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Co-existence of Four Orb Weaving Spiders in the Rice Ecosystem

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Abstract.- Four orb weaving spider species *i.e.*, *Argiope trifasciata* (Forsskål, 1775), *Neoscona theisi* (Walckenaer, 1841) of family Araneidae and *Leucauge decorata* (Blackwall, 1864), *Tetragnatha javana* (Thorell, 1890) of family Tetragnathidae co-exist in the rice agro-ecosystem of Punjab, Pakistan. In the present study we investigated how four species segregate the available resources among themselves to reduce the competition and to make their co-existence possible. The studied species differed significantly in their web architecture and body size. All studied species showed low overall niche overlap values. The four orb weaving species also differed in the frequency with which they captured the different types of prey and prey size. The results of the present study suggested that differences in the selection of prey according to their own body size and construction of webs at different heights (spatial segregation) minimize competition and promote co-existence of studied species in sympatry.

Keywords: Niche overlap, orb weaving spiders, co-existence, spatial segregation.

INTRODUCTION

Spiders with similar ecological requirements are expected to partition the resources to minimize the competition for the available resources (Herder and Freyhoff, 2006; Schwemmer *et al.*, 2008; Richardson and Hanks, 2009) especially when the resources are limited. Partitioning of the available resources is only possible if there is divergence in the utilization of the resources by co-occurring species (Walter, 1991). Different orb weaving spiders can co-exist in the same habitat only if they construct webs at different positions (Enders, 1974; Cumming and Wesolowska, 2004), capture prey of different sizes and types (Harwood *et al.*, 2003) and differ in the timing of their reproduction (Spiller, 1984; McReynolds and Polis, 1987). Although orb weaving spiders compete for available resources (Spiller, 1984; Nyffeler and Benz, 1989) but the differences in their body sizes (*i.e.*, carapace width and body length) and web architecture (*i.e.*, hub height, capture area, mesh size) alter their ability to capturing different types or numbers of prey (Risch, 1977; Uetz *et al.*, 1978; Culin and Yeargan, 1982; McReynolds and Polis, 1987; Nyffeler *et al.*, 1989).

Argiope trifasciata (Forsskål, 1775), *Leucauge decorata* (Blackwall, 1864), *Neoscona theisi* (Walckenaer, 1842) and *Tetragnatha javana* (Thorell, 1890) are orb web spiders of two families, Araneidae and Tetragnathidae, that co-exist in the rice fields of central Punjab, Pakistan (Tahir and Butt, 2008). These species utilize same macrohabitat, food resources and ecological time. If these species live sympatrically, they must be able to partition the available resources in a way that reduces niche overlap. Present study is aimed to test the hypothesis that how these species segregate the available resources (food and habitat) among themselves to reduce the competition and to make their co-existence possible. The study of niche diversification will increase our ability to identify the species that will ultimately be helpful in the biological control of insect pests.

MATERIALS AND METHODS

Study area

The study was conducted over a two year period (2008-2009) at rice fields (rice variety grown was super basmati) of Adaptive Research Farm (31°43’N, 73°59’E) in district Sheikupura, Punjab, Pakistan. For the study two plots (about 4000 square meter each) were selected. Each plot was surrounded by other rice plots from all sides.

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Selected plots were not treated with any type of pesticides or herbicides. Tillage activity was done in both plots in mid-September (2008) and late-September (2009). During the study, the daily temperature ranged from 25±5°C (at night) to 34±5°C (during the day). The relative humidity was highly variable (65-86%) due to rainy season.

Relative abundance of orb web spiders

The relative abundance of orb-weaving spider species in the study area was measured twice per month per year (from August through November). During the study data of only adult females was collected. We did not use males in our study as they often do not spin webs (Wise, 1993). To assess the relative abundance of orb web spiders in the study area rice plants (n = 30 each year) were randomly selected in each plot during each sampling data and each plant was visually searched for two minutes from top to the bottom. At each sampling date number of plants was same (n =30) but plants were not same. Spiders were removed from each web with forceps, placed in small jars filled with 70% ethanol and transported to the laboratory for sorting and identification. Orb weaving web spiders were identified with the help of available literature.

