were conducted for 9 consecutive wk, from mid-June to mid-August 1988, during the daylight hours (the majority between 1200 and 1800 hours CST). Lockley & Young (1987) noted that predator activity was higher in the morning hours compared with the afternoon hours in Mississippi. In a previous study conducted in Texas cotton, the feeding activity of the numerically dominant predators did not differ significantly between the morning and afternoon hours (Nyffeler et al. 1987a, b), although we cannot rule out that the unknown feeding activities of some less abundant species may peak in the morning (see also Culin & Yeargan 1982). In total, 108 person-hours of visual observation were spent in the field; 34 h in June, 50 h in July, and 24 h in August, with an average of 3 h/d. The numbers of predators were monitored by counting them on plants during 1-h periods (walking speed ≈0.8 km/h along the field rows). During each observation period, the following data were recorded: (1) Date, (2) time of day, (3) numbers of predators without prey per observation hour, (4) numbers of predators with fleahopper prey per observation hour, (5) numbers of predators with alternate prey per observation hour, and (6) numbers of potential fleahopper prey per observation hour.

Versatile predators (nonweb-building spiders and insects) with prey in their chelicerae–mandibulae were captured by hand with a transparent cup (7.5 cm upper diameter, 10 cm depth). This method monitored "observational evidence of predation in action" (*OE* values [see Sterling 1989]). One fire ant worker transporting a wiggling fleahopper was listed in the category of "predators feeding," although the ant was not actually seen eating; however, subsequent feeding by the colony could be expected (Breene et al. 1989b).

For sedentary web-building spiders, evidence of predation was obtained in two ways: (1) by capturing spiders with prey in their chelicerae (observational evidence of predation in action [*OE*], see above), and (2) by collecting the remains of dead fleahoppers from the spider webs ("durable evidence" [*DE*] sensu Sterling [1989]). "Total evidence" is defined as the combined data of "observational evidence" plus "durable evidence" (*OE* + *DE*).

Predators in possession of prey were killed, preserved (along with their prey) in 70% ethyl alcohol, and later identified in the laboratory under a dissecting microscope. At the same time, the age (instar) of each fleahopper prey was determined and recorded. For methodological details see Nyffeler et al. (1987a, b, c; 1988a, b; 1989).

Estimate of Predation Rate of *Oxyopes salticus* Hentz. According to Edgar (1970) and Kiritani et al. (1972), the predation rate of nonweb-building spiders can be estimated based on the average proportion of prey-carrying spiders observed in the field. It is necessary to know the average time required to handle an individual prey (handling time) and the hunting time (hours per day), so that the data obtained in the field can be converted into the number of prey eaten per day (Edgar 1970, Kiritani et al. 1972). The predation rate in this study was estimated in the middle of the growing season, when the *O. salticus* population had a nearly uniform age–size class structure dominated by larger stages (late instars–adults, sensu Whitcomb & Eason [1967]). Young & Lockley (1986) conducted laboratory experiments with *O. salticus* and found that small spiders (0.58 ± 0.04 mm carapace width) killed significantly less prey than medium-sized spiders (0.81 ± 0.07 mm carapace width) or large spiders (1.34 ± 0.29 mm carapace width), whereas the difference between the two larger size categories was not statistically significant. Evidently the difference of the predation rate between the larger *O. salticus* size classes is rather small, which justifies the assessment of a single predation rate for the entire group of larger *O. salticus* in the middle of the growing season.

The daily rate of predation on all prey (Pd_a, number of prey organisms killed per spider per day) of *O. salticus* was assessed with equation 1 (Edgar 1970, Nyffeler et al. 1987a):

$$Pd_a = (T_f \times 60 \times F_t)/(T_h \times 100), \qquad (1)$$

where 60 is minutes and 100 is used to convert to percentage, T_f is the hunting time (hours per day) available for prey capture and feeding in the field, T_h is the average time (minutes) required to handle an individual prey, and F_t is the average feeding frequency at a given time (mean percentage prey-carrying spiders observed in the field [see Edgar 1970]). The proportion of prey-carrying *O. salticus* within the population was recorded on 4 consecutive d (20–23 July, with 3-h observations per day) and the mean (±SE) of the four observation periods used as an estimate for the F_t value. Hunting (finding) time (T_f) and handling time (T_h) of *O. salticus* in Texas cotton had previously been determined in a field study by Nyffeler et al. (1987a). As a polyphagous predator, *O. salticus* feeds on multiple prey species (Nyffeler et al. 1987a, 1992), and the Pd_a value expresses the rate of predation on all prey (fleahopper prey plus alternate prey). The fleahopper prey/all prey ratio was estimated based on field observations (Table 3), and used as a correction factor to convert the rate of predation on all prey (Pd_a value) to the rate of predation on fleahoppers (Pd_c value).

Estimate of Fleahopper Mortality Caused by *O. salticus*. Based on the predation rate by *O. salticus* upon fleahopper prey and on the predator/prey ratio (i.e., number of *O. salticus* individuals per fleahopper), the daily percentage mortality (M) of the cotton fleahopper caused by *O. salticus* was estimated. The M value, in the middle of the growing season, was estimated with the following equation:

$$M = 100 \times Pd_c \times R, \qquad (2)$$

where Pd_c is the predation rate on cotton fleahoppers (number of fleahoppers killed per spider per day), and R is the predator/prey ratio (number of *O. salticus* individuals per fleahopper). In this study, the R values were based on two different density estimates (relative and absolute densities, respectively). Relative population densities (individuals observed per hour) were counted from 1300 to 1400 hours on 14 and 25 July. Absolute population densities (individuals per meter of row) were assessed by whole-plant examination; twenty-five random samples each of 1 m of row were obtained between 1100 and 1200 hours on 19 July.

The predator/prey ratio was assessed as follows for the relative estimate:

$$R_r = S_r/C_r, \qquad (3)$$

where S_r is the average number of striped lynx spiders recorded per hour, and C_r is the average number of cotton fleahoppers recorded per hour.

The predator/prey ratio based on absolute densities was computed as follows:

$$R_a = S_a/C_a, \qquad (4)$$

where S_a is the average number of striped lynx spiders per meter of row, and C_a is the average number of cotton fleahoppers per meter of row.

Statistical Tests. A statistical comparison of the ratio of immature/adult fleahopper prey consumed by the various predator species provides information that can be used to adjust the predator group-specific indices of efficiency used in the tritrophic cotton insect TEXCIM model (see Breene et al. 1989a, Nyffeler et al. 1989, Sterling et al. 1992b). The data were pooled into two principal groups of foragers (web-building spiders versus nonweb-building spiders), because the number of observed predation events was too low for a meaningful between-species statistical analysis. A χ^2 test of independence was used to examine whether the immature/adult fleahopper ratio in the prey differed significantly between the two forager groups.

The same statistical test was used to determine whether the ratio of fleahoppers/alternate prey consumed by the predator complex (monthly pooled data for combined predator species) differed significantly between months, indicating possible temporal shifts of the predator activities (see also Breene et al. 1989a). A χ^2 test of independence was also applied to compare feeding frequencies on fleahopper prey (predators eating a fleahopper per total predators, monthly pooled data) between months, which provides information on the seasonal dynamics of the predator activities. χ^2 values were computed by means of the uncorrected formula (without Yates' correction) (Sokal & Rohlf 1969).

Results and Discussion

Predator Determination and Efficiency. Overall, 3,981 spiders (and numerous uncounted predaceous insects) were encountered by visual observation from June to August in cotton (Table 1). The spider assemblage (Table 1) represents a species complex typical for Texas cotton fields, with lynx spiders (Oxyopidae) predominating (compare Dean et al. 1982; Dean & Sterling 1987; Nyffeler et al. 1987a, b). Spider numbers increased with time (Fig. 1). The phenology of predators is correlated with the fruiting rate of the cotton plant (Dean & Sterling 1992). In the middle of the growing season, the spider density was estimated at 2.84 ± 0.39 individuals per square meter (mean ± SE, whole-plant examination on 19 July).

During this study, a total of 97 cases of arthropod predation upon the cotton fleahopper was documented (total evidence, Table 1). The age structure of fleahoppers killed by predators (Table 1) was: third instar (2 records [2%]), fifth instar (3 records [3%]), unidentified instar (1 record [1%]), and adults (91 records [94%]). However, these observations are biased by the fact that small fleahoppers are not easily observed on the plant. If captured, they are likely consumed rapidly (low handling time) so are less likely to be observed as prey (see Edgar [1970] for an analysis of handling time as a function of prey size). Because they do not fly, immatures are less likely to be observed in spider webs (see below). Therefore, other experimental methods may be needed to assess the predation rates of predators on small immature fleahoppers accurately. Web-building spiders, which are "sit-and-wait" foragers, intercepted with their webs pre-

Table 1. Observations of arthropod predation on the cotton fleahopper in a cotton field near College Station, TX, during summer 1988 (108 h total observation time)

Predator species	Predator stage[a]	Total no. predators observed	No. fleahopper prey[b]		
			Predator feeding (*OE*)	Prey in web (*DE*)	Total evidence (*OE* + *DE*)
Araneae					
Oxyopidae					
Oxyopes salticus Hentz	Imm, ad	2,402	15	—[e]	15[f]
Peucetia viridans (Hentz)	Imm	626	4	—[e]	4[g]
Salticidae					
Phidippus audax (Hentz)	Imm		1	—[e]	1[g]
Metaphidippus galathea (Walckenaer)	Imm		1	—[e]	1[h]
Unidentified	—	213[c]	0	—[e]	0
Thomisidae					
Misumenops spp.	Imm	228	1	—[e]	1[g]
Araneidae					
Cyclosa turbinata (Walckenaer)	Imm, ad	145	1	11	12[g]
Argiope aurantia Lucas	Imm	31	0	1	1[g]
Neoscona arabesca (Walckenaer)	Imm	206[c]	0	2	2[g]
Unidentified	—		0	1	1[g]
Dictynidae					
Dictyna segregata Gertsch & Mulaik	Imm	90	1	53	54[g]
Theridiidae					
Latrodectus mactans (F.)	Ad	2	0	1	1[g]
Unidentified spiders	—	38	0	1	1[i]
Hemiptera					
Nabidae					
Reduviolus alternatus (Parshley)	Ad	—[d]	1	—[e]	1[g]
Unidentified (Reduviidae ?)	Ad	—[d]	1	—[e]	1[g]
Hymenoptera					
Formicidae					
Solenopsis invicta Buren	Ad	—[d]	1	—[e]	1[g]
Total spiders	—	3,981	24	70	94
Total insects	—	—[d]	3	—[e]	3

[a] Only predator individuals in possession of fleahopper prey. Imm, immature; ad, adult.

[b] *OE*, observational evidence of predation in action; *DE*, durable evidence (predator not feeding); *OE* + *DE*, total evidence (observational plus durable evidence).

[c] All Salticidae; *N. arabesca* and unidentified Araneidae.

[d] —, not counted.

[e] These predators do not make a web; therefore, no prey can be found in webs (indicated by a dash).

[f] Third instar, 2 fifth instar, unidentified instar, 11 adults.

[g] Adults only.

[h] Third instar.

[i] Fifth instar.

ponderantly mobile winged adults of the fleahopper (71 adults versus 1 nymph) (Table 1). A significantly ($\chi^2 = 12.84$, df = 1, $P < 0.001$) lower proportion of adult fleahopper prey (17 adults versus 5 nymphs) (Table 1) was captured by the nonweb-building spiders which actively search the plant surface for nymphs and adults of the fleahopper (exception: crab spiders tend toward a "sit-and-wait" foraging strategy). Evidence of predation on fleahoppers was obtained on spiders of 10 different species (six families) and 3 insect species (three families) (Table 1). Among the spider predators ranging from 1.2 to 7.4 mm in length were 5 species each of nonweb-building spiders (Oxyopidae, Salticidae, and Thomisidae) and web-building spiders (Araneidae, Dictynidae, and Theridiidae) (Table 1). With the exception of the black widow spider, *Latrodectus mactans* (F.), all arthropod predators listed in Table 1 have been reported to be predaceous on the cotton fleahopper (Dean et al. 1987; Nyffeler et al. 1987c, 1989; Breene et al. 1988, 1989b).

Total evidence (*OE* + *DE*) presented in Table 1 shows a predominance of web-building spider prey records (mostly *Dictyna segregata* Gertsch & Mulaik and *Cyclosa turbinata* (Walckenaer)), which is deceptive because web-building spiders tend to store prey in their webs for longer time periods (up to several days, "durable evidence" (*DE*) sensu Sterling [1989]), whereas a prey organism remains in possession of a nonweb-building spider for only a short time period (T_h <1 h, *O. salticus*) (Nyffeler et al. 1987a; M.N., unpublished data); whereupon the evidence is destroyed. Total evidence (*OE* + *DE*) for web-building spiders versus nonweb-building spiders (long versus short retention time), therefore, cannot be compared quantitatively. Feeding times, however, can be compared because it takes web-building spiders, nonweb-building spiders, and predaceous in-

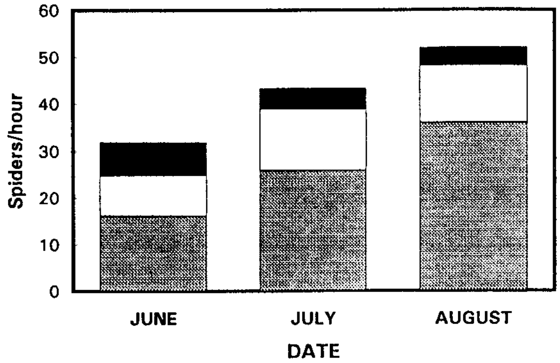

Fig. 1. Seasonal variation in the numbers of spiders encountered per hour (visual observations) in a cotton field near College Station, TX. ▨, *O. salticus;* ☐, other nonweb-building spiders (including *Peucetia viridans*, Salticidae, Thomisidae, Lycosidae, Philodromidae, and others); ■, web-building spiders (including Araneidae, Dictynidae, Theridiidae, Tetragnathidae, Uloboridae, and others). Monthly pooled data collected during daylight hours, June–August 1988.

sects each a short time to consume small-sized prey such as fleahoppers. Observational evidence of predation in action (based on feeding records, *OE*-values from Table 1) provides a less biased quantitative comparison of the various predators (Table 5).

Based on the total numbers of observed predators (*A*) and the number of predators found feeding on fleahoppers (*OE*), the percentage individuals within a particular predator group feeding on fleahoppers ($100 \times OE/A$) was computed, and the values for the various predator groups were compared (Table 2, pooled data for June and July). These values provide an estimate for predation frequency. The predator groups that demonstrated a higher predation frequency were the jumping spiders (Salticidae, 1.3% feeding individuals) and lynx spiders (Oxyopidae, 0.9%). Predator groups with lower predation frequency were the crab spiders (Thomisidae) and web-building spiders (Araneidae, Dictynidae, and Theridiidae, combined 0.5%). A very low predation frequency is attributable to the red imported fire ant (*Solenopsis invicta* Buren, <0.1%). No predation on fleahoppers (0%) was observed for big-eyed bugs (*Geocoris punctipes* (Say)), plant bugs (*Lygus* spp.), lady beetles (*Hippodamia convergens* (Guerin-Meneville) and other Coccinellidae), or lacewings (Chrysopidae) (for a description of these predator groups see Sterling et al. 1992b). In the case of the damsel bugs, ***Reduviolus alternatus*** (Parshley) and other predaceous Hemiptera, no value could be computed.

