

Resource Partitioning among Five Agrobiont Spiders of a Rice Ecosystem

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Abida Butt and Hafiz Muhammad Tahir (2010) Resource partitioning among five agrobiont spiders of a rice ecosystem. *Zoological Studies* 49(4): 470-480. The present study was conducted to investigate possible factors responsible for the coexistence of 3 hunting spiders (*Lycosa terrestris*, *Pardosa birmanica*, and *Oxyopes javanus*) and 2 orb web spiders (*Tetragnatha javana* and *Neoscona theisi*) in a rice ecosystem of central Punjab, Pakistan. For this purpose 2 plots (each of 400 m²) were selected in a monoculture area of Sheikupura District, Punjab, Pakistan. The active density of spiders during the study period was recorded by pitfall trap and a suction device. Data showed that the active density of all spider species significantly differed among different trapping sessions. Members of both guilds fed on the same prey orders but in different proportions. Their reproductive period, abundances of young and adults, and prey size also differed. A positive correlation was found between the carapace width of a spider and prey it took. Values of resource overlap indicated that species of a guild were utilizing time, habitat, prey size, and prey taxa differently. A discriminant function analysis also clearly separated the 5 species in the 3 dimensional space. It was concluded that separation of guild members in time, microhabitat, and prey niche dimensions reduced competition, thus allowing coexistence. <http://zoolstud.sinica.edu.tw/Journals/49.4/470.pdf>

Key words: Niche overlap, Competition, Resource overlap.

Interspecific competition occurs among sympatric species when the availability of a shared resource is reduced in the environment. According to ecologists, competition is the major force that shapes the structure of a community. Different patterns in natural communities such as differential resource utilization, morphological divergences, variable life histories, segregation in activity times, and allotropic distributions can be explained within the framework of competition (MacArthur 1967, Schoener 1974, Toft and Schoener 1983). According to Molles (2007), these niche divergences are the result of directional selection. Sympatric species the niches of which overlap experience selective pressures that cause reduced niche overlap and allow the

species to coexist. Other studies reported that these niche divergences can be explained on the basis of predation, physical factors, or chance (Nieto-Castañeda and Jiménez-Jimenez 2009). If competition occurs in a predator community, it results in a more-reticulated food web, diminished top-down control, and the reduced probability of a trophic cascade (Rosenheim et al. 1995, Finke and Denno 2002).

Various studies reported ambiguous interspecific competition between spiders due to different types of niche segregation among coexisting species (Enders 1974, Finke and Denno 2002 2006, Langellotto and Denno 2006, Toshinori 2007, Uetz 1977 1991). For example, nocturnal sympatric araneids and tetragnathids

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exhibit temporal and spatial niche differentiation (Ward and Lubin 1992), diurnal wandering spiders show seasonal specialization (Uetz 1977, Turner and Polis 1979), and lycosids utilize different microhabitats (Carrel 2003). Cutler and Jennings (1992) also found that lycosids and salticids have habitat partitioning which allows them to coexist in the same area. Habitat complexity also reduces cannibalism among spiders due to lower encounter rates (Wise 2006). Henaut et al. (2001) reported prey partitioning among araneids. However, Spiller (1986), Wise (1983), and Schaefer (1978) reported evidence that interspecific competition may some time be a significant factor in a spider community.

The strength of competition is difficult to measure in the field. Several studies reported that niche overlap indicates current competition in species and also indicates whether competition was present or absent among these species in the past (Schoener 1974). If resources are not in short supply, 2 organisms can share them without detriment to one another, and niche overlap may be high. This represents reduced competition between species (Pianka 1975). So niche differences partially explain the absence of interspecific effects. It may be possible that population densities are not high enough for major competitive interactions to occur (Wise and Barata 1983). Agroecosystems are variable environments with wide niche dimensions. Dimensions of the niches also change with the growth of crops. This environmental variability may also reduce niche overlap between coexisting species.

The present study deals with 5 species of spiders that are very abundant in rice ecosystems of Punjab, Pakistan (Tahir and Butt 2008). All of these species utilize the same macrohabitat, food resources, and ecological time. Their foraging strategies determine that they can be used as biological control agents (Tahir et al. 2009). In conservation biological control, attempts are made to reduce pest problems by increasing the abundance and diversity of natural predators. Evidence suggests that increasing natural enemy diversity may have positive, negative, or neutral effects on a pest population, these effects of which can respectively be caused by niche complementarity, intraguild predation, and functional redundancy (Straub et al. 2008). So the study of niche diversification in organisms that are present on a large spatiotemporal scale will increase our ability to identify the right species that will ultimately help in biological control. On

the basis of these arguments, the present study was designed to understand how the most abundant spider species of a rice ecosystem are segregated in terms of spatial, temporal, and food resources. The answer to these questions will help us understand how the coexistence of 5 spider species takes place in a rice ecosystem. Carnivorous predators like spiders that coexist can provide better control of herbivorous prey.

MATERIALS AND METHODS

Study area

Fieldwork was conducted during 2006 and 2007 in rice fields of the Agriculture Research Farm (31°43'N, 73°59'E) in Sheikhpura District, Punjab, Pakistan. Two plots (each of approximately 400 m²) surrounded by other rice plots were selected for the study. Neither plot was treated with any type of insecticides or herbicides throughout the experimental period. Both fields were tilled in mid-Sept. during both study years. The rice variety grown in the fields was super basmati. During the course of the study, the temperature ranged 25-39°C during the day and 21-34°C at night. The relative humidity was highly variable (63%-86%) due to the monsoon season.

Experimental organisms

Five agrobiont spider species of rice ecosystems of central Punjab, Pakistan were selected for the present study. Of these species, three belonged to a hunting guild (*Lycosa terrestris* Butt et al. 2006, *Pardosa birmanica* Simon 1884, and *Oxyopes javanus* Thorell 1887), and 2 belonged to an orb-web guild (*Tetragnatha javana* (Thorell 1890) and *Neoscona theisi* (Walckenaer 1842)).

