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Original Article

Population dynamics and prey composition of *Tetragnatha* spiders (Araneae: Tetragnathidae) in semi-organic rice fields, Songkhla Province, southern Thailand

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Abstract

Tetragnatha spiders are common predators in rice ecosystems. However, changes in their population numbers and availability of prey types at each rice growth stage are poorly understood. Therefore, this study assessed the population dynamics of *Tetragnatha* spiders and their prey composition during four stages of rice growth, including vegetative, reproductive, ripening, and after-harvesting in semi-organic rice fields in Songkhla Province of southern Thailand. The results showed that species richness and abundance of spiders were significantly higher in the reproductive stage than in other stages. Main prey families captured by *Tetragnatha* spiders varied with different growth stages. Chironomidae and Corixidae were the main prey in the vegetative and reproductive stages, while Delphacidae was the most common prey in the ripening stage and there was dominant prey in the after-harvesting stage. Overall, the different growth stages provided different rice structures for web attachment and different prey, which influenced both the spider populations and prey composition.

Keywords: biological control, long-jawed spider, generalist predator, paddy field, rice growing season

1. Introduction

Predators play an important role in ecosystems by reducing the abundance and growth rates of prey populations (Nyffeler, 2000). In agricultural ecosystems, population dynamics are of special interest because predators can maintain populations of insect pests at low equilibrium levels (Hassell, 1978).

Spiders are common generalist predators in agricultural ecosystems. They feed on various kinds of prey, especially insects. They exhibit a high diversity in agroecosystems and serve to limit the numbers of prey populations (Nyffeler, 2000; Venturino, Isaia, Mona, Chatterjee, & Badino, 2008). Many agricultural entomologists and arachnologists have demonstrated the importance of spiders as the major natural control agents which can regulate insect pest populations, especially in rice fields (Ludy, 2007; Nyffeler & Sunderland, 2003; Sebastian, Mathew, Pathummal, Joseph, & Biju, 2005; Sigsgaard, 2000; Tahir, Butt, & Sherawat, 2009). For example, researchers reported that spiders were the main predators of leaf folders, cut worms and stem borers.

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Additionally, they also trap small insect pests, such as thrips, planthoppers, and aphids (Landis, Wratten, & Gurr, 2000).

Tetragnatha (Latreille, 1804), or long-jawed spiders, are a dominant group of web-building spiders that exhibit prominent spatial and temporal dynamics in rice ecosystems (Rattanapun, 2012; Sebastian *et al.,* 2005; Tahir & Butt, 2008; Tsutsui, Tanaka, Baba, & Miyashita, 2016). They prefer to live in wet habitats, especially during the rice-growing season. Previous studies showed that *Tetragnatha* species prey on various rice insect pests. Tahir *et al.* (2009) found that the main orders of prey caught in the webs of *Tetragnatha* spiders were Lepidoptera, Diptera, Homoptera, Coleoptera, Hymenoptera, and Orthoptera. Moreover, the webs of *Tetragnatha* spiders either trapped mirid bugs or forced them onto the ground and into the hunting zone of wolf spiders (Takada, Kobayashi, Yoshioka, Takagi, & Washitani, 2013).

An increasing demand for improved sustainability in agriculture has promoted reducing the use of chemicals in rice ecosystems by applying biological control techniques. Since spiders are among the potential biological control agents (Cotes *et al.,* 2018; Nyffeler & Sunderland, 2003; Tahir & Butt, 2008), a better understanding is needed of how their populations and prey preferences change with the rice growing season in tropical rice fields. However, most of the previous studies on spider populations and their prey were conducted in only one particular stage of rice growth (Tahir *et al.,* 2009; Tsutsui *et al.,* 2016; Wang, Yuan, Song, & Zhu, 2004) and only one study covered all stages of rice plant development (Butt & Tahir, 2010). Here, we examined population changes of *Tetragnatha* spiders and the composition and availability of prey in all of the development stages of rice plants throughout the rice growing season in insecticide-free rice fields. Since prey composition can change with the rice planting period, this study hypothesizes that the population dynamics and prey utilization patterns of *Tetragnatha* spiders are closely associated with the progression of the growth stages of the rice. The results of this study can provide future uses of *Tetragnatha* spiders as biological control agents in rice fields.