These values ($100 \times OE/A$) were converted into a standardized value ("efficiency index" $[100 \times OE]/[1.3 \times A]$), ranging between 0.0 and 1.0. The predator group with the highest predation frequency (jumping spiders), considered to be the most efficient natural enemy, is weighted with an efficiency index of 1. Other predators are compared in efficiency with the jumping spiders (concept according to Sterling et al. [1989]). The standardized values obtained in our study (Table 2) agree fairly well with efficiency indices previously used by the Texas Cotton Insect Model (TEXCIM; see Breene et al. 1989a).

Percentage Fleahoppers in Predators' Diet. Approximately 20% ($n = 134$) of the overall diet of combined predators was composed of fleahoppers (Table 3). The proportion of fleahoppers in the diet of combined predators did not differ

Table 2. Frequency of predation on cotton fleahoppers observed in a cotton field near College Station, TX (data pooled for June and July 1988)

Predator taxon	Total no. predators observed (*A*)	No. predators feeding on fleahoppers (*OE*)	% predators feeding on fleahoppers ($100 \times OE/A$)	Standardized value ("efficiency index") ($(100 \times OE)/(1.3 \times A)$)[a]
Striped lynx (*O. salticus*)	1,645	15	0.9	0.7
Green lynx (*P. viridans*)	460	4	0.9	0.7
Jumping spiders (Salticidae)	157	2	1.3	1.0
Crab spiders (Thomisidae)	201	1	0.5	0.4
Web-building spiders (Araneidae, Dictynidae, Theridiidae)	398	2	0.5	0.4
Fire ants (*S. invicta*)	—[c]	1	<0.1	<0.1
Damsel bugs (*R. alternatus*) and unidentified bugs (Reduviidae)[b]	—[c]	2	(0.8)[d]	(0.6)[d]
Big-eyed bugs (*G. punctipes*)[b]	—[c]	0	0.0	0.0
Plant bugs (*Lygus* spp.)[b]	—[c]	0	0.0	0.0
Lady beetles (Coccinellidae)[b]	—[c]	0	0.0	0.0
Lacewings (Chrysopidae)[b]	—[c]	0	0.0	0.0

[a] Standardized value as an estimate of "predator efficiency", ranging between 0.0 and 1.0. The predator group with highest predation frequency (jumping spiders), considered to be the most efficient natural enemy of the cotton fleahopper, is weighted with an efficiency index of 1. Other predators are compared with jumping spiders.

[b] For a description of these predator groups, see Sterling et al. (1992b).

[c] —, not counted.

[d] Empirical estimate.

Table 3. Cotton fleahoppers in diet of polyphagous arthropod predators, observed in a cotton field near College Station, TX, during summer 1988

Predator taxon	Month	No. predators observed feeding[a]	No. predators feeding on fleahopper
O. salticus	June	24	6
	July	31	9
	Aug.	8	0
P. viridans	June	13	3
	July	15	1
	Aug.	3	0
Salticidae	June	6	1
	July	7	1
	Aug.	5	0
Thomisidae	June	2	0
	July	8	1
	Aug.	0	0
Web-building spiders	June	6	2
	July	1	0
	Aug.	0	0
Predaceous insects	June	3	2
	July	2	1
	Aug.	0	0
Combined total	June	54	14 (25.9%)a[b]
	July	64	13 (20.3%)b
	Aug.	16	0 (0.0%)ab
	Total	134	27 (20.1%)

[a] Fleahopper prey plus alternate prey.

[b] Percent fleahoppers in diet of combined predators. Values followed by the same letter are significantly different ($P < 0.05$, χ^2 test of independence).

significantly ($\chi^2 = 0.52$, df = 1, $P > 0.05$) between June and July (26 versus 20%) (Table 3) but declined significantly ($\chi^2 = 3.88$, df = 1, $P < 0.05$) from July to August (20 versus 0%) (Table 3).

In June, we found 24 prey-carrying *O. salticus* spiders with a fleahopper prey/all prey ratio of 1:4 (Table 3). In July, we collected 31 prey-carrying *O. salticus* spiders, with a corresponding ratio of approximately 1:3.5 (Table 3). This implies that overall, approximately one in four prey captured by *O. salticus* was a fleahopper during June and July.

Mussett et al. (1979) obtained a correlation ($r = 0.62$) between the abundance of combined predators and cotton fleahoppers. Whitcomb & Bell (1964) and Mussett et al. (1979) suggested that fleahoppers are among the cotton arthropods serving as a food source which help maintain the abundance of polyphagous predators. The high percentage of fleahoppers in the diet of polyphagous predators observed in this study (Table 3) supports Whitcomb & Bell's hypothesis.

Estimate of Predation Rate of *O. salticus*. This estimate was conducted in the middle of the cotton-growing season when the *O. salticus* population had a nearly uniform age–size class structure dominated by larger stages (mean body length 4.34 ± 0.23 mm, $n = 18$, on 20 July); low-SEM carapace width (1.55 ± 0.08 mm, $n = 18$) implies that the *O. salticus* population was at that time composed of individuals with similar energy requirements, which justifies the evaluation of a single predation rate for this entire group of larger spiders (see Methods).

The predation rate (Pd_a) of *O. salticus* was estimated with equation 1, using the following values: $F_t = 3.0 \pm 0.61$ ($\bar{x} \pm$ SE of four samples, $n = 74$, $n = 77$, $n = 77$, $n = 102$ observed spiders), $T_f = 24$ (based on Nyffeler et al. [1987a]), and $T_h = 49$ (mean value for penultimate–adult *O. salticus* [Nyffeler et al. 1987a]). Because the handling time is a function of the spiders' prey size (Edgar 1970), a low SE of mean prey length (2.72 ± 0.36 mm, $n = 10$) observed during midseason justifies the use of a single average T_h value for the entire group of larger *O. salticus*. On this basis, we estimated that an *O. salticus* spider captured, in the middle of the cotton-growing season, an average of approximately one prey daily ($Pd_a = 0.9$). This estimate is slightly lower than the daily predation rate of *O. salticus* assessed in another Texas cotton field (Nyffeler et al. 1987a) and in laboratory feeding tests (Guillebeau & All 1989), where the larger stages of this spider captured on the average a little more than one prey per day.

Because *O. salticus* is a polyphagous feeder (Nyffeler et al. 1987a), the obtained Pd_a value expresses the rate of predation on multiple prey species (see above). About every fourth prey organism captured by *O. salticus* was a cotton fleahopper (see above), which suggests that one fleahopper may have been killed per spider about every 4 d in the middle of the growing season ($Pd_c = 0.25$). This is a rough estimate that appears to be rather conservative compared with the Pd_c values for *O. salticus* evaluated in other studies. Ten to thirteen times higher mean Pd_c values estimated for *O. salticus* were reported by Breene et al. (1989a, 1990).

The average population density of *O. salticus*, in the middle of the growing season, was 1.48 ± 0.24 individuals per square meter (S_a value for 19 July) in the investigated cotton field, which implies that one fleahopper may have been killed per square meter about every 3 d ($Pd_c \times S_a = 0.25 \times 1.48 = 0.37$).

Killing Power of Dominant Predator, *O. salticus*. The killing power of the dominant predator species, *O. salticus*, was evaluated quantitatively based on estimates of predation rate, spider density, and fleahopper density.

The daily percentage mortality (M) of the cotton fleahopper caused by the most abundant spider species (*O. salticus*) in the middle of the growing season was assessed with equation 2. In the relative estimate, values used were $S_r = 29.50$ and $C_r = 48.50$ (mean value of 14 and 25 July) (Table 4), which resulted in $R_r = 0.61$. In the absolute estimate, values used were $S_a = 1.48 \pm 0.24$ and $C_a = 2.04 \pm 0.36$ (data for 19 July), which resulted in $R_a = 0.72$. Assuming that

Table 4. Numbers of cotton fleahoppers and striped lynx spiders counted per hour on cotton foliage in a field near College Station, TX, during summer 1988

Date	No. individuals/h[a]		Predator/ prey ratio $R_r = (S_r)/(C_r)$
	(C_r)	(S_r)	
4 July	92.9[b]	32.6	0.35
7 July	84.5[b]	31.0	0.37
9 July	76.0[c]	30.4	0.40
14 July	55.0[c]	27.8	0.51
25 July	42.0[c]	31.2	0.74
26 July	9.0[d]	32.0	3.60
4 Aug.	5.3[d]	34.0	6.42

Records made between 1200 and 1500 hours CST.

[a] C_r, cotton fleahoppers; S_r, striped lynx spiders. Abundance of striped lynx spider apparently not changing with time. Based on larger data (June to August), however, a visible change in the abundance of *O. salticus* with the progressing season was found (Fig. 1).

[b] All adult.

[c] >90% adult.

[d] <90% adult.

$Pd_c = 0.25$ is an accurate predation estimate (see above), the daily mortality was computed to be $M_r = 15\%$ per day (relative estimate) and $M_a = 18\%$ per day (absolute estimate), respectively. The two estimated values are of similar magnitude (only 3% difference). The other predaceous arthropods such as the green lynx spider *Peucetia viridans* (Hentz), jumping spiders, crab spiders, web-building spiders, predaceous Hemiptera, and red imported fire ants contributed additional mortality (Tables 1–3) (see also Breene et al. 1989a, b).

Because data for predators and prey were limited, fleahopper mortality could not be quantitatively assessed except for the middle part of the growing season. A comparison of predation records per hour (number of fleahopper prey counted per hour, monthly pooled data) in different months (Fig. 2) suggests a declining trend of fleahopper predation by the predator complex with the progressing season (decrease of ≈40% from June [≈0.5 record per hour] to July [≈0.3 per hour], down to zero in August) (Fig. 2). Observed predation on fleahoppers by *O. salticus* alone, however, did not differ visibly between June and July (≈0.2 record per hour). A low predation rate of *O. salticus* on fleahoppers was monitored in August (Table 3; Fig. 2) after the decline of fleahopper numbers in late July (Table 4).

Another way of examining the seasonal dynamics of predation on the cotton fleahopper is given by comparing feeding frequencies (predators eating a fleahopper per total predators, monthly pooled data) between months. The feeding frequency on fleahopper prey by the spider complex decreased significantly ($\chi^2 = 4.12$, df = 1, $P < 0.05$) from June (12 in 893 spiders eating a fleahopper) to July (12 in 1,994) and further declined significantly ($\chi^2 = 6.61$, df = 1, $P < 0.01$) from July to August (0 in 1,094).

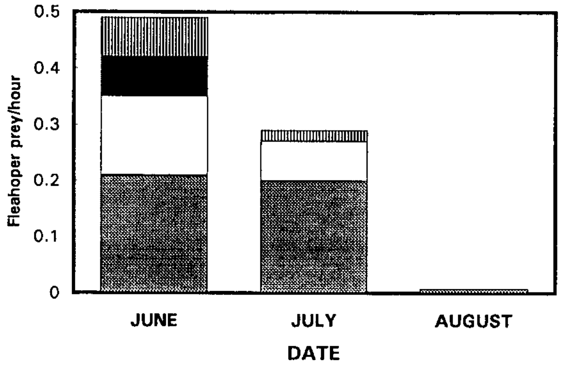

Fig. 2. Seasonal variation in the frequency of predation on the cotton fleahopper (measured as number of fleahopper prey records per observation hour) in a cotton field near College Station, TX. ▩, *O. salticus;* □, other nonweb-building spiders (including *Peucetia viridans*, Salticidae, and Thomisidae); ■, web-building spiders (including Araneidae, Dictynidae, and Theridiidae); ▥, insects (including *Solenopsis invicta* and predaceous Hemiptera). Monthly pooled data collected during daylight hours, June–August 1988.

Relative Importance of Various Predator Groups (Observational Versus Experimental Evidence). In another Texas cotton agroecosystem, Breene et al. (1989b) conducted a field experiment by releasing ≈30,000 fleahopper nymphs labeled with ^{32}P and thereafter recovered radioactive predators. Although this experimental design has the limitation that it cannot distinguish primary from secondary predation (Breene & Sterling 1988), it has the advantage that evidence is based on much larger samples compared with the very time-consuming visual observation method ($n = 282$ versus $n = 24$ for spiders) (Table 5). In addition to this, the ^{32}P method is advantageous by measuring the combined activity of diurnal and nocturnal predation. The observational data of our project (*OE* values in Table 1) and Breene's data are comparable because both studies were conducted in insecticide-free cotton fields in the same geographic area (near College Station, TX). Table 5 compares the relative importance of various predators between the two studies. The comparison reveals that the results of the present observational study are strongly supported by Breene's experimental work.

In our study, 89% of the predators found feeding on fleahopper prey (*OE*) were spiders, and 97% of all predation events recorded (total evidence, *OE* + *DE*) were attributable to spiders (Table 1). This is basically confirmed by the work of Breene et al. (1989b) and the observations of Reinhard (1926), who also concluded that spiders are superior as predators compared with the predaceous insects. In our study, the

Table 5. Relative importance of various spider taxa as predators of cotton fleahopper; comparison of two methods

	Observational evidence Spiders feeding on fleahopper[a]		Experimental evidence Radioactive spiders (previous feeding on fleahopper)[b]		Difference (*A*−*B*)
	No. events recorded	% Total (*A*)	No. events recorded	% Total (*B*)	
O. salticus	15	62.5	163	57.8	4.7
P. viridans	4	16.7	5	1.8	14.9
Salticidae	2	8.3	81	28.7	−20.4
Thomisidae	1	4.2	6	2.1	2.1
Other nonweb-building spiders	0	0.0	8	2.8	−2.8
Web-building spiders	2	8.3	19	6.7	1.6
Total	24	100	282	100	—

Both studies conducted in insecticide-free cotton fields near College Station.

[a] Numbers of spiders feeding on fleahoppers observed in a cotton field during summer 1988 (*OE*-values from Table 1).

[b] Numbers of radiolabeled spiders recovered with a D-Vac following release of radiolabeled fleahoppers in a cotton field (summers 1986–1987, data from Breene et al. 1989b). Predation evidence based on assumption that predators became radioactive while feeding on radiolabeled fleahoppers (Breene & Sterling 1988).

only insects predaceous on the fleahopper were two individuals of Hemiptera and one individual red imported fire ant (Table 1). Breene et al. (1988, 1989b) provided experimental evidence for red imported fire ants feeding on the fleahopper. They pointed out that the rate and extent of such ant predation cannot be reliably estimated using ^{32}P. In the course of this project, during 108 h of direct observation in the field, we witnessed only one case of a red imported fire ant (minor worker) carrying a wiggling fleahopper (Table 1). In other cases (not listed in Table 1), red imported fire ant workers were transporting dried-out (unnatural coloration) fleahopper carcasses, which suggests a scavenging foraging behavior. Thus, ant feeding traced by Breene et al. (1988, 1989b) using ^{32}P may consist of both scavenging and predation.