Web architecture and body size

Web architecture (*viz*., height of hub above ground, web capture area, mesh size, number of spirals and number of radii) and body size (viz., body length, carapace width and wet weight) of each spider were also recorded. Web characteristics were measured directly in the field after removing corresponding spider from the web (numbers of web studied varied for each species due to difference in their availability). For recording the web data, each web was sprayed with a fine mist of water and cornstarch using Knapsack hand sprayer (THS-119428) to improve the resolution (Tahir *et al.*, 2010). The occupant of each web was collected in a glass tube (5 cm long and 2 cm wide, mouth covered by mesh cloth) and brought to the laboratory for the measurement of body length (in mm), carapace width (in mm) and wet weight (mg).

Prey recorded from webs of spiders

To record the data of prey of orb weaving spiders arthropod prey remains from webs of all spiders were identified directly in the field up to order level. Those preys which could not be identified in the field were preserved in 70% ethanol and brought to the laboratory for identification. In the laboratory size (length) of each prey was also measured. The general abundance of potential prey within study plots was also estimated in mid-September (peak of crop season) each year. For this purpose total number of prey items (flying insects) from 1 m^2 area (randomly chosen from ten different areas) were covered all of a sudden by two plastic bags and then all plants were cut just above the root. The entire rice stem thus cut were brought to the laboratory and carefully examined for the insects.

Statistical analyses

Kolmogorov-Smirnov test was used to check the normality of the data before statistical analyses. For all of the analyses performed in this study, means (±SE) were calculated by totaling data within years and then averaging across years. Abundance of spiders during different trapping sessions (sampling dates) was compared using Mann-Whitney test. Differences in the web characteristics and body size were tested by ANOVA. Bar graphs were plotted showing the mean spider length, mean carapace width, mean wet weight and mean hub height above ground, mean capture area of web, mean mesh size, mean number of spirals and mean number of radii. Friedman's test was used to determine whether individuals of different species differed in the type of prey that were captured or whether the prey they captured differed from a random sampling of available prey in the study area. Kruskal-Wallis test was used to compare the size of prey taken by different spider species. Pearson's correlation was used to determine the relationship of prey size with the predator size. To determine the niche overlap for habitat (height of webs), prey size (total length) and prey taxa (relative proportion) formula developed by MacArthur and Levins (1967) was used.

$$Mjk = \Sigma\, pij\, pik / \Sigma\, pi^2 j$$

where M is the MacArthur and Levins niche overlap measure of species *k* on species *j*, *pij* is the proportion of the resource *i* that species *j* utilizes, and *pk* is the proportion of the resource *i* that species *k* utilizes. Hutchinson (1959) was consulted to calculate the body size (cephalothorax width) ratio of species. For the discrimination among species in habitat and prey utilization discriminant function analysis was performed using linear discriminant function. Statistical software *i.e.*, Minitab 13.2 and Statistica 6 and Spdivers.bas were used for these statistical analyses.

RESULTS

A total of 330 spiders were captured during the sampling period of two years (Table I). *Tetragnatha javana* was the most abundant species while *Argiope trifasciata* was represented by the lowest number. Each of the four species was represented in each trapping session from August through November 2008 and 2009. However their abundance differed significantly among different trapping sessions each year (Mann–Whitney U during 2008: P = 0.014 for *A. trifasciata*; P = 0.03 for *Leucauge decorata*; P = 0.023 for *Neoscona theisi* and P = 0.015 for *T. javana*. Mann–Whitney U during 2009: P = 0.014 for *A. trifasciata*; P = 0.07 for *L. decorata*; P = 0.013 for *N. theisi* and P = 0.019 for *T. javana*).

The four species of orb weaving spiders differed significantly in their web architecture *i.e.*, height of hub above ground (df: 3,116; F= 11.89; P< 0.001), capture area (df: 3, 116; F= 26.33; P< 0.001) and mesh size (df: 3,116; F= 111.43; P< 0.001), (Fig. 2). Body length (df: 3, 116; F= 84.24; P< 0.001), carapace width (df: 3, 116; F = 99.09; P< 0.001) and wet weights (df: 3, 116; F= 52.75; P< 0.001) of studied species also differ significantly (Fig. 1).

Table I.- Abundance of four orb web spider species recorded from the study plots in 2008-2009.