2. Materials and Methods

2.1 Study site

This study was conducted in Bankhao, Ranot District, Songkhla Province in southern Thailand (7°50'N, 100°13'E). Rice farming is the major agricultural occupation in this area. In this study, three semi-organic rice fields that used chemical fertilizers but not chemical insecticides or herbicides were selected because a small proportion of each area was semi-organic compared to conventional rice fields. All fields were limited areas and were under the supervision of the Agricultural Extension Office of Ranot District, Songkhla Province for the purpose of producing safe, good quality rice. Rice in all of the selected fields was planted by the seed sowing method. More or less space was provided between the rice plants in all of the selected fields. Each rice field covered around 5 ha and was at the same growth stage as the other fields (planting was done simultaneously). Landscape structures surrounding the rice fields were generally similar among the three sites, namely other semi-organic rice fields, ditches, small tracks of road, and small patches of oil palm plantations. The cultivated rice variety was Pathumthani fragrant rice which is the most common cultivar in this area.

2.2 Vegetation measurements

Vegetation complexity of the rice crop was estimated by placing a 1.5-m measuring pole vertically in the ground and recording the height of the rice plants and the number of contacts between rice plants and the pole (Corcuera, Jiménez, & Valverde, 2008; McNett & Rypstra, 2000). The height of the rice plants continuously increased from the vegetative growth stage to the reproductive stage. Thereafter, it stayed relatively constant until the rice was harvested. Rice complexity changed between the different growth stages which increased from the vegetative stage to the reproductive stage and from the reproductive stage to the ripening stage (Table 1).

2.3 Field observations

Fieldwork was done from November 2015 to March 2016 covering the four stages of rice growth: vegetative (tillering sub-stage); reproductive (flowering sub-stage); ripening (maturity sub-stage); and after-harvesting stages. In this study, each sub-stage was chosen to represent each stage because rice plants are used by many groups of insects. All observations were conducted between 1900 h to 2200 h because the feeding activity of *Tetragnatha* spiders is at its highest during this time (Kiritani, Kawahara, Sasaba, & Nakasuji, 1972; V. Saksongmuang, personal observation). During this rice growing season, the means±SDs of the air temperature and relative humidity were recorded by data loggers which were around 26.14±0.40 °C and 90.77±3.09,

Table 1. Description of rice growth in each stage of Pathumthani fragrant rice variety.

	Vegetative	Reproductive	Ripening	After-harvesting
Days after planting	40–50	70–80	100–110	After 120
Height (cm)	40–50	90–100	80–90	10–20
Vegetation complexity *	3.0 (low)	5.5 (moderate)	7.9 (high)	-
Important characteristics	Active tillering	Culm elongation, emergence of the flag leaf, heading and flowering.	Grain increases in size and weight, changes from green to gold color at maturity.	Straw

*Vegetation complexity defined as the mean number of rice plants in contact with the measuring pole.

respectively. In the study period, rain fall ranged from 290–500 mm/month in November and December (2015) and ranged from 0–200 mm/month in January, February and March (2016) (Meteorological Department, 2016). However, the sampling was done during the night with no rain.

2.4 Spider collection

Tetragnatha spiders were collected at 15 sampling points in each rice field during each growth stage. Sampling points were 10 m apart from each other. Specimens were collected by both visual searching and sweep netting adjacent to each other at each sampling point. In visual searching, spiders were captured by hand within a 1x1 m quadrat. Sweep netting was carried out with a 35-cm diameter insect net that was swept five times over and around the rice plants at each sampling point which was 1 m from the paddy edge. The sweeping net was used at the canopy of the rice plants to collect hiding spiders in rice leaves since spiders may not be in their webs. Spider sampling was conducted for three days per rice field in each stage of rice growth. The captured *Tetragnatha* spiders were preserved in 75% alcohol. Adult spiders were identified to the species level using Riceland Spiders of South and Southeast Asia (Barrion & Litsinger, 1995).