Among the spider predators found feeding on fleahoppers, <10% were web-building spiders (two feeding records, *OE*-values in Tables 1 and 5), which agrees with Breene's results where, likewise, a low proportion (<10%) of monitored predation activity was attributable to web-building spiders (Table 5). The flight paths of the fleahoppers spatially–temporarily coincide with the web positions of the spiders (M. N. & W.L.S., unpublished data). Based on the fairly large numbers of winged fleahoppers observed in the field during the first half of the growing season (Table 4), one may expect frequent capture of these insects in spider webs. However, <1 in 250 webs contained a spider feeding on fleahopper prey. This is a very low feeding frequency, indicating that the predation rates on fleahopper prey by web-building spiders are very low; the question arises whether this eventually reflects some type of web avoidance or prey defense–escape behavior by these insects (sensu Nyffeler & Benz 1981), but no avoidance or escape behaviors could be observed in the field (M. N. & W.L.S., unpublished data). Our data and those of Breene indicate that under the conditions of these studies, web-building spiders are of less importance than *Oxyopes* as predators of the fleahopper.

In our study (*OE* values) and in the experimental work by Breene et al. (1989b), ≈90% of the monitored spider predation on fleahoppers was attributable to the nonweb-building spiders (Table 5). A higher relative frequency of predation events attributable to jumping spiders was monitored in Breene's study compared with the present project. The apparent difference observed in *P. viridans* is based on a low number of predation records in both studies. *O. salticus* was the dominant predator of the fleahopper in both studies (more than half of the predation events recorded in Table 5). As in our study, high fleahopper mortality caused by lynx spider predation was also monitored by Breene et al. (1989b), indicating a high killing power of these predators.

The present observational project is based on the data of 1 yr (1988) only. Breene's project (1986–1987), however, was conducted in the same geographic area in an insecticide-free field; hence, the two projects complement each other, providing combined data over a continuous 3-yr period (1986–1988). The similarity of the predation patterns observed in the two projects (Table 5) provides strong mutual support for their accuracy.

Ecological Significance of Predation on Cotton Arthropods by *O. salticus*. The dominant predator in this study, *O. salticus* (Table 5), is generally considered a prominent agroecosystem spider species in the United States (Whitcomb & Eason 1967, Riechert & Lockley 1984, Young & Lockley 1985, Young & Edwards 1990). For a detailed predation analysis of *O. salticus*, see Young & Lockley (1986), Lockley & Young (1987), and Nyffeler et al. (1987a). As polyphagous feeders, the lynx spiders kill pest insects,

Table 6. Prey records obtained per hour; comparison between two insecticide-free cotton agroecosystems in Texas based on total evidence data (predators observed feeding plus fleahopper carcasses found in webs)

Predator taxon	Central Texas (summer 1988)[a]		East Texas (summer 1985)[b]	
	Total no. fleahopper prey	No. records/h[c]	Total no. fleahopper prey	No. records/h[d]
Nonweb-building spiders	22	0.20	0	0.00
Web-building spiders	72	0.67	3[e]	0.03
Predaceous insects	3	0.03	0	0.00
Combined total	97	0.90	3[e]	0.03

[a] Present paper.

[b] Based on Nyffeler et al. (1986; 1987a, b, c; 1988a, b; 1989), Dean et al. (1987).

[c] Total number of fleahopper prey divided by 108 h.

[d] Total number of fleahopper prey divided by 85 h.

[e] Fleahopper carcasses found in webs, but spiders not observed feeding (durable evidence) based on Nyffeler et al. (1987c, 1989).

insects of a neutral economic status, and predaceous arthropods as well. High levels of "intraguild predation" (sensu Polis et al. 1989) by lynx spiders were recorded in Texas cotton fields (Nyffeler et al. 1987a, b; 1992); the overall ecological and economic implications of this phenomenon, however, are not yet known.

Oxyopes salticus is predaceous on various cotton insect pests (Young & Lockley 1985, Nyffeler et al. 1990). Although no experimental evidence for "irreplaceable mortality" (sensu Sterling et al. 1989) of fleahoppers caused by *O. salticus* exists currently, these spiders show several characteristics suggesting that they are major predators of fleahoppers in the Texas cotton agroecosystem:

(1) They have good dispersal capabilities (Dean & Sterling 1985, 1990) and appear to be excellent colonizers well adapted for survival (foraging and reproducing) in the cotton agroecosystem (Dean & Sterling 1987, Nyffeler et al. 1987a). Therefore, they colonize cotton fields in high abundance relative to other predators (Table 1) (Johnson et al. 1986, Dean & Sterling 1987, Nyffeler et al. 1987a). Because these spiders can build up large numbers, they may sometimes become more abundant than their fleahopper prey (Table 4) (Breene et al. 1989a). Because of their polyphagous feeding behavior, these spiders can survive in a field with low fleahopper numbers (Nyffeler et al. 1987a).

(2) They are among the first predators arriving in spring in the cotton fields (Nyffeler et al. 1987a). Even the smaller immature *O. salticus* (<3 mm long) are already capable of overpowering fleahoppers (Nyffeler et al. 1992).

(3) They forage for prey throughout the entire cotton plant, from the top to the ground and even under leaves, which enables them to detect fleahoppers hiding in refuges (Whitcomb et al. 1963; Dean et al. 1982; M. N., unpublished data).

(4) They forage for prey day and night (nocturnalism reported by Nyffeler et al. [1987a]). Thus, this spider is a "time generalist," which increases the probability of encountering fleahopper prey.

(5) These spiders readily feed on the various stages of the fleahopper (Table 1) and exhibit a sigmoid functional response to fleahopper availability (Breene et al. 1990).

The high values of fleahopper mortality estimated in our study and in that of Breene et al. (1989b) provide evidence that these spiders contribute to fleahopper mortality in Texas cotton. The contribution of these spiders as mortality agents, however, varies between the different fields and within different years because of the spatial and temporal fluctuations of the abundance patterns of spiders and fleahoppers (Dean & Sterling 1987, Breene et al. 1989a). We recorded ≈30 times higher frequency of predation on fleahoppers compared with another Texas cotton field (0.90 versus 0.03 prey record per hour) (Table 6). Consequently, the economic benefit attributable to these predators varies in different situations.

With the TEXCIM50 model (Sterling et al. 1992b), the economic value of lynx spiders, other spiders, fire ants, and predaceous bugs in the control of cotton fleahoppers can be forecast for each field. The value of spiders and other predators depends on many variables such as predator density, cotton fleahopper density, weather, insecticides, crop value, other herbivores, crop growth, etc. TEXCIM50 takes these and many other factors into consideration in forecasting the value of spiders. During a 5-yr study, the value of all predators of cotton fleahoppers ranged from $2.12 to $38.30 per ha (Sterling et al. 1992a).

Few quantitative evaluations of the predation effect of spiders have been published (review in Nyffeler & Benz 1987, 1989). The mortality estimates presented here suggest that nonweb-building spiders can exert predation pressure on herbivores, which agrees with the quantitative evaluations by Van Hook (1971) and Kiritani et al. (1972) in other habitats.

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BIOLOGICAL CONTROL

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

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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 ≈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 & Futuyma 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 ≈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-

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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[a]										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[b]	1	2	8
Lepidoptera	0	1	0	0	0	0	0	0	1	3[c]	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	—[d]	100	—[e]	—[e]	16	23	—[e]	111	15	44	>300

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

[b] Including one adult cotton fleahopper.

[c] Including one bollworm moth.

[d] Active searcher that does not spin webs.

[e] 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 glomosus* (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 ≈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 manpower 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

	Relative utilization of prey group (j)[a]										
	(1)	(2)	(3)	(4)	(5)	(6)	(7)	(8)	(9)	(10)	(11)
Spider species[b]											
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.

[a] (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.

[b] *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):

$$C_{1,2} = 1 - ½ \Sigma \,|(p_{1j} - p_{2j})|, \qquad (1)$$

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) ± 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:

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

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

where

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

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

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):

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

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

The test statistics has a χ^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 χ^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 1×10^{-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):

$$H' = -\Sigma p_{ij} \ln p_{ij}, \qquad (8)$$

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[a]									
	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

[a] *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):

$$H'/H'_{max} = H'/\ln R. \qquad (9)$$

[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:

$$\mathrm{var}(H') = \frac{\Sigma\, p_{ij}\ln^2 p_{ij} - (\Sigma\, p_{ij}\ln p_{ij})^2}{N} + \frac{R-1}{2N^2} + \ldots. \qquad (10)$$

[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):

$$t = \frac{H_1' - H_2'}{[\mathrm{var}(H_1') + \mathrm{var}(H_2')]^{1/2}}. \qquad (11)$$

The null hypothesis is $H_o : H_1' = H_2'$. The degrees of freedom of the test is (Poole 1974):

$$\mathrm{df} = \frac{[\mathrm{var}(H_1') + \mathrm{var}(H_2')]^2}{[\mathrm{var}(H_1')^2/N_1 + \mathrm{var}(H_2')^2/N_2]}, \qquad (12)$$

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:

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

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[a]	Leafhoppers[a]	Fire ants[b]	Diptera	Coleoptera	Araneae	Heteroptera
F. pyramitela	+0.10	-1.00	-1.00	-1.00	-1.00	-1.00	-1.00
U. glomosus	+0.09	-1.00	-0.37	+0.33	-1.00	-1.00	-1.00
T. laboriosa	+0.02	+0.08	-0.62	+0.71	-1.00	-1.00	-1.00
L. mactans	-0.90	-0.71	+0.70	-1.00	+0.95	-0.67	-1.00
C. turbinata	-0.06	-0.09	-0.73	+0.73	+0.43	-1.00	-1.00
D. segregata	-0.14	-1.00	-0.08	+0.87	-1.00	-1.00	-1.00
G. heptagon	-0.16	+0.25	-0.04	+0.78	+0.43	-1.00	0.00
N. arabesca	-0.25	-0.09	-1.00	+0.43	+0.97	-1.00	+0.67
A. stellata	-0.36	+0.20	-0.86	+0.88	+0.95	-0.33	+0.33
O. salticus	-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).

[a] Homoptera.

[b] Hymenoptera.

(0.08–0.94, overall mean = 0.57 ± 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 Petraitis' (1979) test statistics (see Ludwig & Reynolds 1988). For forty-three of the forty-five examined species pairs computed χ^2s 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 χ^2s 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 spider'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 ± 0.04 SEM], *A. stellata* [0.58 ± 0.05], *F. pyramitela* [0.59 ± 0.09], *U. glomosus* [0.64 ± 0.09], *T. laboriosa* [0.65 ± 0.09], *D. segregata* [0.65 ± 0.07], *C. turbinata* [0.68 ± 0.07], *G. heptagon* [0.69 ± 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[a]
Oxyopidae		
Oxyopes salticus	Small active searcher on plants and near the ground	67.2
Linyphiidae		
Frontinella pyramitela	≈Horizontal, small space webs (not sticky), on plants	<1.0
Uloboridae		
Uloborus glomosus	≈Horizontal, small orb webs (cribellate silk), on plants	<1.0
Theridiidae		
Latrodectus mactans (small- to medium-sized immatures)	Small to medium-sized space webs (partly sticky), near and on the ground	1.0
Dictynidae		
Dictyna segregata	Small space webs (cribellate silk), on plants	3.3
Tetragnathidae		
Tetragnatha laboriosa	Small (sticky) orb webs, on plants	2.2
Araneidae		
Cyclosa turbinata	Small (sticky) orb webs, on plants	<1.0
Gea heptagon	Small (sticky) orb webs, on plants	1.1
Neoscona arabesca	≈Vertical, large (sticky) orb webs, between and on plants	<1.0
Acanthepeira stellata	≈Vertical, large (sticky) orb webs, between and on plants	3.5

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

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

[a] 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 ± 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 ± 0.03) (Table 3). This indicates that *L. mactans* was an 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 (≈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 ≈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 (≈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 (Bohmfalk 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 ≈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).

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FORUM

How Spiders Make a Living

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ABSTRACT Although the beneficial status of the spiders as insectivores has been widely recognized for quite some time, biologists by and large seem to be rather unfamiliar with the specific feeding habits of this very diverse order. We present an overview of the feeding patterns of 10 groups of common agroecosystem spiders to inform entomologists and ecologists concerned with issues of natural biological control. The various spider groups discussed in this article exhibit a very diverse range of life styles and foraging modes, which is reflected in the diversity of their feeding patterns. Implications of the insectivorous activities of these predators for natural pest control are discussed.

KEY WORDS spiders, predation, diets

SPIDERS (ARANEAE) ARE a very diverse order of ubiquitous carnivores within the class Arachnida. At the present time, >30,000 species of spiders are described (Coddington & Levi 1991). Over 3,000 species occur in North America alone (Young & Edwards 1990). The vast majority of spiders occupy terrestrial habitats. Some lycosids and pisaurids, however, can walk and *sail* on the water surface (and at times even dive and swim under water); they forage on aquatic and semiaquatic organisms when they inhabit marshes, flooded rice fields, and other wetlands (Greenstone 1979, Oraze & Grigarick 1989, Zimmermann & Spence 1989). One agelenid species (the *water spider*) actually lives under water (see subsection *Foraging Patterns of Web Weavers*). Most spiders are highly cannibalistic solitary creatures and practice bizarre courtship rituals (Turnbull 1973). Several species produce sounds (acoustic communication) during courtship and agonistic displays (Rovner 1975, Uetz & Stratton 1982). These animals live in a world full of vibrations (e.g., Rovner & Barth 1981). Sexual dimorphism occurs in many species, the female normally being significantly larger than the male (hereafter *adult length* always refers to the female). Spiders disperse by walking on the ground, by using silk-thread bridges between plants, as well as *ballooning* through the atmosphere from place to place on silken threads (Foelix 1982, Dean & Sterling 1985, Young & Edwards 1990). All spiders produce silk from abdominal glands though only the *web weavers* construct webs that are used to catch prey. Spiders are equipped with a pair of jaws (chelicerae) and possess venom glands (exception, Uloboridae do not produce venom). Immobilization of prey is assisted by the use of silk and by the injection of venom. These animals cannot ingest solid food and must, therefore, inject digestive enzymes into the immobilized prey (external digestion) and then suck in the dissolved tissue in liquid form. Spiders generally have a very low rate of metabolism compared with other poikilothermic organisms of comparable body weight (Greenstone & Bennett 1980). They can store energy and starve for considerable time periods, which makes them excellent survivors under conditions of food shortage (see Nyffeler & Breene 1990a).

According to traditional foraging theory, spiders are considered to be predators of live, moving prey only (e.g., Turnbull 1960, 1973). More recent studies have modified this view when evidence was found that spiders utilize a much broader range of foraging strategies, including feeding on arthropod eggs (oophagy), dead animals (scavenging), plant pollen, and even artificial diets (see McDaniel & Sterling 1982, Nyffeler et al. 1990a). Stealing of prey from other spiders (kleptoparasitism) plays an important role as an alternative foraging strategy of various web spinners (Vollrath 1987). Spiders have been reported feeding on a wide range of different animal groups including some unusual prey such as small mice, bats, birds, fish, crayfish, crabs, frogs, lizards, snakes, and scorpions (Nyffeler & Benz 1981, McCormick & Polis 1982); however, in general they tend to concentrate on insect prey and to a lesser degree on other spiders (Wise 1993). Most spider species forage on multiple prey species (generalist predators), which Greenstone (1979) has suggested may be advantageous by optimizing a balanced essential amino acid composition in the diet. Spiders feed predominantly on small-sized prey relative to their own size (prey length ≤ predator length) (Nyffeler & Benz 1981, Wise 1993); feeding ex-

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periments with a variety of spider species and a model prey (crickets) conducted in the laboratory revealed that the optimal prey length ranges from 50–80% of the spider length (Nentwig 1987).