Species	Abundance 2008	Abundance 2009	Total (% of grand total)
Argiope trifasciata (Forsskål, 1775)	19	23	42 (12.73)
Leucauge decorata (Blackwall, 1864)	27	31	58 (17.58)
Neoscona theis (Walckenaer, 1841)	37	34	71 (21.52)
Tetragnatha javana (Thorell, 1890)	82	77	159 (48.18)
	165	**165**	**330**

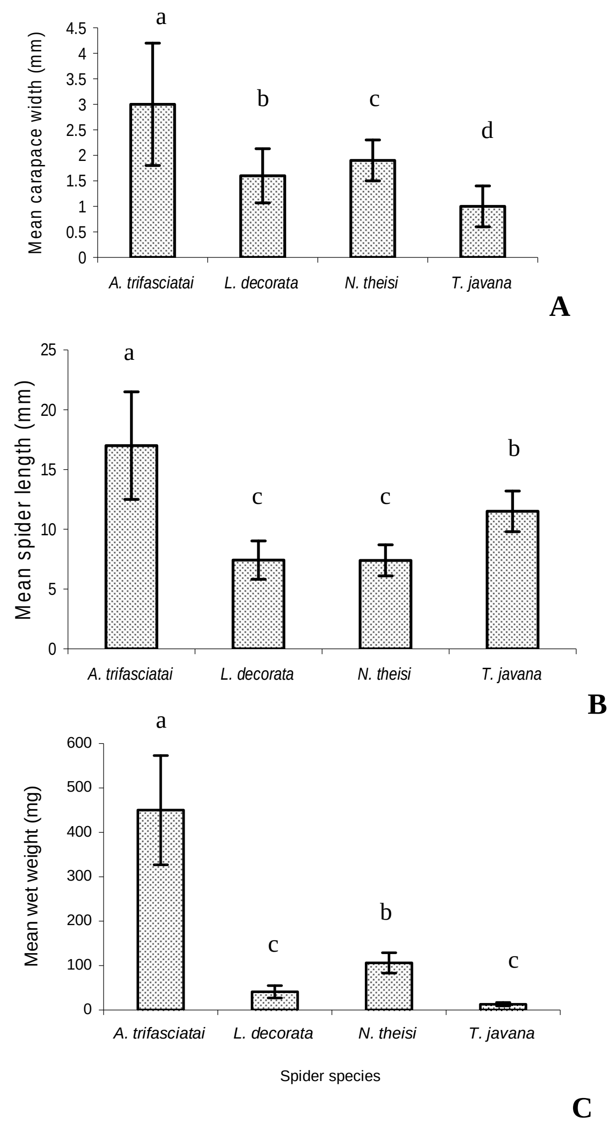
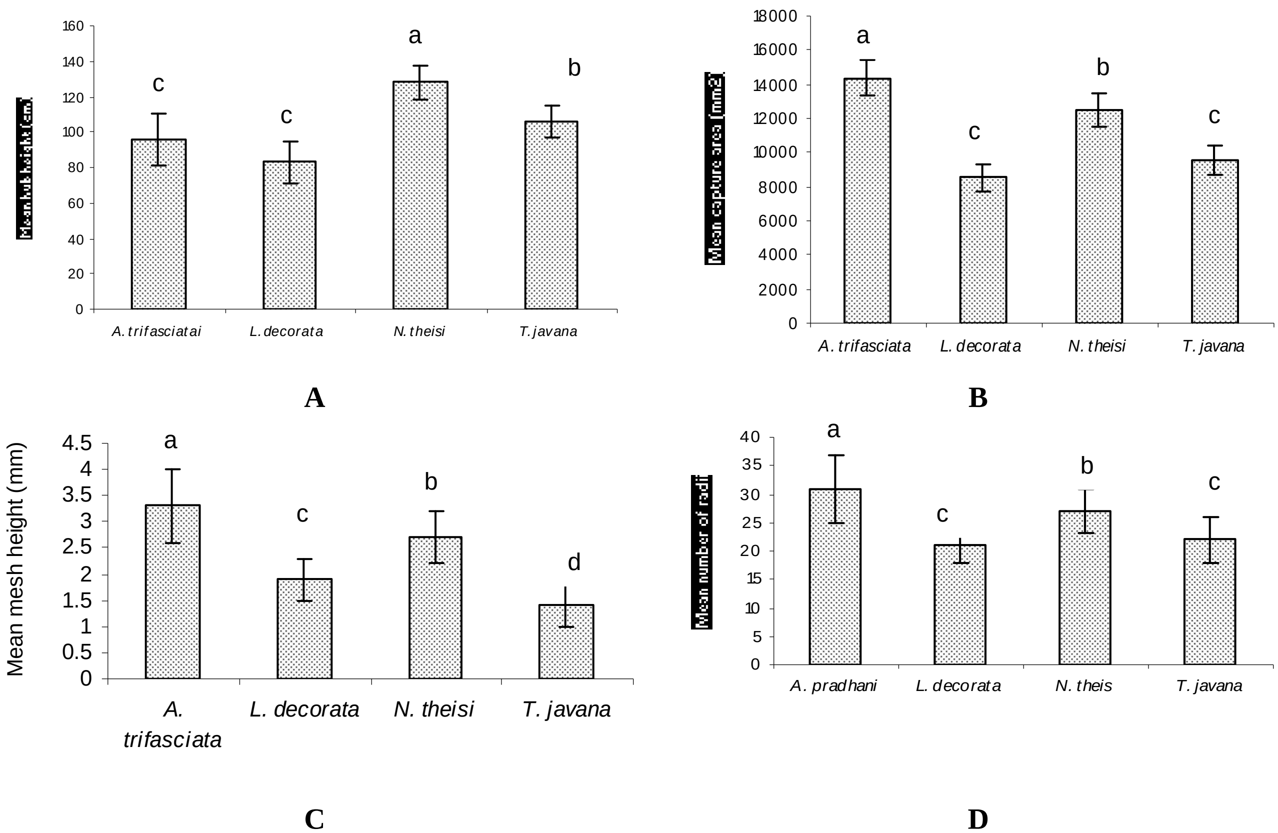