Collection of spiders

The activity density of spiders throughout the growth period of the crop was investigated using 2 types of sampling methods (pitfall traps and suction devices) every 2 wk from June to the end of Nov. (harvest time). To collect ground spiders in each plot, 20 pitfall traps consisting of wide-mouth glass jars (6 cm in diameter × 12 cm deep) were used. Four pitfall traps (on a 5 × 5 m grid pattern) were installed at each corner of the plots, and 4 in

the center. Ethylene glycol (95%; 250 ml) and 2 drops of 1% liquid detergent were added to each trap to break the surface tension. A rain cover (18 × 18 cm) constructed of 0.6 cm plywood, and supported by 3 nails (9 cm long) was placed over each trap (the height of rain cover over the mouth of the glass jar was 30 cm) to prevent flooding. At each field, traps were consecutively operated for 72 h (which was 1 trapping session).

Foliage organisms (spiders and other invertebrates) were collected using a suction device (Siemens VK 20C01, Gultig in der Bundesrepublik, Deutschland) from Aug. to Nov. Fifty rice plants were randomly selected from each plot, and each plant was vacuumed for 1 min from top to the bottom. Captured organisms were placed in small jars with 70% ethanol and transported to the laboratory for sorting and identification. Spiders were identified using Dyal (1935), Tikader and Malhotra (1980), Tikader and Biswas (1981), Barrion and Litsinger (1995), and other related literature. For orb-web spiders, data regarding web height and web diameter were also recorded.

Diet composition

To investigate the diet composition of hunting and orb-web spiders, direct observations were conducted in Sept. 2006 and 2007 for 1 h at dawn (06:30-07:30) and 1 h at dusk (17:00-18:00) for 3 d in every week by 3 different observers. In earlier studies, the highest activity of studied species was recorded at dawn and dusk (Tahir and Butt 2009, Tahir et al. 2009). Whenever, a spider was found eating prey, the spider and prey in the mouth of this spider, were collected and placed in a vial and preserved with 70% ethanol. Specimens were returned to the laboratory for measurements and prey identification. Prey groups were identified only up to order level. The size of the predator (carapace width and length of leg IV) and prey (length from the head to the tip of the abdomen) were measured to determine if correlations existed between predator size and prey length.

Statistical analyses

As there was no significant difference in the data of 2 yr, an average of the data of the 2 yr was used for the statistical analyses. The active density of spiders during different trapping sessions was compared using the Mann-Whitney

test. The active density of spiders captured from the ground during the 2 sampling years was compared by *t*-test. The numeric proportion of different prey orders taken by each guild member was compared using the Friedman test. The Wilcoxon signed-rank test was used to compare the size of prey taken by different spiders. Values of niche breadth and niche overlap were calculated to examine habitat, time, and prey relationships between species. Niche breadth was calculated using Levin's formula (1967), which measures how uniformly resources are being utilized by each species:

$$B = 1 / \sum pi^2;$$

where B is the Levin's measure of niche breadth, and pi is the proportion of individuals found using resource i . Niche breadth values nearer to 1 represent generalization, while values nearer to 0 represent specialization. The Kruskal-Wallis test was used to compare niche-breadth values of the 2 study years. A *t*-test was used to compare the activity densities of spider species collected during the 2 sampling years. To determine the niche overlap with time (on the basis of the total abundance of predators in different trapping sessions), a habitat (ground and foliage data), prey size (total length), and prey taxa (relative proportion) formula developed by MacArthur and Levins (1967) was used:

$$M_{jk} = \sum P_{ij} P_{ik} / \sum pi^2j;$$

where M is MacArthur and Levin's niche overlap measure of species k on species j , P_{ij} is the proportion resource i is of the total resource that species j utilizes, and P_{ik} is the proportion resource i is of the total resources that species k utilizes. Statistical software of Ludwig and Reynolds (1988) was used for niche breadth and overlap estimations. The body size (cephalothorax width) ratio of species pairs was calculated using a method described by Hutchinson (1959). To discriminate among species in time, habitat, and prey utilization, a discriminant function (DF) analysis (DFA) was performed using a linear DF. Pearson's correlation was used to determine the relationship of prey size with carapace width and IV leg length of spider species. Minitab 13.2 (Minitab inc. Pennsylvania, USA) and Statistica 6 (Statsoft inc. Oklahoma USA) were used for these statistical analyses.

RESULTS

In the present study, differences in the utilization of resources (i.e., time, habitat, prey size, and prey taxa) by 3 species of the hunting guild (*L. terrestris*, *P. birmanica*, and *O. javanus*) and 2 species of the orb-web guild (*T. javana* and *N. theisi*) were investigated. Table 1 shows the total number of individuals of each guild member collected from fields during the 2 sampling years. Of 5432 spider specimens, 3781 belonged to the studied species. Of these, 1566 were recorded from the ground and 2215 from foliage. There was no difference in the active densities of different species captured from the ground during the 2 sampling years ($t = 1.40$; $p = 0.23$). However, a significant difference was recorded in the foliage data of the 2 yr ($t = 3.33$; $p = 0.02$). Differences in the abundance patterns of the 5 agrobiont spiders are presented in figure 1 (the average of 2 yr of data was used for the plots in figure 1). The active densities of adults and young of *L. terrestris* vs. *P. birmanica* (Mann-Whitney *U*-test; $p = 0.014$ for

adults and $p = 0.011$ for young), *L. terrestris* vs. *O. javanus* (Mann-Whitney *U*-test; $p = 0.04$ for adults and $p = 0.02$ for young), and *N. theisi* vs. *T. javana* (Mann-Whitney *U*-test; $p = 0.023$ for adults and $p = 0.015$ for young) significantly differed among different trapping sessions. *Neoscon theisi* and *T. javana* also differed in their vertical utilization of habitat. The average height of the web from the ground for *T. javana* was 107 cm (SD = 6.31), and for *N. theisi* was 126 cm (SD = 5.41), whereas the average diameters of the webs were 26 cm (SD = 2.2, $n = 20$) for *T. javana* and 32 cm (SD = 5.2) for *N. theisi*.