Spiders are among the numerically dominant insectivores in terrestrial ecosystems and exhibit a very diverse range of life styles and foraging behaviors (Turnbull 1973, Wise 1993). Two basic groups of foraging strategies can be distinguished: (1) *web spiders* (i.e., foraging with a catching web) (Tables 1–5), and (2) *hunters* or *wanderers* (i.e., foraging without the use of a web) (Tables 6–9). Some prominent representatives of web spinning spiders are orb weavers (Araneidae and Tetragnathidae), sheet web weavers (Linyphiidae), mesh web weavers (Dictynidae), comb-footed spiders (Theridiidae), and funnel-web weavers (Agelenidae). Prominent representatives of hunters are wolf spiders (Lycosidae), lynx spiders (Oxyopidae), crab spiders (Thomisidae), and jumping spiders (Salticidae). These 10 families are among the most abundant spider predators in agroecosystems (e.g., Whitcomb 1974, Luczak 1979, Nyffeler 1982, Dean & Sterling 1987); and because of their high colonization power and insectivorous feeding behavior, they are of interest to the entomologist and ecologist concerned with issues of natural biological control (compare Turnbull 1973, Riechert & Lockley 1984, Nyffeler & Benz 1987, Sterling et al. 1989). In this article, we present an overview of the feeding patterns of these 10 groups of spider predators.

Materials and Methods

There are different methods to evaluate spider diets. The prey spectra of spiders can be assessed by directly collecting prey organisms or their remains from spider webs (i.e., prey analyses of web weavers) (Tables 1–5), or collecting spiders with prey in their chelicerae in the field (i.e., prey analyses of hunters) (Tables 6–9). Spider predators (along with their prey) are placed in 70% ethyl alcohol and later identified in the laboratory, using a dissecting microscope (see Nyffeler et al. [1987b, 1989] for details). Additionally, sophisticated methods (e.g., release of prey radiolabeled with ^{32}P, ELISA techniques, chromatography) are used to detect feeding on insect eggs, tiny aphids, and mites, and other *hidden* predation activities that may otherwise be overlooked with visual observation methods (Greenstone 1979, McDaniel & Sterling 1982, Nyffeler et al. 1990a). The prey spectra presented in this article (Tables 1–9) are all based on observational data from field studies previously published in literature (see references in tables); a large portion of this information had been collected in the course of research projects conducted at Texas A&M University and the Swiss Federal Institute of Technology, respectively.

Results and Discussion

Foraging Patterns of Web Weavers. High feeding frequencies (up to 90% spiders feeding simultaneously during peak activity) were observed in field populations of certain larger-sized orb weavers (Araneidae) that rebuild (recycle) their webs daily (Nyffeler 1982). The high feeding frequencies indicate that the web is a very efficient prey capturing device. Large orb weavers often kill prey in excess of their energy requirements. As many as 1,000 small insects have been found entangled at one time in a single orb web; however, not all insects caught by the web are eaten. Sheet-web weavers, mesh web weavers, comb-footed spiders, and funnel-web weavers that do not renew their nets daily, feed less frequently (<10% spiders feeding simultaneously) (M.N. & Benz 1988a; unpublished data). Relatively low feeding frequencies were also observed in small orb weavers that spin small delicate nets (LeSar & Unzicker 1978, Culin & Yeargan 1982, Nyffeler 1982). The designs and functions of different types of spider webs are discussed explicitly by Eberhard (1990).

Orb Weavers. Orb weavers (Araneidae and Tetragnathidae) spin spiraling sticky webs on and between plants in a wide variety of field crops and natural habitats. Many orb weavers spin their webs preferentially at the beginning or end of the nocturnal period (Foelix 1982). Orb weavers wait in a head-down position for prey in the web center (hub) or in a retreat connected to the hub by a signal line. Alerted by the vibrations of an insect struggling in the web, the spider rushes to its victim; subsequently, the prey is wrapped in silk followed by a venomous bite (in some cases, the prey is first bitten and then wrapped) (Foelix 1982). The immobilized prey is later carried to the hub or retreat where it is eaten. *Tetragnatha laboriosa* Hentz (Tetragnathidae), a slender elongate orb weaver (≈6 mm adult length) of yellowish color with a silvery abdomen, is one of the most abundant spider predators of field crops in the United States (Young & Edwards 1990). With their fragile webs (≈10–15 cm in diameter) oriented at various angles, these spiders trap small soft-bodied insects predominantly of the orders Diptera and Homoptera (Table 1). Leafhoppers (Cicadellidae) represented an essential component (>30% of total) in the prey of *T. laboriosa* in soybean fields in Illinois and Kentucky (Table 1) (LeSar & Unzicker 1978, Culin & Yeargan 1982). In a cotton field in Texas, the prey of this species was composed largely of aphids (75% of total) (Table 1; Nyffeler et al. 1989). Coleoptera are often excluded as prey of small orb weavers (≤5% of total prey) (Table 1). *T. laboriosa* was seen eliminat-

Table 1. Prey spectrum (in percent) of small orb-weaver, *Tetragnatha laboriosa* Hentz (Tetragnathidae), based on three different field studies

Prey type	Study 1[a]	Study 2[b]	Study 3[c]
Diptera	40.5	17.5	12.2
Cicadellidae	36.7	50.0	7.3
Aphididae	0.0	12.5	78.0
Other Homoptera	1.3	7.5	0.0
Heteroptera	17.7	2.5	0.0
Coleoptera	0.0	5.0	0.0
Formicidae	2.6	2.5	2.5
Lepidoptera	0.0	2.5	0.0
Others	1.2	0.0	0.0
Total	100.0	100.0	100.0
No. prey records	79	40	41

[a] In soybeans in Illinois (LeSar & Unzicker 1978).
[b] In soybeans in Kentucky (Culin & Yeargan 1982).
[c] In cotton in Texas (Nyffeler et al. 1989).

ing entangled beetles from the web by the following tactics: (1) by the spider violently shaking the web until the beetle fell, (2) by ignoring the beetle until it worked itself free and could escape, (3) by cutting the web around an adult beetle allowing it to drop from the web (LeSar & Unzicker 1978, Culin & Yeargan 1982). Fragile, small nets of small orb weavers such as *T. laboriosa* are suitable for interception of small insects only (narrow feeding niche) (LeSar & Unzicker 1978, Culin & Yeargan 1982).

In contrast, large orb weavers of the family Araneidae are able to overcome the defenses of a wider diversity of prey types, with their strong nets (broad feeding niche), which include insects with strong sclerotization, chemical protection, and aggressive behavior (Culin & Yeargan 1982, Nentwig 1987). Large orb weavers of the genus *Argiope* frequently kill grasshoppers (Orthoptera) and large stinging bees (including *Apis mellifera* L.) (Table 2; Nyffeler & Breene 1991). Grasshoppers (genera *Melanoplus, Encoptolophus,* and *Schistocerca*) constituted 18% of the total prey intercepted in the ≈30 cm diameter webs of *Argiope aurantia* Lucas in a cotton field of East Texas (Table 2); this spider (≈20–25 mm adult length) kills prey up to ≈200% of its own size (Nyffeler et al. 1987a).

Table 2. Prey spectrum (in percent) of large orb-weavers (Araneidae) based on three different field studies

Prey type	Study 1[a]	Study 2[b]	Study 3[c]
Diptera	26.8	77.8	69.2
Aphididae	30.0	0.0	11.1
Orthoptera	17.9	12.2	0.1
Apis mellifera L.	1.1	4.4	15.5
Other Apidae	2.1	0.0	0.0
Formicidae	8.4	0.0	0.0
Other Hymenoptera	1.0	0.0	2.2
Coleoptera	5.8	1.1	0.0
Araneae	0.0	3.3	0.0
Lepidoptera	0.0	0.0	0.0
Others	6.9	1.2	1.9
Total	100.0	100.0	100.0
No. prey records	190	90	215

[a] *Argiope aurantia* Lucas in cotton in Texas (Nyffeler et al. 1987a).
[b] *Argiope bruennichi* (Scopoli) in grassland in Switzerland (Nyffeler 1982).
[c] *A. bruennichi* in grassland in Switzerland (Nyffeler 1982).

Orb weavers generally seem to be rather ineffective in trapping moths and butterflies. Eisner et al. (1964) stated: "Moths, by virtue of the loose scales that cover their wings and bodies, are admirably adapted to elude capture by orb-weaving spiders. Rather than sticking to the web, they may simply lose some of their scales to the viscid threads, and fly on." Nyffeler (1982) recorded that flying lepidopterans made up a very low percentage of the prey of various temperate orb weaver species. Several species of orb weavers, however, spin highly modified orb webs (e.g., *ladder web* and *bolas spider*) that function as effective moth traps (Foelix 1982, Eberhard 1990).

Sheet-Web Weavers. The family of sheet-web weavers (Linyphiidae) includes the subfamilies Linyphiidae-Linyphiinae and Linyphiidae-Erigoninae (=Erigonidae or Micryphantidae). These spiders hang inverted below the sheet waiting for prey, which they pull through the sheet (Wise 1993). Linyphiid webs include some viscid silk though it does not seem to be much involved in prey capture. Various small to medium-sized species of the subfamily Linyphiinae can reach high abundance in woodlands and grasslands where they kill numerous small insects primarily from the orders Diptera, Hymenoptera, Homoptera, and Heteroptera (Turnbull 1960, Nyffeler & Benz 1981). Lepidopterans and coleopterans often escape from the fragile sheet webs and, thus, compose an insignificant fraction of these spiders' diet (Turnbull 1960). Dwarf spiders of the subfamily Erigoninae (*Erigone* spp. and *Oedothorax* spp.), <3 mm in length, numerically dominate the spider faunas on the ground surface of agricultural fields in the temperate-northern zones (Sunderland et al. 1986, Nyffeler & Benz 1988a). With fragile small sheet webs spun horizontally over small depressions on the ground, these tiny spiders capture small soft-bodied insects, including numerous springtails (Collembola), dipterans, and homopterans (Table 3). Agriculturally harmful cereal aphids can form a significant portion (≈12–40%) in the prey of the dwarf spiders in European winter wheat fields (Table 3) (Sunderland et al. 1986, Nyffeler & Benz 1988a). Green rice leafhoppers, *Nephotettix cincticeps* (Uhler), and brown planthoppers, *Nilaparvata lugens* (Stal), composed ≈60% of the prey of *Oedothorax insecticeps* Boes. & Str. in rice fields in Asia (Table 3; Kiritani et al. 1972).

Mesh-Web Weavers. Mesh-web weavers (Dictynidae) are small spiders (≤3 mm in length) of brownish, greyish, or green color that use the

Table 3. Prey spectrum (in percent) of sheet-web weavers (Linyphiidae) based on three different field studies

Prey type	Study 1[a]	Study 2[b]	Study 3[c]
Nilaparvata lugens (Stal)	0.0	0.0	23.9
Nephotettix cincticeps (Uhler)	0.0	0.0	38.9
Aphididae	38.7	12.1	—[d]
Collembola	37.8	71.7	—[d]
Diptera	13.5	5.6	—[d]
Thysanoptera	—[d]	4.0	—[d]
Araneae	0.0	1.5	16.3
Others	10.0	5.1	20.9
Total	100.0	100.0	100.0
No. prey records	111	198	226

[a] *Erigone* spp./*Oedothorax* spp. in winter wheat in Switzerland (Nyffeler & Benz 1988a).

[b] Various linyphiid species in winter wheat in England (Sunderland et al. 1986).

[c] *Oedothorax insecticeps* Boes. & Str. in rice fields in Japan (Kiritani et al. 1972).

[d] Information not available.

Table 4. Prey spectrum (in percent) of comb-footed spiders (Theridiidae) based on three different field studies

Prey type	Study 1[a]	Study 2[b]	Study 3[c]
Solenopsis invicta (Buren)	0.0	75.3	0.0
Other Formicidae	92.0	0.4	0.0
Coleoptera	0.0	15.1	3.1
Diptera	0.0	0.0	27.8
Aphididae	0.0	4.6	42.6
Cicadellidae	3.0	0.8	0.0
Thysanoptera	0.0	0.0	9.0
Ephemeroptera	0.0	0.0	7.6
Others	5.0	3.8	9.9
Total	100.0	100.0	100.0
No. prey records	101	258	223

[a] *Achaearanea riparia* (Blackwall) under overhanging grass in Switzerland (Nyffeler & Benz 1981).

[b] *Latrodectus mactans* (F.) in cotton in Texas (Nyffeler et al. 1988).

[c] *Theridion impressum* L. Koch in wheat fields in Switzerland (Nyffeler 1982).

calamistrum to comb out *cribellate silk* from a sieve-like plate just forward of the other spinnerets called the cribellum. Soft-bodied insects, predominantly small adult dipterans and homopterans, are intercepted in the small irregular mesh webs that the dictynids spin on leaves of various field crops and wild plants (Nyffeler & Benz 1981, Nentwig 1987). Agriculturally harmful dipterans and aphids can compose a high percentage in the diet of dictynid spiders (Heidger & Nentwig 1989). In other studies, dictynids were recorded foraging on small bugs (Heteroptera) (Nyffeler et al. 1992b).

Comb-Footed Spiders. This family (Theridiidae) of small to medium-sized species, are characterized by a globular abdomen. Theridiids spin irregular webs and throw viscid silk on their victim before biting it (Nentwig 1987). Theridiids are, in general, exceedingly polyphagous (Nyffeler & Benz 1981). However, in environments where ants occur in large numbers, these spiders can switch to predominantly feeding on ants (myrmecophagy; Table 4) (MacKay 1982, Nyffeler et al. 1988). Ants compose >90% of the prey of the European species *Achaearanea riparia* (Blackwall) (≈3.5 mm adult length) under overhanging grass (Table 4). Myrmecophagy was also observed in the southern black widow spider, *Latrodectus mactans* (F.), a dangerously venomous species whose black colored females (≈10 mm in length) show a distinct red hourglass marking on the ventral part of the abdomen. *L. mactans* was observed to capture primarily red imported fire ants, *Solenopsis invicta* (Buren), (75% of total prey; Table 4) in cotton fields of East Texas, where this spider builds 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 plants (Nyffeler et al. 1988). Black widow immatures, third instar or older, can capture fire ant workers. Black widow spiders also frequently capture beetles (15% of total prey; Table 4) including the boll weevil, *Anthonomus grandis grandis* Boheman (Whitcomb 1974, Nyffeler et al. 1988). The western widow spider, *Latrodectus hesperus* Chamberlin & Ivie, known to feed primarily on various beetles (Pratt & Hatch 1938), was observed foraging on harvester ants in California (MacKay 1982). Some theridiids (*Steatoda* spp. with ≈6 mm adult length) feed primarily on a diet of various flies and meal-infesting insects in stables and barns (Nyffeler & Benz 1987). Aphids constituted ≈10–90% of the prey of theridiids in European field crops (Nyffeler & Benz 1981).