Fig. 1. Body size (±SE) of orb weaving spiders; A, carapace width; B, spider Length; C, wet weight. Means with different letters are significantly different (LSD, P<0.05).

Overall 1211 arthropods were recorded from the webs (n =145) of four species (detail of data of each species webs and arthropod prey recorded from the webs is given in the Table II). Most of the prey recorded from the webs belonged to orders Homoptera, Diptera, Coleoptera, Lepidoptera, Orthoptera and Hymenoptera. The four orb weaving species differed in the frequency with which they captured the different types of prey (Friedman test, P <0.001, Fig. 3). Average number of prey per web



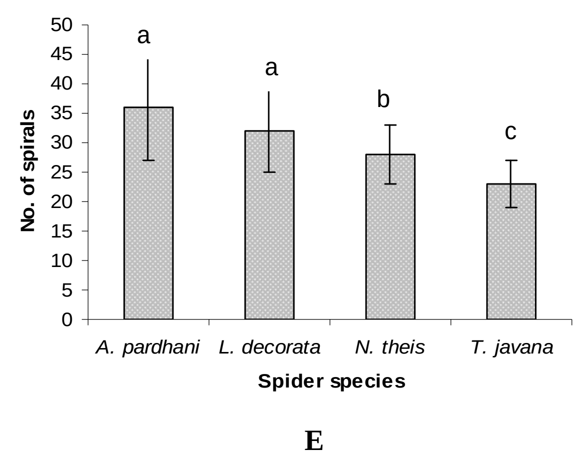


Fig. 2. Structural characteristics of webs A, height of hub above ground; B, capture area; C, mesh size; D, No. of radii; E, No. of spiral. Means with different letters are significantly different (LSD, P<0.05).

was highest in the webs of *A. trifasciata* and lowest in the webs of *T. javana* (Table II). The four species of orb-weaving spiders captured prey of different size (Kruskal-Wallis, P = 0.03). The sizes of the preys that were captured in the webs were also found to be strongly positively correlated with the carapace width of spiders (Table III). However, prey size was not related to the length of spiders or their wet weight (Pearson's correlation, P > 0.05 for all species).

Mean number of pests recorded from 1 m^2 of study field was 134±31 (SE). There was no significant difference in the proportion of different prey orders recorded randomly from 1 m^2 of studied fields and the prey collected from the spider webs (Friedman test, P>0.05).