2.5 Captured prey and prey availability

Captured prey were all arthropods found in *Tetragnatha* webs along a 50-m line transect. Searches lasted 60 min per rice field each night. All prey items (dead, alive, partially eaten, or even still in the possession of the spider) as well as *Tetragnatha* spiders were collected using forceps, and preserved in 75% alcohol. Captured prey and *Tetragnatha* spiders were collected on three consecutive nights per rice growth stage per rice field. The time taken to remove the spider and its prey from each web was not included in the 50 min of searching time. Prey availability was estimated by sweep netting simultaneously with *Tetragnatha* spider collection. The prey captured by spiders and the available prey were assessed at the same time and in the same rice fields where the spiders were collected. However, different sampling points were used for sampling *Tetragnatha* spiders, captured prey and available prey. All preys were identified to the family level using Rice-Feeding Insects of Tropical Asia (Shepard, Banion, & Litsinger, 1995) and Arthropod Biodiversity, Taxonomy and Identification (International Rice Research Institute [IRRI], 2010).

2.6 Statistical analysis

To analyze the effect of the growth stages of the rice (vegetative growth, reproductive, ripening and after-harvesting) on the total spider abundance and the abundance of each prey, the study used a generalized linear model (GLM) with a Poisson error distribution because the dependent variables were count data. The fixed factor in the model was the rice stage, and the random factor was the identity of the rice field. The model with the lowest Akaike's information criterion value was selected as the best predictive model. The function lsmeans from the package lsmeans was used to perform pairwise comparisons, and Tukey's honestly significant differences adjustment was applied. All statistical analyses were conducted with R-3.3.2 (R Development Core Team, 2016).

Prey selectivity of the spider webs was determined using Ivlev's electivity index (Ivlev, 1961) based on prey availability and captured prey compositions (Alderweireldt, 1994; Diehl, Mader, Wolters, & Birkhofer, 2013; Nentwig, 1985). These indices were calculated only for dominant prey families that were present at all rice stages. The Ivlev index (IE) was estimated using the following formula:

$$IE = \frac{r-p}{r+p}$$

where r is the percentage contribution of individuals from a prey family to the captured prey composition and p is the percentage contribution of the same prey family to the available prey composition. The Ivlev index ranges from +1 (prey family over-represented in webs) to –1 (prey family under-represented in webs), where 0 indicates random feeding (i.e. prey family appears with the same percentage in captured prey and available prey).

3. Results

A total of 192 spiders of *Tetragnatha* were collected in three semi-organic rice fields over four stages of rice plant growth. Among them, 83 adults and 27 juveniles were collected by visual searching, and 54 adults and 28 juveniles were collected by sweep netting. Only adult *Tetragnatha* spiders were identified to the species level. We found six species that included *Tetragnatha javana* (Thorell, 1890), *Tetragnatha mandibulata* (Walckenaer, 1841), *Tetragnatha maxillosa* (Thorell, 1895), *Tetragnatha nitens* (Audouin, 18 26), *Tetragnatha vermiformis* (Emerton, 1884), and *Tetragnatha virescens* (Okuma, 1979). *T. javana* and *T. maxillosa* were the two most abundant species that represented 40.1% and 29.9% of the total adults, respectively, while *T. nitens*, *T. Mandibulata*, *T. virescens*, and *T. vermiformis* represented 11.6%, 9.5%, 8.0%, and 1.4%, respectively.

3.1 Effect of rice stage on *Tetragnatha* spiders

The growth stage of rice plants in the semi-organic rice fields significantly affected the abundance of *Tetragnatha* spiders, collected by visual searching (GLM, X^2=44.66, df=3; P<0.001) as well as net sweeping (GLM, X^2=35.72, df=3; P<0.001). The abundance of *Tetragnatha* spiders from both sampling techniques was significantly higher in the reproductive stage of rice plant growth than in the other stages (P<0.05) but not significantly different between the vegetative stage, the ripening stage, and the after-harvesting stage (P> 0.05) (Figure 1).