Small kleptoparasitic theridiids, *Argyrodes* spp. (≈4 mm adult length), live in the webs of other spider species and forage by stealing prey from the host or taking prey below the threshold of acceptability (in size) of the host, or occasionally attacking the host or its young (Nyffeler et al. 1987a, Vollrath 1987).

Funnel-Web Weavers. These weavers (Agelenidae) trap their prey by means of funnel-like sheet webs. At the entrance of the funnel, the spider waits for prey. When an insect lands on the sheet, the spider runs quickly to the victim, bites it, and carries it to the funnel entrance where feeding takes place. Mass occurrences of *Agelena labyrinthica* (Cl.), a dark brown European species, with ≈10 mm adult length, can sometimes be seen in minimally disturbed grassland (old fields). In the strong extensive funnel webs, these spiders capture a wide variety of different insect groups (Table 5), which includes at times numerous agriculturally harmful lepidopterans from the family Pieridae. Honey bees, *A. mellifera*, and grasshoppers (Orthoptera) constitute high proportions in the prey of this spider in some habitats (Table 5; Nyffeler 1982).

In the litter of European woodlands, the dark brown *Coelotes terrestris* (Wider) (≈10 mm

Table 5. Prey spectrum (in percent) of funnel web-weavers (Agelenidae) based on three different field studies

Prey type	Study 1[a]	Study 2[b]	Study 3[c]
Apis mellifera L.	23.3	1.9	0.0
Formicidae	13.3	5.7	1.0
Other Hymenoptera	8.3	1.9	1.0
Orthoptera	0.0	26.4	0.0
Coleoptera	5.0	7.5	64.0
Lepidoptera	18.3	37.7	0.0
Diptera	11.7	15.1	17.0
Trichoptera	10.0	0.0	0.0
Dermaptera	0.0	0.0	8.0
Other	10.1	3.8	9.0
Total	100.0	100.0	100.0
No. prey records	60	53	306

[a] *Agelena labyrinthica* (Cl.) in grassland in Switzerland (Nyffeler 1982).

[b] *A. labyrinthica* in grassland in Switzerland (Nyffeler 1982).

[c] *Coelotes terrestris* (Wider) in hedges in Germany (Petto 1990).

adult length) builds tube-like funnels that end several centimeters under ground. Most of the remains found in such ground funnels were the elytra of beetles (including numerous Carabidae), which indicates that *C. terrestris* concentrates largely on beetle prey (Table 5; Nyffeler & Benz 1981, Petto 1990). The hard-sclerotized beetles are probably not optimal diet for most smaller-sized spiders, because the chelicerae cannot penetrate the thick cuticle of these insects (Nentwig 1987). Some spider species, which inhabit microhabitats rich in beetle prey such as *C. terrestris*, exhibit a specialized predatory behavior by biting into the intersegmental membranes of beetles (Nentwig 1987). Spiders that live in tubes under ground, e.g., Atypidae, Ctenizidae, and Eresidae (≈10–15 mm in length), concentrate largely on beetle prey (Nyffeler & Benz 1981).

Another agelenid, the water spider *Argyroneta aquatica* Clerck (≈10 mm adult length), lives in a bell (air bubble attached to water plant) under water in ponds and streams. This palaearctic species mostly hunts fly larvae and small crustaceans (Foelix 1982). (Recently *Argyroneta* has been placed into its own family, Argyronetidae [Platnick 1993]).

Foraging Patterns of Hunters. Low feeding frequency (≤10% spiders feeding simultaneously in a given population) was observed in each of the four families of hunters described in this article (wolf spiders, lynx spiders, crab spiders, and jumping spiders) (Nyffeler & Breene 1990a). With a visual method based on average percentage of spiders with prey in their chelicerae observed in the field, average hunting (searching) time, and handling time assessed in the laboratory, the predation rate (number of prey per spider per day) of a spider individual can be roughly estimated (Nyffeler et al. 1987b). With this method we estimated that adult wolf spiders and lynx spiders may capture an average of ≈1 prey per spider per day in the field (Nyffeler & Benz 1988b, Nyffeler et al. 1992a). Field populations of hunting spiders were observed in an underfed condition by researchers in North America, Europe, and Japan (see Nyffeler & Breene [1990a] for a review). Apparently, low feeding frequency is a pattern characteristic for spiders foraging without a web in the natural environment (Zimmermann & Spence 1989, Wise 1993). Significantly higher feeding frequencies can be observed in laboratory experiments when food is offered ad libitum (Nyffeler & Breene 1990a, Nyffeler et al. 1992a). High levels of cannibalism, observed in hunting spiders, may be crucial for their survival under conditions of food limitation.

Wolf Spiders. These spiders (Lycosidae) are small to large-sized animals, characterized by the specific arrangement of their eight eyes; they form three rows with the anterior row consisting of four small eyes and the two back rows consisting each of two larger eyes. These spiders are vagrant hunters that forage on the ground surface well-camouflaged by their brownish to greyish coloration. Contrary to common belief, wolf spiders do not necessarily run down their prey (Wise 1993). More recent studies suggest that they tend towards a *sit-and-wait* foraging strategy. With their stout chelicerae they chew down their prey to a "meat ball" (Kiritani et al. 1972). Wolf spiders of the genus *Pardosa* (5–8 mm adult length) are often characterized as diurnal foragers (e.g., Yeargan 1975); but nocturnal predation activities could be monitored as well (Whitcomb 1974, Hayes & Lockley 1990). *Pardosa* spp. wolf spiders are abundant in field crops, grasslands, and woodlands where they forage on small soft-bodied arthropods. Their diet includes springtails (Collembola), small dipterans, and homopterans (Table 6; Edgar 1970, Nyffeler & Benz 1988b, Nyffeler & Breene 1990a). Agriculturally harmful cereal aphids can constitute an essential portion in the diet of *Pardosa* spp. in European winter wheat fields (Table 6; Nyffeler & Benz 1988b). Leafhoppers and dipterans constitute essential components in the diet of *Pardosa ramulosa* (McCook) in field crops in California (Table 6; Yeargan 1975, Oraze & Grigarick 1989). In rice fields in Asia, green rice leafhoppers, *N. cincticeps*, and brown planthoppers, *N. lugens*, composed ≈80% of the diet of wolf spiders (Table 6; Kiritani et al. 1972). Mosquitoes (*Aedes*), shore flies (*Ephydra*), and bugs (waterboatman *Trichocorixa*) are the primary food source for *P. ramulosa* in marshes (Greenstone 1979).

Large nocturnal wolf spiders, genera *Rabidosa* and *Hogna* (previously known as *Lycosa*, ≈15–20 mm adult length), often feed on bulky prey including large grasshoppers, crickets, bee-

Table 6. Prey spectrum (in percent) of wolf spiders (Lycosidae) based on three different field studies

Prey type	Study 1[a]	Study 2[b]	Study 3[c]
Nilaparvata lugens (Stål)	0.0	0.0	24.9
Nephotettix cincticeps (Uhler)	0.0	0.0	52.6
Other Cicadellidae	0.0	19.3	—[d]
Aphididae	27.1	4.8	—[d]
Diptera	27.1	22.1	—[d]
Collembola	25.4	1.8	—[d]
Heteroptera	0.0	11.5	—[d]
Orthoptera	0.0	6.3	—[d]
Coleoptera	5.1	6.0	—[d]
Araneae	6.8	19.6	8.9
Others	8.5	8.6	13.6
Total	100.0	100.0	100.0
No. prey records	59	331	1,553

[a] *Pardosa* spp. in winter wheat in Switzerland (Nyffeler & Benz 1988b).

[b] *Pardosa ramulosa* (McCook) in alfalfa fields in California (Yeargan 1975).

[c] *Pardosa* (=*Lycosa*) *pseudoannulata* (Boes. & Str.) in rice fields in Japan (Kiritani et al. 1972).

[d] Information not available.

tles, noctuid moths, and other spiders (Van Hook 1971, Whitcomb 1974, Hayes & Lockley 1990).

Lynx Spiders. These predators (Oxyopidae) are characterized by the erect long spines on their legs and by a hexagonal eye arrangement. Lynx spiders can be active day or night (Nyffeler et al. 1987b). The striped lynx spider, *Oxyopes salticus* Hentz, a light-colored species with an average adult length of ≈6 mm, was found to be the most abundant spider predator in cotton fields and other agricultural crops in parts of the southern United States (Dean & Sterling 1987, Young & Edwards 1990). *O. salticus* is a pouncing hunter that actively searches the plant surface for prey. This spider captures a wide variety of small-sized arthropods (up to ≈6 mm maximum prey length) and shows considerable flexibility in switching its dietary composition in response to prey availability (Table 7). Small bugs (Heteroptera) apparently are optimal diet for *O. salticus* (Lockley & Young 1987; Agnew & Smith 1989; Breene et al. 1990; Nyffeler et al. 1992a, b). Lockley & Young (1987) reported that *O. salticus* fed heavily on tarnished plant bugs, *Lygus lineolaris* (P. de B.) (40% of total prey), cotton fleahoppers, *Pseudatomoscelis seriatus* (Reuter) (8%), and other bugs (6%) in a cotton field in Mississippi (Table 7). In a cotton agroecosystem in Texas, *O. salticus* preyed heavily on cotton fleahoppers (24% of total prey; Table 7), but in another cotton area with low incidence of fleahoppers and other *true* bugs, red imported fire ants (*S. invicta*) were most frequently captured (22% of total prey; Table 7) (Nyffeler et al. 1987b, 1992a).

Table 7. Prey spectrum (in percent) of lynx spider, *Oxyopes salticus* Hentz (Oxyopidae), based on three different field studies

Prey type	Study 1[a]	Study 2[b]	Study 3[c]
Pseudatomoscelis seriatus (Reuter)	8.3	23.8	0.0
Lygus lineolaris (P. de B.)	39.6	1.6	0.0
Other Heteroptera	6.2	9.5	4.7
Diptera	18.7	15.9	17.2
Aphididae	0.0	12.7	14.1
Cicadellidae	16.7	0.0	17.2
Solenopsis invicta (Buren)	0.0	9.5	21.9
Lepidoptera	6.2	0.0	0.0
Araneae	0.0	15.9	14.1
Others	4.3	11.1	10.8
Total	100.0	100.0	100.0
No. prey records	48	63	64

[a] In cotton in Mississippi (Lockley & Young 1987).

[b] In cotton in Central Texas (Nyffeler et al. 1992a).

[c] In cotton in East Texas (Nyffeler et al. 1987b).

Pollinating bees attracted to wild flowers and cotton plants during bloom are frequently encountered and overpowered by the green lynx spider *Peucetia viridans* (Hentz), a larger sized aggressive species (up to >15-mm length), that lies in ambush on the upper surface of leaves well camouflaged by its bright green color and cryptic posture. Bees (including *A. mellifera*) constituted 23% of the prey of green lynx spiders in a Texas cotton field; these spiders also prey on pests such as cotton fleahopper and boll weevil (Nyffeler et al. 1992a).

Crab Spiders. These spiders (Thomisidae) are a family of small to medium-sized species of spiders characterized by their crab-like posture and walking behavior (like crabs they walk laterally). Crab spiders are among the most abundant spider predators in grasslands and agricultural crops. They are considered to be typical sit-and-wait foragers that lie motionless in ambush for prey. McDaniel & Sterling (1982), however, provided evidence that crab spiders may at times actively search for prey (feeding on immobile insect eggs). Feeding can take place day or night. Brown colored crab spiders of the genus *Xysticus* (≈7 mm adult length) feed on small winged Hymenoptera and Diptera most frequently when observed on meadow plants (Table 8); those on the soil surface prey more often on ants, spiders, carabid beetles, and springtails (Table 8; Nyffeler & Breene 1990b). Early-instar crab spiders feed on soft-bodied insects such as tiny dipterans, hymenopterans, aphids, and thrips, whereas later instars and adults occasionally overpower large and well-armed insects including large stinging bees. Large bees comprised <5% of the total prey of *Xysticus* spp. in hay meadows (Nyffeler & Breene 1990b). Morse's (1983) quantitative prey analysis listed large bees (*A. mellifera, Bombus* spp.) as comprising ≈50% (by numbers) of the natural diet of *Misumena vatia* (Clerck) (Table 8). This white, yellow, or pale green colored spider of ≈10 mm adult length is perfectly camouflaged on flowers where it waits in ambush for pollinating insects. *Misumenops celer* (Hentz) (≈6 mm adult length)

Table 8. Prey spectrum (in percent) of crab spiders (Thomisidae) based on three different field studies

Prey type	Study 1[a]	Study 2[b]	Study 3[c]
Diptera	64.8	0.0	7.0
Apidae	4.0	0.0	49.3
Formicidae	4.8	34.3	—[d]
Other Hymenoptera	8.0	2.9	4.2
Lepidoptera	1.6	0.0	29.6
Coleoptera	4.8	8.6	—[d]
Aphididae	0.0	11.4	—[d]
Collembola	0.0	5.7	—[d]
Araneae	6.4	25.7	—[d]
Others	5.6	11.4	9.9
Total	100.0	100.0	100.0
No. prey records	125	35	71

[a] *Xysticus* spp. on meadow plants in Switzerland (Nyffeler 1982).

[b] *Xysticus* spp. on soil surface of meadows in Switzerland (Nyffeler 1982).

[c] *Misumena vatia* (Clerck) on flowers in Maine (Morse 1983).

[d] Information not available.

feeds readily on various bugs in field crops (Dean et al. 1987, Agnew & Smith 1989, Breene et al. 1990). Crab spiders were reported feeding on the Colorado potato beetle (Cappaert et al. 1991).

Jumping Spiders. This is a family (Salticidae) of small to large-sized species with rectangular shape, short stout legs, and greatly enlarged anterior median eyes. Possessing acute vision these diurnal hunters react to visual stimuli such as passing insects (Foelix 1982). They crawl to within striking distance and then jump on their prey with great accuracy. Spiders of this family are highly polyphagous (Table 9) but can narrow their prey spectrum significantly, when a suitable prey species reaches high numbers relative to other prey groups. A form of facultative monophagy was observed in the jumping spider *Plexippus paykulli* (Audouin), a cosmopolitan species of ≈10 mm adult length, that takes up residence in and on buildings and rarely migrates into field crops. This species is known from the literature as a polyphagous feeder on a wide variety of arthropod taxa including Odonata, Orthoptera, Homoptera, Lepidoptera, Diptera, Hymenoptera, and other Araneae (Jackson & MacNab 1989, Nyffeler et al. 1990b). However, in a roach-infested building in Central Texas this spider was observed to concentrate largely on the German cockroach, *Blattella germanica* (L.), as a food source (>90% of total prey; Table 9); regardless of the highly limited diet, the *P. paykulli* females produced viable offspring, which implies that the nutritional quality of the food supply was sufficient for the spiders' growth and reproductive needs (Nyffeler et al. 1990b).

Table 9. Prey spectrum (in percent) of jumping spiders (Salticidae) based on three different field studies

Prey type	Study 1[a]	Study 2[b]	Study 3[c]
Blattella germanica (L.)	0.0	0.0	96.4
Pseudatomoscelis seriatus (Reuter)	44.4	0.0	0.0
Lygus lineolaris (P. de B.)	0.0	22.4	0.0
Other Heteroptera	2.8	8.6	0.0
Diptera	2.8	12.1	0.0
Cicadellidae	5.6	0.0	0.0
Membracidae	0.0	15.5	0.0
Hymenoptera	8.3	1.7	0.0
Lepidoptera	8.3	1.7	0.0
Coleoptera	0.0	22.4	0.0
Orthoptera	5.6	0.0	3.6
Araneae	22.2	15.5	0.0
Others	0.0	0.0	0.0
Total	100.0	100.0	100.0
No. prey records	36	58	28

[a] *Phidippus audax* (Hentz) on wild plants and cotton in Texas (Dean et al. 1987 and M.N. unpublished data).