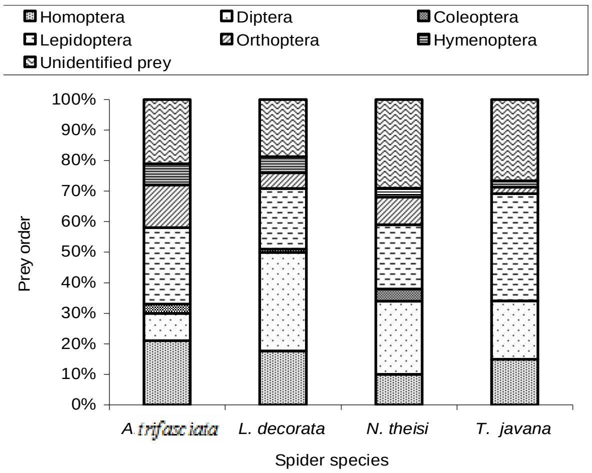


Fig. 3. Percentage of different prey orders collected from the webs of orb-weaving spiders (combined for 2008-2009).

Table II.- Average number of prey/web recorded from webs of orb weaving spiders of four species.

Spider species	No. of webs searched	No. of prey recorded	No. of prey per web
Argiope trifasciata	25	242	9.68
Leucauge decorata	30	249	8.3
Neoscona theis	40	363	9.07
Tetragnatha javana	50	357	7.17

Table III.- Correlation coefficients (r) for carapace widths and prey lengths.

Spider species	Mean carapace width	Prey length	Correlation coefficient (r)	P-value
Argiope trifasciata	2.91±0.210	4.8–39.87	0.47	< 0.05
Leucauge decorata	1.83±0.04	3.19–24	0.44	< 0.05
Neoscona theisi	2.31±0.07	4.9–33.7	0.73	< 0.05
Tetragnatha javana	0.83±0.022	2.2–21	0.42	< 0.05

Note: P-values < 0.05 are representing significant positive correlation.

The niche overlap values between species (four pairs) are given in Table IV. Only one pair (*A. trifasciata* x *L. decorata*) showed overlap values >50% in habitat and only one pair (*L. decorata* x *N. theisi*) in the prey size. All the four species pairs showed overlap values >50% for prey texa. Overall niche overlap values were <50% for all species pairs. Discriminant function analysis clearly separated the four orb weaving spiders in a three dimensional space (Fig. 4). Discriminant function analysis explained 89.8% of the variation among species (collectively along three axes). The first discriminant function (related to hub height) accounted for 64.5% of the variation, the second (related to prey size), explained additional 15.8% of the variation and the third (related to prey proportion) covered 9.5% of the variation among species. Body size ratio was equal to or higher than 1.26 (minimum value for coexistence according to Hutchinson) for all species (Table V).

Table V.- Hutchinsons's ratio (carapace size of larger species/carapace size of smaller species). Spiders are arranged in order of decreasing size.

Spider Species	Carapace width (mm)	Hutchinson's ratio
A. trifasciata	2.91	1.26
N. theis	2.31	1.26
L. decorata	1.88	2.2
T. javana	0.83	–

Note: A body size ratio of 1.26 is required for the coexistence of species according to Hutchinson.

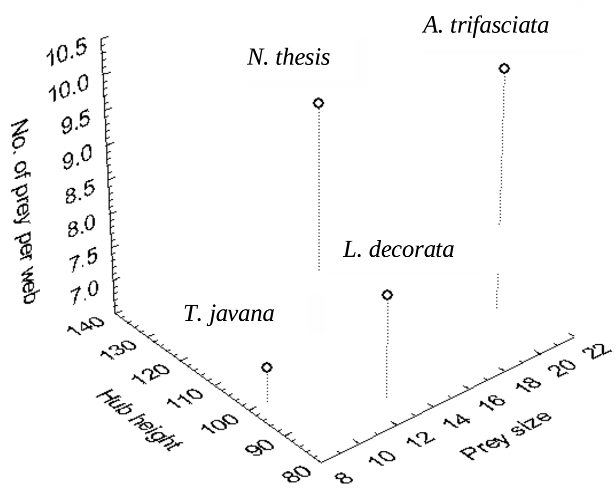


Fig. 4. Discriminant function analysis of four orb web spiders.

Table VI.- Resource overlap values among four orb web spider species (as the overlap in other two species pairs was more than 85% so excluded in the comparison) of rice ecosystem (both years combined) on the basis of exploitation of four niche dimensions (*i.e.*, habitat (hub height), prey size and prey taxa) as well as overall overlap values.