Homoptera, Diptera, Lepidoptera, Hymenoptera, Heteroptera, Coleoptera, Orthoptera, and Araneae were prey items observed in the field. All spiders basically fed on the same prey orders but in different proportions (Friedman test, $p < 0.001$ for hunting spiders and $p = 0.02$ for orb-web spiders) (Table 2). Marked differences were recorded when the prey sizes consumed by 3 species of hunting guild and 2 orb-web spiders were compared (Wilcoxon signed-

Table 1. Total abundances of 5 agrobiont spiders in rice fields

Species	Habitat				Total
	Ground (2006)	Foliage (2006)	Ground (2007)	Foliage (2007)	
<i>Lycosa terrestris</i>	609	201	530	158	1498
<i>Pardosa birmanica</i>	222	-	189	-	411
<i>Oxyopes javanus</i>	4	362	7	311	684
<i>Tetragnatha javana</i>	3	514	2	467	986
<i>Neoscona theisi</i>	-	111	-	91	202
Total					3781

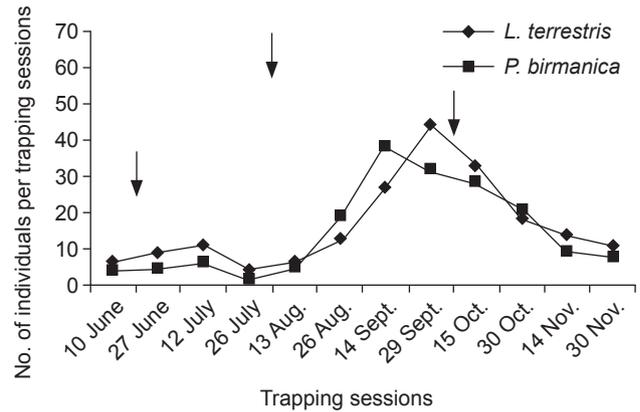
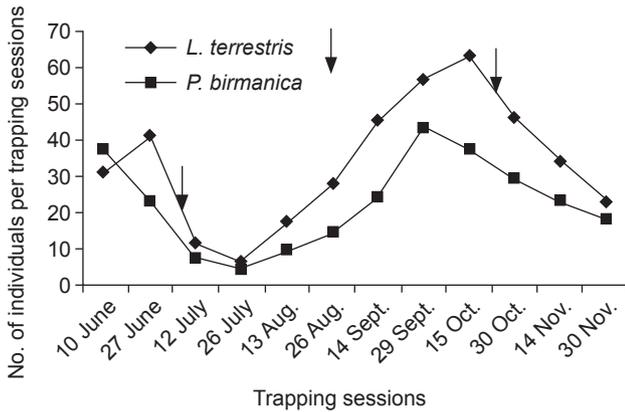
Table 2. Observed diets of hunting and orb-web spiders by prey order. Values given are the average of 2 yr of data (2006-2007)

Order	Hunting spiders			Orb-web spiders	
	<i>L. terrestris</i>	<i>P. birmanica</i>	<i>O. javanus</i>	<i>T. javana</i>	<i>N. theisi</i>
Homoptera	48 (40)	35 (36.08)	17 (25.37)	17 (19.10)	10 (15.87)
Diptera	36 (30)	24 (24.74)	13 (19.40)	22 (24.71)	15 (23.80)
Heteroptera	4 (3.3)	6 (6.18)	3 (4.47)	-	-
Lepidoptera	6 (5)	4 (4.12)	18 (26.86)	37 (41.57)	21 (33.33)
Orthoptera	8 (6.6)	9 (9.27)	4 (5.97)	2 (2.24)	7 (11.11)
Coleoptera	1(0.83)	-	-	-	2 (3.17)
Hymenoptera	-	-	-	2 (2.24)	3 (4.76)
Araneae	8 (6.6)	11(11.34)	8 (11.94)	2 (2.24)	2 (3.17)
Others	9 (7.5)	8 (8.24)	4 (5.97)	7 (7.86)	3 (4.76)
Total observations	120	97	67	89	63

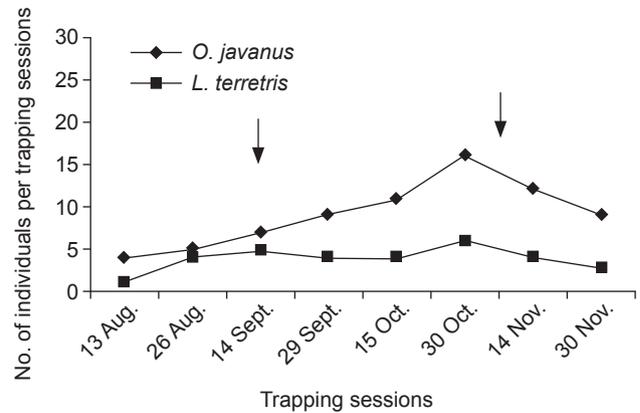
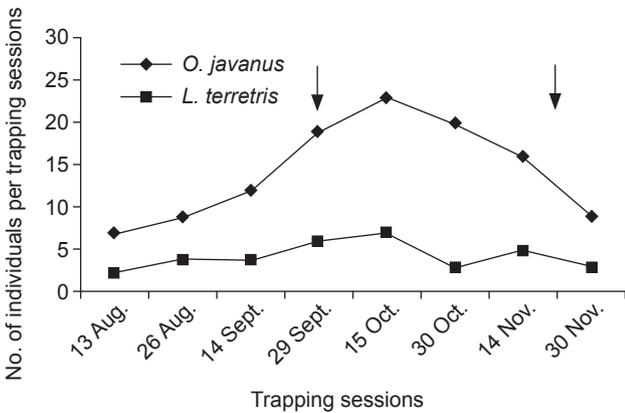
rank test, $p = 0.02$ and < 0.001 , respectively). The prey size taken by each species increased with an increase in the carapace width (Table 3). But

no relationship was observed between prey size and leg (IV) length of all spider species (Pearson's correlation, $p > 0.05$ for all species).