The rice stage generally affected the number of species and also the abundance of each *Tetragnatha* species. Species richness and abundance varied at different stages of rice plant development. The highest number of *Tetragnatha* species (six species) was collected during the reproductive stage while the lowest number (two species) was found in the after-harvesting stage. In the vegetative growth stage, the abundance of *Tetragnatha* spiders did not differ between species. In the reproductive stage, *T. javana* and *T. maxillosa*

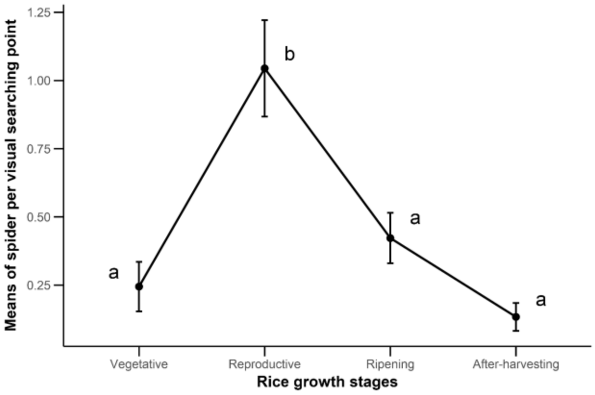

Figure 1. Mean (±SE) number of *Tetragnatha* spiders at each stage of rice by visual searching method. The letters indicate the significant difference of mean numbers between rice stages (Tukey's honestly significant differences test, P<0.05).

were more abundant than the other species. In the ripening stage, *T. javana* and *T. maxillosa* were the most abundant. *T. javana* was also a dominant group in the fields in the after-harvesting stage. The results showed that the abundance of *T. javana* and *T. maxillosa* fluctuated between stages while the abundance of *T. mandibulata*, *T. nitens*, *T. vermiformis*, and *T. virescens* were not significantly different between the stages (Figure 2).

3.2 Prey availability

As estimated from the results of sweep netting, the numbers of insects rapidly increased from the vegetative growth stage to a peak in the reproductive stage. After that, the numbers gradually decreased in the ripening and after-harvesting stages. Dominant families of available prey varied between rice stages. In both the vegetative and reproductive stages, the most dominant family was Chironomidae while Cicadellidae was the second most dominant. In the ripening stage, the number of chironomids decreased while Cicadellidae increased and became dominant. In the after-harvesting stage, Chironomidae and Acrididae were the families most commonly found (Table 2).

3.3 Captured prey

Among 928 prey items collected from *Tetragnatha* webs across all stages of rice plants, Chironomidae and Corixidae dominated. However, the dominant prey varied at different stages of rice growth. In the vegetative growth stage, the main prey families were Chironomidae and Corixidae. In the reproductive stage, a higher number of Corixidae, Chironomidae, and Baetidae were collected. In the ripening stage, Delphacidae and Chironomidae were the main prey of *Tetragnatha*. There was no obvious dominant prey in the after-harvesting stage (Table 3).

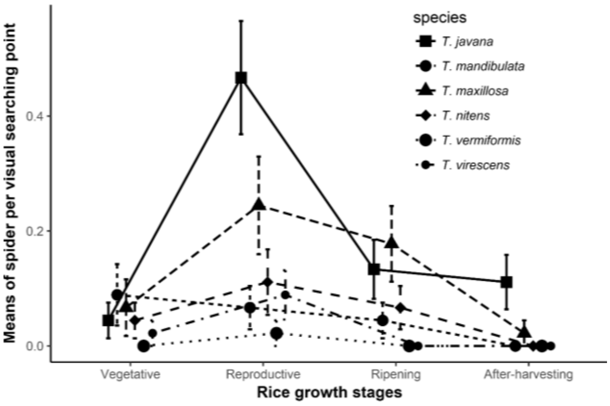

Figure 2. Mean±SE number of *Tetragnatha javana, T. mandibulata, T. maxillosa, T. nitens, T. Vermiformis*, and *T. virescens* in each stage of rice growth.