Species (i,k)	Habitat		Prey size		Prey taxa		Overall	
	(i,k)	(k,i)	(i,k)	(k,i)	(i,k)	(k,i)	(i,k)	(k,i)
A. trifasciata x *L. decorata*	0.51	0.48	0.35	0.28	0.64	0.59	0.35	0.39
A. trifasciata x *N .theisi*	0.31	0.26	0.31	0.36	0.51	0.62	0.41	0.47
A. trifasciata x *T. javana*	0.17	0.21	0.38	0.41	0.58	0.67	0.43	0.38
L. decorata x *N. theisi*	0.37	0.33	0.59	0.62	0.78	0.82	0.44	0.41

Abbreviations used: (i,k) is the overlap of species i (species 1) with species k (species 2); (k,i) is the overlap of species k (species 2) with species i (species 1)

DISCUSSION

Divergence in the resource utilization is thought to reduce the competition for available resources. In the present study, only with the exception of *Leucauge decorata* and *Argiope trifasciata*, the hub height of orb weaving spider species differed significantly in the field (Fig. 2a). This finding supports the hypothesis that orb-weaving spiders use the vertical stratification method of niche partitioning and do not competitively exclude one another. The spiders likely build their webs at different heights to catch different types of prey, effectively reducing niche overlap and promoting coexistence (Perkins, 2009). Differences in the web structure enable orb weaving spiders to capture different types of prey (Bristowe, 1941). Species diets are predicted to diverge only if the shared resources become limiting (Wise, 1993). The results of present study are not consistent with the findings of Perkins (2009) who reported in his study that the largest species (*Nephila clavipes*) had the highest webs and as spider size decreases (*Gasteracantha cancriformis* then *Leucauge* sp.) so does web heights (Fig. 2a). Although size of the *T. javana* is smaller than *A. trifasciata* and *L. decorata* but the location of its web was significantly higher. In the present study, the largest species, *A. trifasciata*, builds a largest web (at the height of 96 ± 14.4cm) whereas the other three species build smaller webs (heights of the webs of *L. decorata*, *N. theis* and *T. javana* were 83±11.9, 128±9.5 and 106±9.4 cm, respectively, Fig. 2b).

Mesh size of the web was found to be related with the prey size in the present study. The prey size was larger in the webs of orb-weaving spider with higher mesh size (Table III). A relationship between mesh size and prey length has also been reported by Uetz *et al.* (1978). He argued that a lower mesh size targets the prey items with smaller body length that otherwise may fly through a web with larger mesh size. However, numerous field studies have failed to find a consistent relationship between mesh size and prey size (McReynolds and Polis, 1987; Herberstein and Elgar, 1994; Herberstein and Heiling, 1998). According to Eberhard (1990), a narrow mesh size may facilitate the retention of larger prey, as more threads are in contact with the prey. However, more spiral turns also reflect more light thus increasing the visibility of web to prey (Craig, 1986; Craig and Freeman, 1991) and reducing the prey capturing efficiency of web. Mesh size may therefore indicate a compromise between prey retention and web visibility.

A larger capture area results in a higher prey interception rate (Craig, 1986; Craig and Freeman, 1991) and by increasing the distance between sticky spirals spiders may enlarge overall capture area without greater energy expenditure. Accordingly, food deprived spiders commonly increase web area to enhance prey encounter (Sherman, 1994; Herberstein *et al.*, 2000).

In the present study, prey size was larger in the webs of orb weaving spiders with larger size (Table III). This finding is also supported by several other researchers (Enders, 1974; Brown, 1981; Castillo and Eberhard, 1983; Murakami, 1983; Richardson and Hanks, 2009). The difference in the prey size may be related to the quality of the web. According to Richardson and Hanks (2009) web of larger orb weaving spiders have thicker thread or greater quantity of adhesive compounds. In the present study we did not studied the quality of the web and further study is required to establish this fact. The larger prey size in the webs of larger orb weaving spiders may be due to the ability of larger prey size to break the relatively weaker thread of the webs of smaller orb weaving spiders, which seems difficult in the webs of larger orb weaving spiders.

Overall niche overlap values were < 50% for all species pairs. All orb weaving spider species spiders can co-exist as none of the species pair showed overlap values higher than the value predicted by MacArthur and Levins (1967) for co-existence (*i.e.,* 54%). It is concluded that studied species partitioned the habitat vertically (constructed web at different height of rice plant), to utilize the available prey of different sizes and according to their own body size. Discriminant function analysis also clearly indicated that the four orb weaving spiders are sufficiently different with respect to the habitat and prey utilization that make their co-existence possible.

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