Plot 1



Plot 2



Adults Plot 3 Young

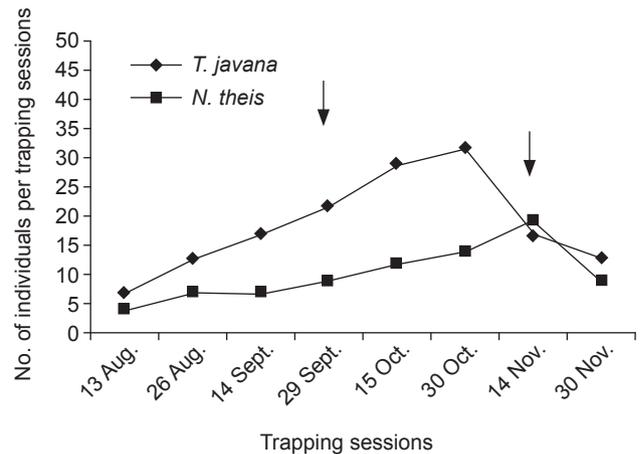
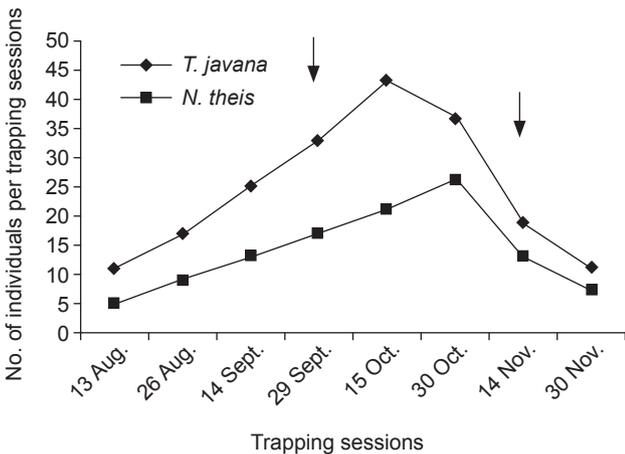


Fig. 1. Seasonal dynamics of ground hunters (plot 1), foliage hunters (plot 2), and orb-web spiders (plot 3). Note: There are 3 arrows in plot 1 and 2 in plots 2 and 3. The 1st arrow in plot 1 indicates transplantation of seedlings in the field, the 2nd and 3rd represent the milking (immature stage before ripening of the fruit) and harvesting stages, respectively. The 1st and 2nd arrows in plots 2 and 3 represent the milking and harvesting stages, respectively.

Niche breadth indices (B) were employed to gain insights into the time, habitat, and prey relationships of the species (Table 4). Comparisons of niche breadth values (for time, habitat, prey size, and prey taxa) of the 2 study years (for both guilds) showed no difference (Kruskal-Wallis test, $p > 0.05$ for both guilds). In the guild of hunting spiders, *P. birmanica* appeared to be a habitat specialist, while *O. javanus* was a time specialist. *Lycosa terrestris* was found to be a generalist in all studied dimensions. In the orb-web guild (i.e., *T. javanas* and *N. theisi*), niche breadth values indicated that both species were specialized in time and habitat while generalized in prey selection.

Niche overlap values between species (6 pairs) are given in table 5. Those species pairs which showed no sort of apparent interaction (*P. birmanica* × *T. javana*; *P. birmanica* × *N. theisi*, etc.) were not included. Of the hunting spiders, only 1 pair (*L. terrestris* × *P. birmanica*) showed overlap values of > 50% in time and prey (both size and taxa) niche dimensions; however this species pair was separated in the habitat niche dimension. Orb-web spiders (*T. javana* × *N. theisi*) also exhibited relatively high overlap (> 55%) in only the time niche dimension, but was separated in the habitat and prey (both size and prey taxa) niche dimensions. Niche overlap values for the other species pairs were smaller (< 45%) for all

Table 3. Correlation coefficients (r) for carapace width and prey length (A) and leg length and prey length (B)

(A)

Spider species	Carapace width (mm)	Prey length (mm)	Correlation coefficient (r)	p value
Hunting spiders				
<i>Lycosa terrestris</i>	2.3 - 2.8	2.4 - 19.5	0.59	< 0.01
<i>Pardosa birmanica</i>	1.9 - 2.7	3.4 - 14.4	0.47	< 0.01
<i>Oxyopes javanus</i>	1.8 - 2.7	4.1 - 23	0.44	< 0.05
Orb-web spiders				
<i>Neoscona theisi</i>	2.3 - 3.1	4.7 - 32.5	0.73	< 0.01
<i>Tetragnatha javana</i>	0.9 - 1.2	2.5 - 26	0.42	< 0.05

(B)

Spider species	Leg length (mm)	Prey length (mm)	Correlation coefficient (r)	p value
Hunting spiders				
<i>Lycosa terrestris</i>	9.5 -10.13	2.4 - 19.5	0.27	> 0.05
<i>Pardosa birmanica</i>	9.7 -11.11	3.4 - 14.4	0.09	> 0.05
<i>Oxyopes javanus</i>	7.9 - 9.7	4.1 - 23	0.12	> 0.05
Orb-web spiders				
<i>Neoscona theisi</i>	9.7 -11.4	4.7 - 32.5	0.19	> 0.05
<i>Tetragnatha javana</i>	9.5 -12.6	2.5 - 26	0.21	> 0.05

p values of < 0.05 represent a significant positive correlation.