[b] *P. audax* on wild plants and cotton in Mississippi (Young 1989).

[c] *Plexippus paykulli* (Audouin) in building in Texas (Nyffeler et al. 1990b).

Another member of the jumping spider family, *Phidippus audax* (Hentz) (≈10 mm adult length), is one of the most abundant spider predators in field crops in the United States (Young & Edwards 1990). *P. audax* feeds heavily on agriculturally harmful bugs such as cotton fleahoppers and tarnished plant bugs (Table 9; Dean et al. 1987, Young 1989). This spider demonstrated a sigmoid functional response to the availability of fleahopper prey in field confinement tests (Breene et al. 1990). *P. audax* also preys on beetles (e.g., spotted cucumber beetle and boll weevil) and larvae of the bollworm, *Helicoverpa zea* (Boddie) (Young 1989). Jumping spiders frequently eat other spiders (Jackson 1977) (Table 9). In different parts of the world, jumping spiders were observed feeding on insect eggs (Whitcomb 1974, McDaniel & Sterling 1982, Nyffeler et al. 1990a). Some salticid species (*Portia* spp.) habitually invade the webs of other spiders and eat the web owners (araneophagy) (Jackson & Blest 1982). Members of the family Mimetidae (pirate spiders) are known to prey exclusively on other spiders in the field (Foelix 1982, Agnew & Smith 1989, Wise 1993) but in the laboratory some mimetids feed on insects as well (Nentwig 1987).

The feeding behaviors of other spider groups are discussed elsewhere (e.g., Nentwig 1987, Wise 1993). The wide variety of spider diets shown in Tables 1–9 reflects the diversity and flexibility of foraging behavioral patterns utilized by these animals in their quest for food.

Ecological Implications of the Insectivorous Activities of Spiders. As generalist predators, spiders destroy pest insects, insects of a neutral economic status, and beneficials alike (Bilsing 1920, Whitcomb 1974, Nyffeler 1982). The same spider species that feeds predominantly on pests at a certain location, may capture mostly beneficials at another location only a few kilometers away. The orb weaver *Argiope bruennichi* (Scopoli) for instance preys primarily on acridid grasshoppers in some grasslands in Central Europe; however, in small old fields dominated by flowering thistles and blackberry bushes, this spider was observed capturing large numbers of honey bees (Nyffeler & Benz 1981). Honey bees, bumble bees, and other pollinating insects are a primary food source for some aggressive spiders that search and wait for prey on or near flowering plants (see above) (Bilsing 1920, Nentwig 1987, Nyffeler & Breene 1991). Agnew & Smith (1989) and Nyffeler et al. (1987b, 1992a) observed that in field crops in the southwestern United States, spiders frequently kill and eat other predators (intraguild predation). Whitcomb (1974) stated that some web weaving spiders destroy large numbers of parasitoids and predators. These negative effects, however, are balanced by spider activities in killing numerous pest insects as well (for a discussion see Agnew & Smith [1989], Nyffeler & Breene [1991], and Nyffeler et al. [1987b, 1992a, b]). Furthermore, predation on beneficials may be helpful in maintaining the number of spiders during a period of food shortage (low pest levels).

Although the ecological significance of spiders in the balance of nature is still largely unexplored, they generally are considered to be important natural enemies of insects (Robinson & Robinson 1974, Whitcomb 1974, Zimmermann & Spence 1989, Young & Edwards 1990). Turnbull (1973) surveyed 37 published censuses of spider numbers in a wide variety of natural and modified environments. He found an overall mean density of 130.8 spiders per square meter (range, 0.6–842/m^2) and concluded that spiders must have an enormous predation impact on insect populations. Especially in minimally disturbed systems such as old fields, marshes, and woodlands colonized by spiders all year long in high numbers (up to a maximum of ≈1,000/m^2) (see Dondale 1971), these animals seem to play an important ecological role as insectivores (Nyffeler & Benz 1987). The prey kill by the spiders of such ecosystems was estimated at ≈50–200 kg fresh weight per hectare per year (Teal 1962, Kajak et al. 1971, Van Hook 1971, Stern & Kullmann 1975), which may be ≈100 times higher compared with average agricultural fields of the temperate-northern zones (Kajak et al. 1971, Luczak 1975, Nyffeler 1982) (Table 10). Nyffeler et al. (1994) surveyed 25 censuses of spider numbers in U.S. field crops published by 11 different research groups (considering a geographic range from North Carolina to California), which gave an overall mean density of ≈1 plant-dwelling spider per square meter (±0.18 SEM). Spider numbers in cotton throughout Texas averaged 0.8/m^2 (Dean & Sterling 1987). Such estimates are based on D-Vac samples, whole plant sampling, and ground cloth technique (e.g., Dean & Sterling 1987). These methods do not take into account those spiders that inhabit cracks in the soil between the rows, and the available data from field crops are, therefore, rather conservative estimates. Nevertheless, mean spider densities in U.S. crops are significantly lower than Turnbull's overall mean value of 130.8/m^2 (see above). Field crops are highly disturbed systems whose beneficial arthropod numbers are drastically reduced by agricultural practices such as frequent mowing, cultivating, combine-harvesting, and use of heavy doses of pesticides (Luczak 1979, Nyffeler 1982, Riechert & Lockley 1984).

Table 10. Prey kill of spiders in various ecosystems (rough estimates computed from literature data [modified after Nyffeler 1982])

Ecosystem	Geographic area	Prey kill kg/ha/yr
Field crops and mown meadows[a]	Central Europe	≤2
Phragmites reed belt of lake (mown once/year)[b]	Central Europe	≈5–10
Minimally disturbed grassland (old field)[c]	United States	≈50
Minimally disturbed grassland (old fields) and forests[d]	Central Europe	≈100–150
Marsh land[e]	United States	≈200
Tropical coffee plantation (insecticide-free)[f]	Oceanic-Australian region	≈160

For purposes of comparison all estimates are converted to Kilograms (freshweight)/ha/yr. Assumptions: ≈80% of the killed prey is consumed; caloric equivalent of prey is ≈5.6 cal/mg dry weight (Moulder & Reichle 1972).

[a] Kajak et al. (1971); Luczak (1975).

[b] Pühringer (1979).

[c] Van Hook (1971).

[d] Kajak et al. (1971); Stern & Kullmann (1975).

[e] Teal (1962).

[f] Robinson & Robinson (1974).

In the literature, methods by which predator numbers in an agroecosystem could be increased are discussed (Nyffeler 1982, Sterling et al. 1989, Wise 1993). Young & Edwards (1990) suggest several management strategies (e.g., reduction of pesticide usage and cultivation frequencies) that could enhance the spider numbers in field crops and adjacent habitats resulting in increased predation activities. In Japan, attempts have been made to raise the fecundity of spiders in rice fields artificially by releasing *Drosophila* flies as a supplementary food supply; this caused an increase in spider numbers (i.e., augmentation of natural enemies) (Kobayashi 1975).

There is evidence that spiders may play an important role as mortality agents of certain crop pests of small body size such as aphids (Aphididae), leafhoppers (Cicadellidae), planthoppers (Delphacidae), and fleahoppers (Miridae) in some agricultural fields where little or no insecticide is used (Kiritani et al. 1972, Liao et al.

1984, Oraze & Grigarick 1989, Nyffeler et al. 1992b). Robinson & Robinson (1974) estimated that spiders may destroy the equivalent of ≈160 kg insects per hectare per year in an insecticide-free coffee plantation in New Guinea (Table 10). These authors cautiously conclude that the absence of coffee pests in their study area may be, at least in part, attributable to the collective predation impact of the rich spider fauna. Sterling et al. (1992) demonstrated with computer modelling techniques that the insectivorous activities of spiders and other arthropod predators are of economic value in certain years in unsprayed cotton in Texas. Experimental evidence for the ecological impact of spiders has been reviewed in detail by Wise (1993) (see his book for original citations).

Coddington & Levi (1991) state that the order Araneae ranks seventh in global diversity after the five largest insect orders (Coleoptera, Hymenoptera, Lepidoptera, Diptera, Hemiptera), and the arachnid order Acari. Wise (1993) considers the spider a 'model predator' in terrestrial ecosystems. Van Hook (1971) and other ecologists recognized that spiders as secondary consumers "may contribute significantly in maintaining community homeostasis." Spiders play an integral part in herbivore- and detritus-based food chains in terms of biomass, energy flow, and nutrient transfers (Turnbull 1973, Schoener 1989, Wise 1993). Surprisingly, the basics of spider predation ecology (i.e., prey preferences, search areas, search times, handling times, predation rates, functional and numerical responses) are still largely unknown for most species. Further detailed investigations on the predatory role and economic impact of spiders in various natural and agricultural habitats are urgently needed. With this article we hope to generate some interest among entomologists and ecologists for future studies on spider impact.

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GENERAL DISCUSSION

Numerically Dominant Spider Groups

The spider assemblages found in cotton in Austonio (East Texas) and Snook (Central Texas) were quite similar and represent a species complex typical for cotton growing areas from the east coast to the southwest, with lynx spiders (Oxyopidae) numerically predominating. Lynx spiders consistently constituted > 50% of the spider total throughout the growing season (see chapters 4, 5, and 6). The second most abundant spider group, the orb-weavers (Araneidae and Tetragnathidae), constituted ≈ 10% of the spider total (see chapters 3 and 7). Other dominant spider groups were crab spiders (Thomisidae), and jumping spiders (Salticidae). The very diverse range of life styles and foraging modes of the various dominant spider groups that occur in these cotton fields have been described in detail in chapter 9 of this thesis.

Two species of lynx spiders occur in these fields: the striped lynx *Oxyopes salticus* and the green lynx *Peucetia viridans*. *Oxyopes*, an excellent survivor / colonizer of agroecosystems (see chapter 8), can constitute up to 90% of the predators found on cotton in some areas of the 'cotton belt' and has been suspected for quite some time by leading U.S. entomologists to be a 'key predator'. *Peucetia* is less frequently found in cotton and is therefore expected to be of minor importance as a potential natural enemy of pests in the cotton fields. However, *Peucetia* can inhabit wild flowers in fairly high numbers; there, *Peucetia* has been seen feeding heavily on cotton pests (see chapter 4) suggesting that this spider may play an important ecological role in suppressing cotton pests prior to their migration into cotton; considering this possibility, data on *Peucetia* are included in this discussion. Our research largely focussed on the numerically dominant lynx spiders and orb-weavers.

Predator Densities and Seasonal Patterns

Early in the season, very few spiders ($< 0.3/m^2$) were found on the small cotton plants. The spider numbers tend to increase gradually with the progressing growing season and reach a peak (up to $\approx 7/m^2$) sometime in late summer at which time the growers periodically destroy the foliage in the course of the cotton harvest (see chapters 3 and 5); the system thereafter becomes an 'ecological desert' (except for soil arthropods) throughout the winter months and must be re-colonized by spiders each spring from so-called 'predator reservoirs'. Wild flowers growing in adjacent grassland areas are assumed to be such predator reservoirs (Nyffeler, Dean & Sterling [1992]: Texas Agricultural Experiment Station Bulletin B-1707, 1-6). The seasonal increase in numbers can be explained partially by migration into the fields early in the season, partially by reproduction within the fields in the second part of the season (see chapters 5).

Spider numbers averaged $2.0/m^2$ and $2.8/m^2$ in the cotton fields of Austonio and Snook, respectively (middle of the growing season, see chapters 5 and 7). The numerically dominant *Oxyopes* occurred in average densities of $\approx 1\text{-}1.5/m^2$ during mid-season in both plantations (see chapters 5 and 7). Thus, the average spider numbers in the two studies were similar.

In order to make our density estimates comparable with those from cropland in other geographic areas, a survey of average spider numbers in field crops across the U.S. was conducted (see chapter 9). The available data originate from 25 censuses published by 11 different research groups and show a bias towards the southern regions of the U.S. Because these estimates are based on sampling methods (D-Vac samples, whole plant sampling, ground clouth technique) which do not take into account those spiders that inhabit cracks in the soil between the rows, these data are rather conservative estimates (= number of plant-dwelling spiders/m^2). This survey resulted in an overall mean density of $\approx$ 1 spider/m^2 ($\pm$ 0.18 SEM) for U.S. field crops (considering a geographic range from the east to the west coast). More than half of these censuses had been conducted in fields where no insecticide was used.

In cotton growing areas where heavy doses of insecticides are used, the spiders occur in extremely low numbers (Sterling, pers. comm.). Compared to sprayed cotton growing areas, the average spider numbers in the insecticide-free cotton fields of Austonio and Snook (2 and 2.8/m^2, respectively) are fairly 'high'.

Feeding Frequencies

One of the most interesting findings of this research was the observation that the lynx spiders in cotton fields in Texas fed both day and night (see chapters 4 and 5). Previously it had been reported in the literature that the lynx spiders are strictly 'diurnal' foragers (e.g., Gertsch [1979]: "American Spiders", Van Nostrand-Reinhold, New York). Our observations in Texas cotton imply that the lynx spiders are 'time generalists' which forage on diurnally and nocturnally active prey groups (see chapter 7). Many orb-weavers spin their webs preferentially at the beginning or end of the nocturnal period; thus, orb-weavers were seen feeding during the day or night (see chapters 3 and 9).

Low feeding frequencies ($\leq$ 5% individuals feeding simultaneously at any given time) were observed in lynx spider populations of Austonio and Snook, respectively (see chapters 4, 5, and 6). Other abundant agroecosystem spiders (e.g., small orb-weavers, crab spiders, and jumping spiders) fed at similar low rates in the field (see chapters 3 and 9). These data indicate that most spiders occurring in the cotton fields fed rather infrequently (see chapter 9).

The predation rate (= no. prey killed/spider/day) was estimated with a visual method based on average feeding frequency (percentage spiders with prey in their chelicerae) observed in the field, average handling time, and hunting (searching) time; it was estimated that a subadult/adult *Oxyopes* (representing a typical agroecosystem spider) may capture $\approx$ 1 prey organism on an average rainfree day in the field (see chapters 5 and 6). Other researchers obtained similar estimates ($\approx$ 1-2 prey/spider/day for adult *Oxyopes*) in field and laboratory cage tests. The same spiders feed at several times higher rates in laboratory feeding experiments if food is offered *ad libitum* (as is known from literature).

This suggests that in the field these spiders often feed below their maximum feeding capacity. Field populations of nonweb-building spiders were often observed in an underfed condition by researchers in North America and other parts of the world. Spiders generally have very low metabolic rates compared to other poikilothermics of equal body weight and possess the capacity to reduce them even more during periods of starvation. Turnbull (1973) (Annu. Rev. Entomol. 18, 305-348) stated that feeding by spiders is erratic, with short intervals of intensive feeding interspersed with periods of fasting. An extensively developed digestive system, a distensible abdomen, and the capacity to store fat allows these animals to feed in excess under conditions of food abundance and to go without food for long periods of time when prey densities drop to low levels. Spiders can be expected to increase their predation rate during severe outbreaks of insect pests (i.e., 'functional response') (see page 73).

