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 &

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):

$$\beta = -\Sigma p_i \log p_i, \tag{2}$$

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 No. prey	Total % Prey	Prey size range, mm	Predator size range, mm
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 No. prey	Total % Prey	Prey size range, mm	Predator size range, mm
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 bigeyed 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).

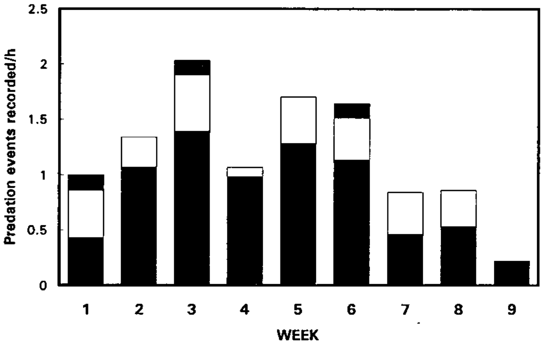

Fig. 1. Number of prey-carrying predators found per hour in a cotton agroecosystem near College Station in central Texas (9 wk during summer 1988). See Table 1 for dates of weeks. Total no. predation events observed = 134. Solid, lynx spiders; empty, other spiders; shaded, insects.

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).

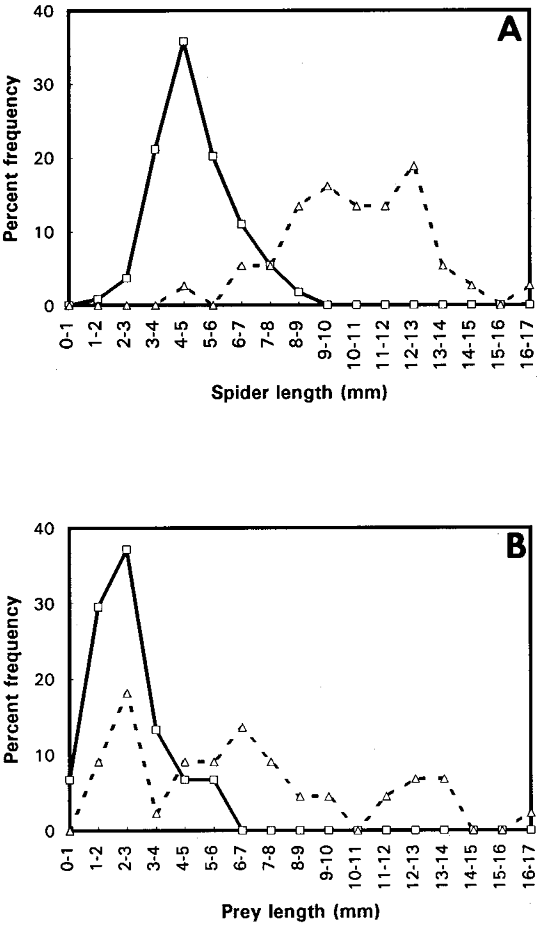

Fig. 2. (A) Body length frequency distribution of *Oxyopes salticus* (squares) versus *P. viridans* (triangles), among 17 size classes. Pooled data for prey-carrying spiders sampled between June and August in two cotton fields in Texas. (B) Prey length frequency distribution for *Oxyopes salticus* (squares)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

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 ($0.5 < \alpha < 0.7$, 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 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* ($\leq$8 mm length) versus the largest individuals of *O. salticus* ($\geq$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 ($\approx$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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