Table 4. Niche breadth (B) values for the 5 most dominant spiders species in the rice ecosystem

Spider	2006				2007				2006-2007			
	Habitat	Time	Prey size	Prey taxa	Habitat	Time	Prey size	Prey taxa	Habitat	Time	Prey size	Prey taxa
Hunting spiders												
<i>Lycosa terrestris</i>	0.64	0.79	0.62	0.59	0.64	0.68	0.66	0.69	0.66	0.81	0.69	0.71
<i>Pardosa birmanica</i>	0.29	0.71	0.58	0.53	0.36	0.61	0.43	0.51	0.38	0.78	0.59	0.63
<i>Oxyopes javanus</i>	0.51	0.39	0.61	0.64	0.69	0.46	0.56	0.37	0.53	0.41	0.64	0.67
Orb-web spiders												
<i>Neoscona theisi</i>	0.11	0.34	0.76	0.73	0.17	0.37	0.61	0.66	0.21	0.34	0.83	0.79
<i>Tetragnatha javana</i>	0.27	0.37	0.78	0.71	0.23	0.35	0.69	0.71	0.29	0.39	0.79	0.73

studied dimensions.

To assess the actual overlap in niches of the various species pairs, the combined effect of 4 niche dimensions was also examined (Table 5). None of the species pairs showed high overall overlap, indicating that species members were sufficiently separated with respect to time, habitat, prey size, and prey taxa. Separation of spider species was clearer after the DFA (Fig. 2). Collectively, the 3 axes of the DFA explained 93.59% of the variation among species. The 1st DF (related to the distribution of species in the habitat) accounted for 68.29% of the variation, the 2nd DF (related to the temporal distribution

of species) explained an additional 13.9% of the variation, and the 3rd DF (related to prey size) covered 11.4% of the variation among species. Body size ratio was higher for all species than 1.26 (minimum value for coexistence according to Hutchinson) (Table 6).

DISCUSSION

The 5 common species of spiders considered in this study belonged to hunting and orb-web guilds. The hunting guild included 2 species of the family Lycosidae (i.e., *L. terrestris* and *P.*

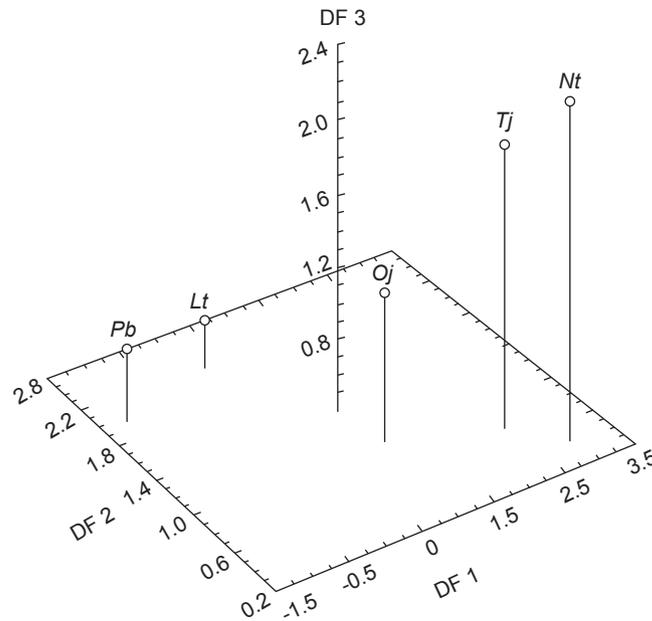


Fig. 2. Separation of 5 coexisting species in a 3 dimensional space by a discriminant function (DF) analysis. Key: *Lt*, *Lycosa terrestris*; *Pb*, *Pardosa birmanica*; *Oj*, *Oxyopes javanus*; *Tj*, *Tetragnatha javana*; *Nt*, *Neoscona theisi*. DF1, vertical distribution; DF2, temporal distribution; DF3, prey type.

Table 5. Resource overlap values among the 5 most dominant spider species of a rice ecosystem (both years combined) on the basis of exploitation of 4 niche dimensions (time, habitat, prey size, and prey taxa) as well as overall overlap values

Species (i,k)	Habitat (i,k) (k,i)	Time (i,k) (k,i)	Prey size (i,k) (k,i)	Prey taxa (i,k) (k,i)	Overall (i,k) (k,i)
<i>L. terrestris</i> × <i>P. birmanica</i>	0.29 , 0.14	0.63 , 0.56	0.43 , 0.54	0.42 , 0.51	0.39 , 0.36
<i>L. terrestris</i> × <i>O. javanus</i>	0.31 , 0.11	0.41 , 0.39	0.23 , 0.38	0.19 , 0.32	0.24 , 0.30
<i>P. birmanica</i> × <i>O. javanus</i>	0.09 , 0.18	0.21 , 0.31	0.05 , 0.38	0.11 , 0.29	0.03 , 0.26
<i>O. javanus</i> × <i>T. javana</i>	0.31 , 0.26	0.19 , 0.41	0.09 , 0.22	0.16 , 0.23	0.10 , 0.22
<i>O. javanus</i> × <i>N. theisi</i>	0.21 , 0.28	0.11 , 0.18	0.34 , 0.21	0.26 , 0.19	0.34 , 0.22
<i>T. javana</i> × <i>N. theisi</i>	0.19 , 0.21	0.58 , 0.61	0.41 , 0.38	0.46 , 0.39	0.31 , 0.41

Genera are defined in table 2.

birmanica) and 1 species of the family Oxyopidae (i.e., *O. javanus*). Both species of orb-web guilds belonged to 2 different families i.e., the Araneidae and Tetragnathidae. Despite the taxonomic diversity, these species occupy the same habitat and had similar ecological and behavioral aspects. Similarity in habitat occupancy indicates that these species should intensively compete with each other (Holt et al. 1994). In order to coexist, these species should segregate in other niche dimensions such as food, time, and microhabitat.