Predator/Prey-Size Ratios

Predator/prey-size ratios are important parameters in evaluating the biocontrol potential of predaceous arthropods towards pest insects. The predator/prey-size ratios of lynx spiders assessed in Snook, Central Texas, resemble those previously observed in Austonio, East Texas. The majority of the captured prey organisms of the lynx spiders were smaller than the length of the predator, which fits the general theory of prey size selection in nonweb-building spiders (see Nentwig [1987]: "Ecophysiology of Spiders", Springer-Verlag). Feeding experiments with a variety of spider species and a model prey (crickets) conducted in the laboratory revealed that the optimal prey length ranges from 50-80% of the spiders' own length (Nentwig 1987). In Texas cotton fields, a mean subduing potential of 56 vs. 68% was observed for *Oxyopes* and *Peucetia*, respectively. Thus, our field observations on lynx spiders strongly support Nentwig's theory. Both lynx spider species never overpowered prey organisms larger than 140% their own size, which again is in good agreement with Nentwig's laboratory feeding experiments where nonweb-building spiders overpowered prey organisms not larger than 150% of the spider's size. In contrast to this, large orb-weavers (genus *Argiope*) can overpower prey organisms up to 200% of the spider's size, but even these large spiders fed predominantly on small insects such as tiny dipterans and aphids in the investigated cotton fields (see Nyffeler, Dean & Sterling [1987]: Entomophaga 32: 367-375).

Of the orb-weavers occurring in cotton, 99% were small-sized spiders which spin delicate (ca. 4 cm diam.) webs. Likewise, the majority of the lynx spiders in cotton were small-sized (i.e., *Oxyopes*). *Oxyopes* captures a wide variety of small-sized arthropods up to 6 mm length ($\approx$ 2.5 mm optimal prey length) (see chapter 8). In contrast to this, the larger *Peucetia* feeds over a broader range of prey size classes and consequently captures a higher proportion of the larger prey organisms (see chapter 6), but because this species is much less abundant than *Oxyopes*, its contribution to the overall predation impact is rather low. Overall, spider individuals of small size (including large percentages of immatures) numerically dominate the faunas of the investigated cotton fields, and these spiders feed primarily on tiny prey organisms ($\leq$ 3 mm in length) (see chapters 3, 5, and 6). Spiders in the cotton fields therefore can be expected to be potentially effective as predators of insect pests of small size.

Spiders as Predators of Selected Key Pests

Cotton Fleahopper *Pseudatomoscelis seriatus* [Heteroptera: Miridae]

With a body length range of 1.1-2.9 mm (third instar to adult) cotton fleahoppers ideally fit the optimal prey length of ≈ 2.5 mm for *Oxyopes*. *Peucetia*, that captures on the average significantly larger-sized prey than *Oxyopes* (see page 72), seems to be less efficient in capturing fleahoppers. Fleahoppers apparently are a suitable prey for the smaller-sized immature *Peucetia* individuals only (< 8 mm in length) (see chapter 6). - *Oxyopes* is a 'active searcher' that forages throughout the cotton plant and even on the ground, and which shows considerable flexibility in switching its feeding patterns in response to prey availability (see chapter 8). The behavioral flexibility of *Oxyopes* comes to light by comparing its feeding patterns recorded in the cotton fields in Austonio and Snook, respectively (see chapters 5 and 7).

In the cotton plantation in Austonio, East Texas, the numbers of cotton fleahoppers counted in 1985 (0.04-1.3 individuals/m^2, early season until bloom) were below the economic threshold. [The Texas Agricultural Extension Service recommended an economic threshold of ≈ 1.5-3.5 fleahoppers/m^2 for this type of field situation.] Consequently very low predation rates on fleahopper prey by spiders were observed in Austonio. Actually, the cotton fleahopper was entirely missing in the diet of *Oxyopes* in the cotton plantation in Austonio (see chapter 5). Instead *Oxyopes* fed heavily on red imported fire ants (22% of the diet), leafhoppers (17%), dipterans (16%), aphids (14%), and other spiders (14%) (see chapter 5).

A totally different scenario was observed in the cotton plantation in Snook, Central Texas, where cotton fleahoppers occurred in fairly high numbers (≈ 2 ind./m^2, during mid-season) in 1988. In this situation, *Oxyopes* fed heavily on these pests (fleahoppers constituting ≈ 24% of the diet); other important components in the diet of *Oxyopes* were dipterans (16%), spiders (16%), aphids (13%), other bugs (11%), and fire ants (9%) (see chapter 6). It was estimated that an *Oxyopes* captured on the average ≈ 1 fleahopper every fourth day in the plantation in Snook (see chapter 7).

These data indicate that *Oxyopes* may feed heavily on other predators such as fire ants when pests are rare; however, when pests become abundant this spider can largely switch to pestiferous species (e.g., fleahoppers) as a major food source. Breene, Sterling & Nyffeler (1990) (Entomophaga 35, 393-401) demonstrated with field confinement tests in an insecticide-free cotton field in Central Texas that *Oxyopes* (and two other spider species) exhibited a sigmoid functional response to availability of fleahopper prey (i.e., increased predation rate at elevated pest levels). - The assessment of the killing power of *Oxyopes*, based on the predation rate and the predator-to-prey ratio (i.e., number of *Oxyopes* individuals per fleahopper), suggests that this spider contributes significantly to fleahopper mortality; additional fleahopper mortality is attributable to other predaceous arthropods such as *Peucetia*, jumping spiders, crab spiders, web-building spiders, damsel bugs, and red imported fire ants (see chapter 7).

Boll Weevil *Anthonomus grandis grandis* [Coleoptera: Curculionidae]

Over a period of ≈ 200 h of visual observations in cotton fields in Austonio and Snook, only 1 spider individual (i.e., *Peucetia*) was seen feeding on an adult boll weevil (see chapter 6). *Oxyopes* and small orb-weavers have not been seen feeding on the boll weevil so far (see chapters 3, 5, and 6). As a rule, spiders rarely capture beetle prey (see chapter 9). The hard-sclerotized beetles are outside the optimal diet for most spiders, because their chelicerae cannot penetrate the thick cuticle of these insects (Nentwig 1987). Though some aggressive spiders (e.g., jumping spider *Phidippus audax*) occasionally penetrate a beetle's body, usually between the head and thorax, other prey groups are attacked and consumed more often in prey choice experiments; in the laboratory, it was observed that *Phidippus* would often attack and then drop a boll weevil after rolling it around between the chelicerae (Roach [1987]: Environ. Entomol. 16, 1098-1102). Likewise, small orb-weavers often eliminate entangled beetles from the web (see chapter 9).

Because the cotton fields are colonized predominantly by spider individuals of small size which feed almost exclusively on tiny soft-bodied prey (see page 72), spiders can be expected to have little impact on the boll weevil. The low percentage of boll weevils in the spider diets recorded in Austonio and Snook seems to reflect this. It is known that the boll weevil is kept at low densities in cotton fields primarily by red imported fire ants, which aggressively attack the immature stages of this pest (Sterling, pers. comm.).

Bollworm *Helicoverpa zea* [= *Heliothis zea*] [Lepidoptera: Noctuidae],
Tobacco Budworm *Heliothis virescens* [Lepidoptera: Noctuidae]

Eisner et al. (1964) (Science 146, 1058-1061) discovered an escape behavior of moths from spider webs which they described as follows: "Moths, by virtue of the loose scales that cover their wings and bodies, are admirably adapted to elude capture by orb-weaving spiders. Rather than sticking to the web, they may simply lose some of their scales to the viscid threads, and fly on." A moth of the bollworm captured by a large orb-weaver (*Acanthepeira*) was the only incidence of spider predation on a lepidopteran pest recorded over a period of ≈ 200 h of visual observations in the field (see chapter 3). The economically important order Lepidoptera was poorly represented in the prey spectrum of orb-weaving spiders, lynx spiders, and other spiders (chapters 3, 4, 5, and 6). The extremely low percentage of lepidopteran pests in the spider diets may partially reflect the moths' success in avoiding predation (see above); partially it may reflect that these pests occurred in low numbers in the investigated cotton fields. In Austonio and Snook, bollworm-budworm numbers monitored with pheromon traps were below the economic threshold.

It is assumed, that these pests were maintained at low levels by predaceous insects (i.e., red imported fire ants, minute pirate bugs, big-eyed bugs, etc.) that colonized the cotton fields and adjacent grasslands in high numbers (Sterling, pers. comm.). The possibility cannot be ruled out that the predation impact of the spiders on lepidopteran pests may have been underestimated due to methodological bias; feeding on the eggs and small larvae of the bollworm and/or tobacco budworm simply may have been overlooked in the field with the method of visual observation. More sophisticated methods (radiolabeling studies, ELISA techniques, etc.) are needed to assess 'hidden' predation activities such as feeding on tiny insect eggs / small larvae (McDaniel & Sterling [1982]: Environ. Entomol. 11: 60-66). Thus, the quantitative impact of spider predation on the very small eggs and larvae of these lepidopteran pests is not known yet.

Spiders as Predators of Beneficials

One of the most important findings of this thesis is the observation that lynx spiders in the cotton fields killed beneficials in relatively large numbers. In the cotton plantation in Austonio, East Texas, beneficial arthropods constituted approx. 42 and 60% of the diet of *Oxyopes* and *Peucetia*, respectively (see chapters 4 and 5). This agrees well with the results from Snook, Central Texas, where benefical arthropods constituted 33 and 66% of the diet of *Oxyopes* and *Peucetia*, respectively (see chapter 6). Similar patterns of feeding on beneficials were observed in crab spiders and jumping spiders (Nyffeler, unpublished data). In contrast to this, beneficials were less frequently captured by the orb-weavers (< 20% of the diet) (see chapter 3).

Honey bees and other bees attracted to cotton during bloom are frequently encountered and overpowered by *Peucetia*, which lie in ambush on the upper surface of leaves in the plant terminal well camouflaged by their vivid green color and cryptic posture (see chapters 4 and 6). In cotton fields, bees can constitute from ≈ 4 to 40% (by numbers) of the diet of *Peucetia*. On wild flowers *Peucetia* also frequently seizes bees (see chapter 4). Randall (1982) (J. Arachnol. 10, 19-22) analysed the natural diet of *Peucetia* in Florida, and came to the conclusion that this spider "...is counterproductive as a predator of economically important insects since it takes beneficial insects as prey more often than it takes harmful insects." Randall reports a 44 : 12 beneficial/harmful prey ratio for *Peucetia* in agroecosystems. By means of a cost/benefit analysis, Louda (1982) (Oecologia 55, 185-191) examined in California the net effect of predation by *Peucetia* for seed production by a native plant (family Asteraceae), and found that "pollination success was lower on branches with spiders [versus branches without spiders], but insect damage to seeds was also reduced on those branches; the net result was an increase [of 18%] in the number of viable seeds where *Peucetia* was present..." The rather low population densities of *Peucetia* in cotton fields (see section 10.1) suggests that the predation impact of this spider upon bees is insignificant in most situations. The smaller-sized *Oxyopes* is incapable of capturing large bees.

Entomophages eaten by lynx spiders include minute pirate bugs, big-eyed bugs, green lacewings, lady beetles, fire ants, and several species of spiders. About a dozen species of entomophages eaten by the spiders are themselves 'key predators' of the eggs and small larvae of bollworms or tobacco budworms; it is well documented in the literature that these key predators (i.e., minute pirate bugs, big-eyed bugs, and others) contribute significantly to mortality of bollworm-budworm eggs and larvae in cotton fields. This begs the question of whether spiders eating other predators (i.e., 'intraguild predation') eventually has negative economic implications by disrupting natural control of bollworm-budworm numbers. I studied this question and found that the bollworm-budworm numbers remained below threshold level in cotton fields where high predator numbers and simultaneously high levels of intraguild predation were monitored (see chapter 6). It is known that bollworm-budworm infestations rarely reach economic levels in insecticide-free cotton fields where an extensive natural enemy complex has been preserved. Cannibalism and interspecific predation within the predator complex may even have positive ecological implications by providing food for predators during time periods of low herbivore numbers which helps to create sustainable predator communities.

Potential Predation Impact

To evaluate the predatory significance of the lynx spiders relative to the other predaceous arthropods occurring in cotton, the total number of predation events observed attributable to lynx spiders versus other arthropod predators was compared based on the data which had been collected in Snook. A total of 134 arthropod predators with prey in their chelicerae/mandibulae were monitored during the 108 h observation period, which included 94 lynx spiders versus 40 other predators. Thus, 70% of all predation events observed were attributable to lynx spiders which indicates that these spiders were the dominant predators in the investigated cotton agroecosystem (see chapter 6).

Based on population density counts in the cotton plantation in Austonio and the assessement of the prey capture rate, it was estimated that lynx spiders killed perhaps ≈ 0.6% of the potential prey per day in the middle of the growing season (assuming an average prey kill of ≈ 1 prey/m^2/day) (see chapter 5).

For comparison, Moulder & Reichle (1972) (Ecol. Monogr. 42, 473-498) measured the predation impact of a forest spider community in Tennessee at different times of the year, based on the ratio of daily food consumption to standing crop of prey (in kcal/m^2). Spiders daily accounted for between 0.44 and 1.16% of the standing crop of prey (in terms of kcal/m^2). Turnbull (1973) (Annu. Rev. Entomol. 18, 305-348) commented as follows: "This may seem to be little but if this consumption were removed from the system presumably the prey populations would increase by from 0.44 to 1.16%/day. At these rates of growth prey doubling times would be from 62-162 days". Turnbull continues "This of course, is a simple-minded approach to the complexity of interactions that constitute an ecosystem, but it does serve to bring some perspective to otherwise rather abstract figures."

The prey mortality estimates by Moulder & Reichle are of the same magnitude as our estimate of ≈ 0.6% assessed in the cotton plantation in Austonio (see above), though a different approach was used in the two studies. Turnbull's considerations may also be applied to our estimate, indicating that the collective predation impact of spiders in cotton may contribute significantly in maintaining cotton pests (i.e., cotton fleahopper) below numbers that cause economic crop losses.

FINAL CONCLUSIONS

Our studies led to the assumption that spiders (i.e., *Oxyopes*) are the most effective arthropod predators of the cotton fleahopper. Natural predation upon the cotton fleahopper had also been investigated by a graduate student from Texas, who conducted a field experiment by releasing ≈ 30,000 fleahopper nymphs labeled with ^{32}P, and thereafter recovered radioactive predators evidencing predation on the fleahopper (Breene [1989]: Ph.D. Diss., Texas A&M Univ.). Breene's experimental design has the limitation that it cannot distinguish primary from secondary predation, but it has the advantage that evidence is based on much larger samples compared to the very time-consuming method of visual observation (see chapter 7). In addition to this, the ^{32}P-method is advantageous by measuring the combined activity of diurnal and nocturnal predation. Breene's data and ours (see chapter 7) are comparable since both studies were conducted in insecticide-free cotton fields of the same geographic area. Breene's project (1986-1987) and ours (1988) complement each other, providing combined data over a continuous 3-year period (1986-1988) for this particular cotton growing area. The relative importance of the various predators of the fleahopper was compared between the two studies and very similar patterns were found. The data from both studies suggest that spiders were highly superior as predators of the fleahopper compared to the predaceous insects (in Snook, spiders accounted for ≈ 90% of the fleahopper mortality attributable to specific predators). In both cases, lynx spiders were the dominant predators of the fleahopper; other predators including orb-weaving spiders, crab spiders, jumping spiders, damsel bugs, and red imported fire ants have proven to be less effective natural enemies. The similarity of the predation patterns observed in the two projects provides strong mutual support for their accuracy.

