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-

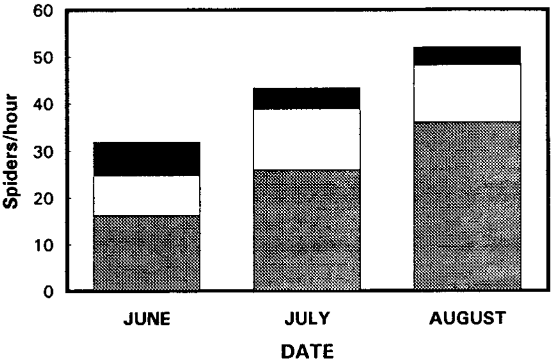

Fig. 1. Seasonal variation in the numbers of spiders encountered per hour (visual observations) in a cotton field near College Station, TX. ▩, *O. salticus;* ☐, other nonweb-building spiders (including *Peucetia viridans*, Salticidae, Thomisidae, Lycosidae, Philodromidae, and others); ■, web-building 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 × *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 × *OE*/*A*) were converted into a standardized value ("efficiency index" [100 × *OE*]/[1.3 × *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 × *OE*/*A*)	Standardized value ("efficiency index") (100 × *OE*)/(1.3 × *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.

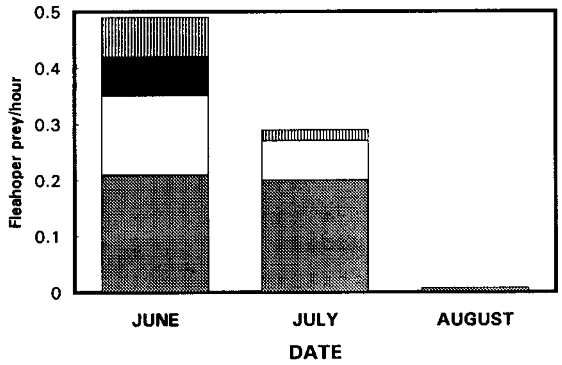

Fig. 2. Seasonal variation in the frequency of predation on the cotton fleahopper (measured as number of fleahopper prey records per observation hour) in a cotton field near College Station, TX. ▨, *O. salticus;* ☐, other nonweb-building spiders (including *Peucetia viridans*, Salticidae, and Thomisidae); ■, 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.

$Pd_c = 0.25$ 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).

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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