All studied species were present in different strata of the same habitat. According to niche breadth values, *L. terrestris* should be the most abundant species and *N. theisi* should be the rarest and most restricted in the range of macrohabitat occupied. This pattern is shown in table 1. This indicates that although both macrohabitats (ground and foliage) were available for each species, large interspecific differences were present in the tolerance and avoidance of a particular habitat. Among the hunters, *L. terrestris* used habitat resources horizontally as well as vertically, while *O. javanus* only used them vertically and *P. birmanica* only horizontally. Both orb-web spiders (*N. theisi* and *T. javana*) used the habitat only vertically but further partitioned it by making webs at different heights (Tahir et al. 2009). Habitat overlap values were also low in the present study, which indicates that all of these abundant species were well segregated in spatial dimensions of the niche. Many other workers also reported that sympatric spider species segregate by vertical and horizontal stratification of habitat (Greenstone 1980, Henaut et al. 2001, Nieto-Castañeda and Jiménez-Jimenez 2009). It was shown in both mathematical models and the laboratory that habitat complexity allows the coexistence of species (Huffaker 1966, Levin

1974, Prokop 2006). Selection of microhabitats in a complex field environment also reduces intraguild predation among spiders due to lower encounter rates (Finke and Denno 2002 2006). However, habitat heterogeneity may act as a limiting factor by increasing the mortality of dispersers (Morris 1963) or by reducing host-finding ability (Tahvanian and Root 1972). If populations are limited by these factors, then competition might never occur.

Niche breadth values calculated on the basis of seasonal activity were low for the orb-web guild members and 1 hunter species, i.e., *O. javanus*. However, these values were broader for *L. terrestris* and *P. birmanica*. Broader niche values for *L. terrestris* and *P. birmanica* were due to their early appearance in the field. These species were present in the field even at the seedling stage, whereas the other species invaded the crop after the development of foliage. During the study, the population size and structure of all species changed with the crop phenology. The density of each spider species in the field increased with an increase in the crop foliage but began to decline after senescence of the crop. The increasing complexity of the habitat with time offers more shelter, food, and microhabitats for the spiders (Öberg and Ekblom 2006). Members of both hunter and foliage guilds also differed in their reproductive period as shown in figure 1. All hunters reproduced earlier (Sept.) than orb-web spiders (Oct.) in the field. This also showed that the same field was stratified in time by these species in terms of reproduction, which is also an important means of reducing competition. According to the prediction of Hutchinson (1959), larger spiders (congeners) breed first and thus maintain the size differential. This prediction was not true in the present study. For example among the hunters, *P. birmanica* (body length 3.13-6.63 mm) bred first compared to *L. terrestris* (body length 6.25-7.38 mm). According to Tahir et al. (2009), both studied orb web spiders are nocturnal and begin web construction at almost the same time so cannot be segregated in time. Similarly, all of the hunting spiders were diurnal, and their activities and activity times overlapped each other. Turner and Polis (1979) and Uetz (1977) also stated that temporal segregation is an important factor in reducing niche overlap. This type of segregation was also reported for coexisting species of spiders on soybean farms in Ohio (Marshall et al. 2002).

Spiders are generalist predators, and prey compositions do not usually greatly differ among coexisting species when similar-sized species

Table 6. Hutchinson's ratio (carapace size of larger species/carapace size of smaller species). Spiders are arranged in the order of decreasing size

	Carapace size (mm)	Hutchinson's ratio
Hunters		
<i>Lycosa terrestris</i>	2.70	1.17
<i>Oxyopes javanus</i>	2.59	1.13
<i>Pardosa birmanica</i>	2.3	-
Orb-web spiders		
<i>Neoscona theisi</i>	1.9	1.72
<i>Tetragnatha javana</i>	1.1	-

are compared (Nyffeler and Benz 1987, Eberhard 1990, Miyashita 1991). In the present study, all studied species basically fed on the same orders but in different proportions (Table 2). Similar results were reported by Nyffeler (1999). Utilization of prey taxa in different proportions helps reduce competition among coexisting species. Dietary mixing also optimizes a balanced nutrient composition needed for the survival and reproduction of spiders (Uetz et al. 1992). A high proportion of Lepidoptera was observed in the diet of orb-web spiders (the main prey item of orb web spiders) in the present study. This might be expected as most of the insects were caught in the webs of both the orb-web spiders mainly during night. Slowly flying insects with relatively large surface areas like Lepidoptera which are also highly active at night can easily be caught in freshly prepared webs of these spiders when visibility is low (Kraker et al. 1999). Specimens of Homoptera and Diptera formed a major portion of the diet of all studied spiders, but their frequency patterns differed.

Niche breadth values for prey (on the basis of prey size and prey taxa) in the present study were broader for orb-web spiders (*N. theisi* and *T. javana*) compared to hunting spiders (Table 4). These results are in contrast with the findings of Nyffeler (1999), which showed greater niche breadth of hunters compared to web-weavers in agro-ecosystems. Broader niche breadth values for orb-web spiders were due to their dependence on food captured in the web. Web spiders can capture prey items in their webs which cannot be captured by the species individuals themselves due to their physical activity.

Food size was the most tractable niche dimension, and therefore the one most used in theoretical models of resource allocation and species packing. Differences in the reproductive periods of closely related species also enable them to diverge in food because prey size depends on the body size of the predator. Hunting spiders consume prey of similar size to themselves (Nentwig and Wissel 1986). According to Hutchinson (1959) the mean body size ratio of ≥ 1.26 is required for the coexistence of species. This was suggested as a mean for a community to allocate food size among its members and minimize competition. The body size ratios of these 2 species of the hunting guild were lower than the predicted value of 1.26 indicating that *L. terrestris* and *O. javanus* compete for prey with *P. birmanica*. This is true for *L. terrestris* but not for

O. javanus, because there is no direct interaction between *O. javanus* and *P. birmanica* (*O. javanus* is a foliage hunter while *P. birmanica* is a ground hunter). The overlap values of prey dimensions, i.e., size and taxa, also indicated that competition exists between *L. terrestris* and *P. birmanica* for this resource. Data showed that spiders with a larger carapace take larger prey. A larger carapace is advantageous for capturing prey but suppresses starvation tolerance. A larger carapace has bigger muscles and therefore consumes more energy. Thus, there is a tradeoff between the carapace width and hunting ability of hunting spiders (Iida and Fujisaki 2005).