High values of fleahopper mortality estimated in Snook (see chapter 7) and in Breene's study provide evidence that spiders contribute significantly to fleahopper mortality in Texas cotton. The contribution of spiders as mortality agents, however, varies between the different fields and within different years, due to the spatial and temporal fluctuations of the numbers of spiders and fleahoppers. An approximately 30 times higher frequency of predation on fleahoppers was recorded in Snook compared to Austonio (see chapter 7). Consequently the economic benefit due to these predators varies in different situations.

The boll weevil, bollworm, and tobacco budworm occurred in Austonio and Snook in numbers far below economic injury levels; they were probably maintained at these low levels by red imported fire ants and other predaceous insects (Sterling, pers. comm.). Various groups of entomophages evidently complement each other in their activities as natural biocontrol agents.

In conclusion, the data presented in this thesis imply that lynx spiders (i.e., *Oxyopes*) were among the most important natural control agents in Texas cotton. *Oxyopes* had been suspected to be a major natural enemy in other crop systems, too; this species is a typical 'agroecosystem spider' (sensu Young & Lockley [1985]: Entomophaga 30, 329-346). Surprisingly, the feeding patterns of this ecologically important spider predator had not been known until recently. During our studies the feeding patterns of *Oxyopes* in the field could be identified in detail, which is of interest in a broader sense: this information can be translated to other crop systems as well.

ZUSAMMENFASSUNG

Die ökologische Bedeutung der Spinnen als Prädatoren von Baumwollinsekten wurde in texanischen Baumwollfeldern untersucht. Insbesondere wurde untersucht, mit welcher Häufigkeit vier 'Schlüsselschädlinge' - nämlich die Baumwollwanze *Pseudatomoscelis seriatus* [Heteroptera: Miridae], der Baumwollkapselkäfer *Anthonomus grandis grandis* [Coleoptera: Curculionidae], der Amerikanische Baumwollkapselwurm *Helicoverpa zea* [= *Heliothis zea*] [Lepidoptera: Noctuidae] und die Baumwolleule *Heliothis virescens* [Lepidoptera: Noctuidae] - von Spinnen erbeutet werden und inwieweit die Mortalität der Schädlinge dadurch beeinflusst wird. Der Beutefang der Spinnen wurde mittels Dauerbeobachtungen direkt im Feld ermittelt (insgesamt ca. 200 Stunden Beobachtungszeit). Ein erstes Projekt wurde im Sommer 1985 in einer ungespritzten Baumwollplantage (6.5 ha Ausdehnung) bei Austonio, Houston County, im östlichen Teil von Texas durchgeführt. Im Sommer 1988 fand dann ein ergänzendes Projekt in einer ungefähr 100 km südwestlich vom ersten Untersuchungsgebiet gelegenen, ungespritzten Baumwollplantage (13.6 ha Ausdehnung) bei Snook, Burleson County, im zentralen Teil von Texas statt.

Die Resultate dieser Untersuchungen wurden zwischen 1987 und 1994 in Form von sieben separaten Publikationen in der Zeitschrift "Environmental Entomology" (Entomological Society of America) veröffentlicht. Die letzte dieser Veröffentlichungen stellt einen FORUM-Artikel dar, in welchem sämtliche im Verlauf meiner Freilanduntersuchungen in Texas und anderswo gesammelten Informationen zur Nahrungsökologie der Spinnen vergleichend analysiert wurden.

Die in den beiden Plantagen vorkommenden Spinnengemeinschaften waren grundsätzlich sehr ähnlich. In beiden Fällen handelt sich um einen Artenkomplex, der typisch ist für manche Anbaugebiete im amerikanischen Baumwollgürtel. Während der gesamten Baumwollsaison herrschten die Luchsspinnen (Oxyopidae) zahlenmässig vor ($>$ 50% der gesammelten Spinnen). Radnetzspinnen (Araneidae und Tetragnathidae) waren die zweithäufigste Spinnengruppe (ca. 10% der gesammelten Spinnen). Zwei Arten von Luchsspinnen kommen in diesen Feldern regelmässig vor: die 'gestreifte Luchsspinne' *Oxyopes salticus* und die 'grüne Luchsspinne' *Peucetia viridans*. *Oxyopes*, die häufigste Spinnenart der Baumwollfelder, trat in beiden Plantagen in der Mitte der Baumwollsaison in durchschnittlichen Populationsdichten von $\approx$ 1-1.5/m^2 auf. [*Peucetia* kommt in den Baumwollfeldern weniger häufig vor und ist vermutlich als potentieller natürlicher Feind von Baumwollschädlingen eher unwichtig.] Die durchgeführten Untersuchungen konzentrierten sich vor allem auf die bezüglich Individuenzahl vorherrschenden Luchsspinnen und Radnetzspinnen.

Basierend auf Daten, die in Snook gesammelt worden waren, wurden die räuberischen Aktivitäten von Luchsspinnen und anderen räuberischen Arthropoden vergleichend analysiert. Total 134 beutetragende räuberische Arthropoden waren während der 108 stündigen Beobachtungsperiode registriert worden; darunter befanden sich 94 Luchsspinnen und 40 andere Prädatoren. Die Luchsspinnen waren folglich für schätzungsweise 70% der beobachteten räuberischen Aktivitäten verantwortlich. Es könnte daher sehr wohl sein, dass die Luchsspinnen in der Baumwollwollplantage bei Snook die wichtigsten Prädatoren waren. Auch in Austonio gehörten die Luchsspinnen zu den wichtigsten Prädatoren.

Die Beutefangrate (= Anz. Beutetiere/Spinne/Tag) wurde mittels einer visuellen Methode in der Mitte der Baumwollsaison für *Oxyopes* geschätzt. Basierend auf der im Freiland beobachteten durchschnittlichen Fresshäufigkeit (= % beutetragende Spinnen) und Suchzeit (= für die Suche und den Verzehr von Beute verfügbare Zeit / 24 Stunden), sowie der im Labor gemessenen 'Handlungszeit' (= für den Verzehr eines Beutetieres benötigte Zeit) wurde mittels dieser Methode geschätzt, dass eine subadulte/adulte *Oxyopes* an einem regenfreien Tag im Durchschnitt vielleicht ca. 1 Beutetier fängt. In Laborexperimenten nehmen diese Spinnen unter *ad libitum*-Fütterungsbedingungen ein Mehrfaches an Nahrung zu sich (wie aus der Literatur bekannt ist). Dies weist darauf hin, dass die maximale Fresskapazität bei diesen Spinnen im Feld oft nicht erreicht wird. Man kann folglich annehmen, dass die Spinnen während einer Massenvermehrungen von Schadinsekten ihre Beutefangrate zu steigern vermögen (falls es sich dabei um Schädlinge handelt, die im entsprechenden Stadium für die Spinnen fangbar sind; 'funktionelle Reaktion').

Ein grosser Teil der in den Baumwollfeldern vorkommenden Luchsspinnen (*Oxyopes*) waren von geringer Körpergrösse. *Oxyopes* erbeutet verschiedenartige kleine Arthropoden zwischen 0.6 und 6 mm Länge, wobei die optimale Beutelänge ca. 2.5 mm beträgt. [Demgegenüber frisst die in Baumwolle wesentlich seltener vorkommende *Peucetia* im Durchschnitt grössere Beutetiere, was allerdings der niedrigen Dichte dieser Spinnen wegen weniger ins Gewicht fällt.] Die in den Baumwollfeldern vorkommenden Radnetzspinnen sind ebenfalls grösstenteils von geringer Körperlänge. Gesamthaft betrachtet werden die Baumwollfelder vor allem von kleinen Spinnen (einschliesslich hohe Prozentsätze von Jungtieren) besiedelt, welche primär winzige Beutetiere fangen ($\leq$ 3 mm Körperlänge).

Mit einer Körperlänge von 1.1-2.9 mm (drittes Stadium bis Imago) sind Baumwollwanzen der Gattung *Pseudatomoscelis* ein idealer Beutetyp (optimale Beutelänge $\approx$ 2.5 mm) für *Oxyopes*. [*Peucetia* frisst mehrheitlich grössere Beutetiere als *Oxyopes* und ist folglich weniger effizient als Prädator von Baumwollwanzen.] *Oxyopes* weist ein bemerkenswert flexibles Fressverhalten auf. Diese Spinnenart ist offenbar in der Lage ihr Beutespektrum je nach Verfügbarkeit geeigneter Beutearten weitgehend umzustellen. - In der Baumwollplantage bei Austonio, lag die Populationsdichte der Baumwollwanzen unterhalb der Schadenschwelle, und entsprechend fehlten hier Baumwollwanzen in der Nahrung der Spinnen weitgehend (0% Baumwollwanzen in der Nahrung von *Oxyopes*); *Oxyopes* fing hier recht häufig rote importierte Feuerameisen (22% der Nahrung). - Völlig anders war die Situation in der Baumwollplantage bei Snook; dort kamen die Baumwollwanzen in recht hoher Populationsdichte vor, und entsprechend machten diese Schädlinge einen beachtlichen Prozentsatz (24%) der Nahrung von *Oxyopes* aus. - Diese Daten zeigen an, dass eine niedrige Verfügbarkeit von Schädlingen als potentielle Beute (unter Bedingungen niedriger Schädlingsdichten) von *Oxyopes* dadurch kompensiert werden kann, dass diese Spinne sich zumindest vorübergehend zu einem erheblichen Teil von anderen Prädatoren (z.B. Feuerameisen) ernährt; wenn die Schädlingsdichten ansteigen, können diese Spinnen weitgehend auf Schädlinge (von geeigneter Grösse wie etwa Baumwollwanzen) als Nahrungsquelle umstellen.

Auf Grund des in der Plantage bei Snook ermittelten Verhältnisses 'Räuberdichte : Beutedichte' (= Anz. *Oxyopes*-Individuen pro Baumwollwanze) sowie der Beutefangraten von *Oxyopes* wurde das Tötungspotential dieser Spinne in der Mitte der Baumwollsaison quantitativ bestimmt. Die Berechnung ergab, dass *Oxyopes* signifikant zur Mortalität der Baumwollwanze in der Plantage in Snook beiträgt (≥ 15% Beutemortalität pro Tag); andere Spinnen und räuberische Insekten leisten einen zusätzlichen Beitrag zur Mortalität der Baumwollwanzen. - Die anderen Schlüsselschädlinge (Baumwollkapselkäfer, Amerikanischer Baumwollkapselwurm und Baumwolleule) fehlten in der Spinnennahrung in beiden Plantagen weitgehend; dies dürfte darauf zurückzuführen sein, dass diese Schädlinge dort nur in ganz unbedeutend niedrigen Dichten auftraten (weit unterhalb der Schadenschwelle) (es wird angenommen, dass vor allem Feuerameisen für diese niedrigen Schädlingsdichten verantwortlich waren). - Der Einfluss der Spinnen und anderer Prädatoren auf die Mortalität der Baumwollwanzen variiert allerdings von Feld zu Feld und von Jahr zu Jahr (als Folge der räumlich-zeitlichen Schwankungen der Populationsdichten von Prädatoren und Baumwollwanzen. Die beobachtete Häufigkeit des Fangs von Baumwollwanzen durch Prädatoren war in Snook ungefähr 30 mal höher als in Austonio. Daraus folgt, dass der durch die Prädatoren bewirkte ökonomische Nutzen je nach Situation unterschiedlich gross sein kann.

Basierend auf Daten, die in der Baumwollplantage bei Austonio gesammelt worden waren, konnte ausgerechnet werden, dass in der Mitte der Baumwollsaison vielleicht ≈ 0.6% der potentiellen Beute pro Tag durch Luchsspinnen getötet wurden. Dieser Wert stimmt recht gut überein mit Mortalitätsschätzungen aus anderen terrestrischen Oekosystemen; in der Literatur wurde postuliert, dass Mortalitätsraten von dieser Grössenordnung bereits eine stabilisierende Wirkung auf die Populationsdynamik der Beutepopulationen in gewissen terrestrischen Oekosystemen haben können (vergleiche Turnbull, 1973, "Ecology of the true spiders", in: Annu. Rev. Entomol. 18, 305-348).

Die in Austonio und Snook gesammelten Daten deuten an, dass Luchsspinnen (insbesondere *Oxyopes*) in den texanischen Baumwollfeldern zu den wichtigsten natürlichen Feinde gehören. *Oxyopes* (generell ein typischer Kolonisator von Agroökosystemen) war bereits verdächtigt worden, auch in anderen Feldkulturen ein wichtiger natürlicher Feind von landwirtschaftlichen Schädlingen zu sein. Erstaunlicherweise waren die Fressgewohnheiten dieser ökologisch bedeutungsvollen Spinnenart bis anhin unbekannt gewesen. Im Verlauf meiner in Texas durchgeführten Untersuchungen waren die Fressgewohnheiten von *Oxyopes* im Detail erforscht worden. Dies ist von weitreichender Bedeutung, da die hiermit gesammelten Erkenntnisse über das Fressverhalten dieser Spinne sehr wohl auch auf Baumwollanbaugebiete in anderen geographischen Regionen der USA sowie auf andere Feldkulturen übertragen werden können. Ferner waren im Verlauf dieser Freilandstudien zahlreiche grundlegende, neue Erkenntnisse über die Fressgewohnheiten verschiedener anderer Spinnenarten gesammelt worden, welche wesentlich zu einem besseren Verständnis der Spinnenökologie beitragen.

CURRICULUM VITAE

Research & Teaching

1950	Born in Zurich, Switzerland, where I attended schools
1982	Graduation ("Promotion") from ETHZ with Doctorate in Natural Sciences
1983-84	Swiss NSF postdoc c/o Canada Department of Agriculture, Ottawa
1985-86	Swiss NSF postdoc c/o Dept. of Entomology, Texas A&M University USA
1988-94	Visiting scientist c/o Dept. of Entomology, Texas A&M University USA
1994-95	Lectureship ("Lehrauftrag") c/o Zoological Institute / University of Berne

Awards

1968	Silver medal in Earth Sciences at the 2nd Swiss Science Fair in Basle
1971	Second prize in Earth Sciences at the 5th Swiss Science Fair in Basle
1983	Silver medal of ETHZ for excellence of my doctoral thesis in entomology
1983	Schläfli prize of the Swiss Academy of Natural Sciences for my thesis
1994	Department of Entomology Special Award, Texas A&M University (College of Agriculture and Life Sciences), College Station / USA

Reviewer in USA

1990	Reviewer for the "Entomological Society of America, College Park / USA"
1993	Reviewer for the "Entomological Society of America, College Park / USA"
1994	Reviewer for the "Entomological Society of America, College Park / USA"
1994	Reviewer for the "National Geographic Society - Evaluation of a grant proposal f. Committee for Research & Exploration, Washington, D.C. / USA"