According to May (1975), the total niche overlap can be either overestimated (e.g., a large overlap is found for prey taxa when in actuality, taxa are being partitioned by size or microhabitat) or underestimated (e.g., prey taxa are highly correlated with size and/or microhabitat, but are being treated as an independent dimension). Values of total niche overlap are given in table 5. All species pairs had niche overlap values of $< 54\%$, implying a minimal degree of competition in resource utilization (MacArthur and Levins 1967). All studied species can coexist because none of the species pairs in the present study showed total overlap values exceeding 54%. The entire community appears to be staggered in the total niche space.

The lower overlap values of all species pairs showed that resources were not limited in the habitat. This may have been due to interspecific and intraspecific predation, which limits the population of each guild species below the carrying capacity of an agro-ecosystem (Kuroda et al. 2005). It was also observed that utilization of resources peaked after all resources had reached their maximum carrying capacities. According to Lotka (1925), Volterra (1926), and Gause (1934), no 2 species can occupy the same niche. But according to Vandermeer et al. (2002), formulating the classical equations on the basis of nonlinearities of niche dimension increases the probability of coexistence even with higher levels of competition. In rice fields, agrobiont spiders appeared to be well adopted due to minimized competition. However, in the rice fields of Punjab, Pakistan, many species of the same guilds are present, although in fewer numbers (Tahir and Butt 2008). The presence of other guild members in lower numbers indicated that resources in rice fields are not completely utilized by only agrobiont species. However, it also indicated that

competition may have been present in the species of a guild in the past due to severe environmental conditions or resource limitations. These conditions produced periodic crunches (Wiens 1977), which led towards the present community patterns.

The results of our experiments indicate that competition among agrobiont spider species has minimal or no effect on their microhabitat segregation, growth, survival, or quality and type of prey captured. So the conservation of these species in rice fields can increase their biological control potential. However, before doing that, we have to check whether intraguild predation occurs in these spider species or not. It may also be possible that other physical factors are controlling resource utilization patterns.

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REFERENCES

- Barrion AT, AJ Litsinger. 1995. Rice land spiders of South and Southeast Asia. Wallingford, England: CAB International.
- Butt A, R Anwar, M Tahir. 2006. Some new species of family Lycosidae from agricultural fields of Punjab, Pakistan. *Pakistan J. Zool.* **36**: 185-190.
- Carrel JE. 2003. Ecology of true burrowing wolf spiders (Araneae: Lycosidae). *J. Kansas Entomol. Soc.* **76**: 16-30.
- Cutler B, DJ Jennings. 1992. Habitat segregation by species of *Metaphidippus* (Araneae: Salticidae) in Minnesota. *J. Arachnol.* **20**: 88-93.
- Dyal S. 1935. Fauna of Lahore: spiders of Lahore. *Bull. Zool. Punj. Univ.* **1**: 119-252.
- Eberhard WG. 1990. Function and phylogeny of the spider webs. *Ann. Rev. Ecol. Syst.* **21**: 341-372.
- Enders F. 1974. Vertical stratification of orb-web spiders (Araneidae: Araneae) and consideration of other methods of coexistence. *Ecology* **57**: 238-251.
- Finke DL, RF Denno. 2002. Intraguild predation diminished in complex-structured vegetation: implication for prey suppression. *Ecology* **82**: 643-652.
- Finke DL, RF Denno. 2006. Spatial refuge from intraguild predation: implications for prey suppression and trophic cascades. *Oecologia* **149**: 265-275.
- Gause GF. 1934. The struggle for existence. New York: Hafner, 163 pp.
- Greenstone MH. 1980. Contiguous allotopy of *Pardosa ramulosa* and *Pardosa tuoba* (Araneae: Lycosidae) in the San-Francisco Bay Region and its implications for patterns of resource partitioning in the genus. *Am. Midland Nat.* **104**: 305-311.
- Henaut Y, J Pablo, G Ibarra-Nuñez, T Williams. 2001. Retention, capture and consumption of experimental prey by orb-web weaving spiders in coffee plantations of southern Mexico. *Entomol. Exp. Appl.* **98**: 1-8.
- Holt RD, J Grover, D Tilman. 1994. Simple rules for interspecific dominance in systems with exploitative and apparent competition. *Am. Nat.* **144**: 741-771.
- Huffaker CB. 1966. Competition for food by phytophagous mites. *Hilgardia* **37**: 553-561.
- Hutchinson GE. 1959. Homage to Santa Rosalia or Why are there so many animals? *Am. Nat.* **93**: 145-159.
- Iida H, K Fujisaki. 2005. Adaptive significance of gregarious phase in nymphs of wolf spiders *Pardosa pseudoanulata* (Araneae: Lycosidae). *J. Appl. Entomol. Zool.* **40**: 649-657.
- Kraker De J, A Van Huis, KL Heong, IC Van Lenleren, R Robbinge. 1999. Population dynamics of rice leafhopper and their natural enemies in irrigated rice fields in Philippines. *Bull. Entomol. Res.* **89**: 411-421.
- Kuroda M, K Wada, M Kamada. 2005. Factors influencing coexistence of two brachyuran crabs, *Helice tridens* and *Parasesarma plicatum*, in an estuarine salt marsh, Japan. *J. Crustacean Biol.* **25**: 146-153.
- Langellotto GA, RF Denno. 2006. Refuge from cannibalism in complex-structured habitats: implications for the accumulation of invertebrates. *Ecol. Entomol.* **29**: 566-577.
- Levin SA. 1974. Dispersion and population interactions. *Am. Nat.* **108**: 207-228.
- Lotka AJ. 1925. *In* Chapman R.N. 1931. Elements of physical biology. Baltimore, MD: Williams and Wilkins Baltimore.
- Volterra, V. 1926, pp. 409-448.
- Ludwig JA, JF Reynolds. 1988. Statistical ecology: a primer on methods in computing. New York: J Wiley, 337 pp.
- MacArthur R, R Levins. 1967. The limiting similarity, convergence, and divergence of coexisting species. *Am. Nat.* **101**: 377-385.
- Marshall J, WP Kelley, SS Rubakhin, JP Bingham, JV Sweedler, WF Gilly. 2002. Anatomical correlates of venom production in *Conus californicus*. *Biol. Bull.* **203**: 27-41.
- May RM. 1975. Some notes on estimating the competition matrix. *Alpha Ecol.* **56**: 737-741.
- Miyashita T. 1991. Direct evidence of food limitation for growth rate and body size in the spider *Nephila clavipes*. *Acta Arachnol.* **40**: 17-21.
- Molles M. 2007. Ecology: concepts and applications. 4th ed. New York: McGraw Hill, pp. 309-317.
- Morris RF. 1963. The dynamics of epidemic spruce budworm populations. Canada: Memorial Entomology Society of Canada, **31**: 1-332.
- Nentwig W, C Wissel. 1986. A comparison of prey lengths among spiders. *Oecologia* **68**: 595-600.
- Nieto-Castañeda IG, ML Jiménez-Jiménez. 2009. Possible niche differentiation of two desert wandering spiders of genus *Syspira* (Araneae: Miturgidae). *J. Arachnol.* **37**: 299-305.
- Nyffeler M. 1999. Prey selection of spiders in the field. *J. Arachnol.* **27**: 317-324.
- Nyffeler M, G Benz. 1987. Spiders in natural pest control: a review. *J. Appl. Entomol.* **103**: 321-339.
- Öberg S, B Ekbohm. 2006. Recolonisation and distribution of spiders and carabids in cereal fields after spring sowing. *Ann. Appl. Biol.* **149**: 203-211.
- Pianka ER. 1975. Niche relations of desert lizards. *In* M Cody,

- J Diamond, eds. Ecology and evolution of communities. Cambridge, MA: Harvard Univ. Press, pp. 292-314.
- Prokop P. 2006. Prey type does not determine web design in two orb-weaving spiders. *Zool. Stud.* **45**: 124-131.
- Rosenheim JA, HK Kaya, LE Ehler, JJ Marois, BA Jaffee. 1995. Intraguild predation among biological control agents: theory and evidence. *Biol. Control* **5**: 303-335.
- Schaefer M. 1978. Some experiments on the regulation of population density in the spider *Floronia buccelenta* (Araneida: Linyphiidae). *Symp. Zool. Soc. Lond.* **42**: 203-210.
- Schoener TW. 1974. Resource partitioning in ecological communities. *Science* **185**: 27-39.
- Simon E. 1884. Les arachnides de France, Tome V, troisième partie contenant la famille des Theridionidae. (fin). Paris: Roret, pp. 421-885.
- Spiller DA. 1986. Interspecific competition between spiders and its relevance to biological control by general predators. *Environ. Entomol.* **15**: 177-181.
- Straub CS, DL Finke, WE Synder. 2008. Are the conservation of natural enemy biodiversity and biological control compatible goals? *Biol. Control* **42**: 225-237.
- Tahir HM, A Butt. 2008. Activities of spiders in rice fields of central Punjab, Pakistan. *Acta. Zool. Sin.* **54**: 701-711.
- Tahir HM, A Butt. 2009. Predatory potential of three hunting spiders inhabiting the rice ecosystems. *J. Pest. Sci.* **82**: 217-225.
- Tahir HM, A Butt, MS Sherawat. 2009. Foraging strategies and diet composition of two orb-web spiders of rice ecosystem. *J. Arachnol.* **37**: 357-362.
- Tahvaninan JO, RB Root. 1972. Influence of vegetational diversity on the population ecology of a specialized herbivore, *Phyllotreta cruciferae*. *Oecologia* **10**: 321-346.
- Tikader BK, B Biswas. 1981. Spider fauna of Calcutta and vicinity. *Rec. Zool. Surv. India* **30**: 1-48.
- Tikader BK, MS Malhotra. 1980. The fauna of India. *Rec. Zool. Surv. Calcutta India* **1**: 272-439.
- Toft CA, TW Schoener. 1983. Abundance and diversity of orb spiders on 106 Bahamian islands: biogeography at an intermediate trophic level. *Oikos* **41**: 411-426.
- Toshinori O. 2007. Prey of two species of jumping spiders in the field. *Appl. Entomol. Zool.* **42**: 663-668.
- Turner M, GA Polis. 1979. Pattern of coexistence in a guild of raptorial spiders. *J. Anim. Ecol.* **4**: 531-341.
- Uetz GW. 1977. Coexistence in a guild of wandering spiders. *J. Anim. Ecol.* **46**: 531-541.
- Uetz GW. 1991. Habitat structure and spider foraging. In SA Bell, ED McCoy, HR Mushinsky, eds. *Habitat Structure: The Physical Arrangement of Objects in Space*. Chapman & Hall, London, pp. 325-348.
- Uetz GW, J Bischoff, J Raver. 1992. Survivorship of wolf spiders (Lycosidae) reared on different diets. *J. Arachnol.* **20**: 207-211.
- Vandermeer J, MA Evans, P Foster, T Hook, M Reiskind, M Wund. 2002. Increased competition may promote species co-existence. **99**: 8731-8736.
- Volterra V. 1926. Variazioni e fluttuazioni del numero d'individui in specie d'animali conviventi. *Mem. Acad. Lincei* **1**: 31-113.
- Ward D, Y Lubin. 1992. Temporal and spatial segregation of web-building in a community of orb-weaving spiders. *J. Arachnol.* **20**: 73-87.
- Wiens JA. 1977. On competition and variable environment. *Am. Sci.* **65**: 259-267.
- Wise DH. 2006. Cannibalism, food limitation, intraspecific competition, and the regulation of spider populations. *Ann. Rev. Entomol.* **51**: 441-465.
- Wise DH, JL Barata. 1983. Prey of two syntopic spiders with different web structures. *J. Arachnol.* **11**: 271-281.