Table 2. Prey availability estimated by sweep netting in each rice stage (A = Vegetative growth stage, B = Reproductive stage, C = Ripening stage, D = After-harvesting stage).

Main families of available prey		Number of individuals (Mean±SE)			
		A	B	C	D
Diptera	Chironomidae	132.7±17.3	109.0±7.8	6.0±1.0	47.7±8.5
	Cecidomyiidae	-	2.3±0.7	0.3±0.3	5.3±1.5
	Tipulidae	-	15.3±2.2	6.7±2.2	3.0±2.1
Hemiptera	Cicadellidae	8.0±3.0	59.3±10.8	103.7±9.8	9.7±2.7
	Delphacidae	1.3±0.7	3.0±2.5	2.7±0.9	2.7±1.5
	Corixidae	4.3±1.5	5.0±2.1	2.3±1.2	1.0±0.6
	Miridae	3.0±0.6	14.7±4.8	3.3±1.2	3.0±0.9
Orhtoptera	Tettigoniidae	9.7±2.2	4.0±1.2	12.0±2.1	9.0±3.0
	Acrididae	4.3±1.5	0.7±0.7	7.0±1.7	16.0±2.3
Odonata	Coenagrionidae	4.3±1.2	5.0±2.0	3.3±1.9	-
Coleoptera	Coccinellidae	7.7±1.8	12.3±2.0	7.7±2.4	4.0±1.7
Lepidoptera	Pyralidae	2.3±1.3	16.3±2.6	3.7±0.3	-
Ephemeroptera	Baetidae	0.3±0.3	4.0 ±0.6	1.7±0.9	-
Aranea	Spiders	33.0±5.5	91.3±7.7	101.7±8.4	49.3±2.7
Others		50.7±6.6	125.0±14.4	66.7±7.3	66.0±9.6
Total number		279.0±12.7	469.7±35.4	348.0±30.6	217.7±20.7

Table 3. Numbers of main insect prey captured by spider webs in each rice stage (A = Vegetative growth stage, B = Reproductive stage, C = Ripening stage, D = After-harvesting stage).

Main family of captured prey		Number of individual (Mean±SE)			
		A	B	C	D
Diptera	Chironomidae	5.1±0.9	19.2±1.8	0.4±0.2	0.2±0.1
	Cecidomyiidae	0.2±0.1	0.7±0.2	0.2±0.1	0.1±0.1
	Tipulidae	-	1.2±0.4	0.1±0.1	-
Hemiptera	Corixidae	2.6±0.4	33.3±7.0	-	-
	Delphacidae	-	0.8±0.3	0.7±0.2	0.1±0.1
	Notonectidae	-	1.2±0.6	-	-
Odonata	Coenagrionidae	0.2±0.1	0.7±0.3	-	-
Ephemeroptera	Baetidae	-	2.7±0.3	-	0.2±0.2
Others		1.0±0.4	5.9±1.1	1.7±0.6	0.1±0.1
Unidentified		1.7±0.5	15.7±1.8	6.8±1.0	0.3±0.2

From the proportions of captured prey and available prey estimated in each stage of rice growth, Corixidae was clearly over-represented in *Tetragnatha* webs in the vegetative and reproductive stages (Ivlev index 0.85 and 0.95, respectively). In the ripening stage, Cecidomyiidae, Delphacidae, and Chironomidae were over-represented (Ivlev index 0.99, 0.97, and 0.81, respectively), as were Baetidae and Cecidomyiidae in the after-harvesting stage (Ivlev 1 and 0.83, respectively). In general, Acrididae, Cicadellidae, and Pyralidae were under-represented in spider webs in almost all stages of rice (Ivlev index < 0) even when they were more available as prey (Figure 3).

4. Discussion

4.1 Population dynamics of *Tetragnatha* spiders

Our study showed that both the abundance and species richness of *Tetragnatha* spiders was the highest in the reproductive stage of rice plants, while they were the lowest in the after-harvesting stage. That the highest spider abundance and species richness should occur in the reproductive stage of rice growth could result from the concurrence of certain conditions. The availability and diversity of prey peaked in this stage due to the wet habitat and the appearance of rice

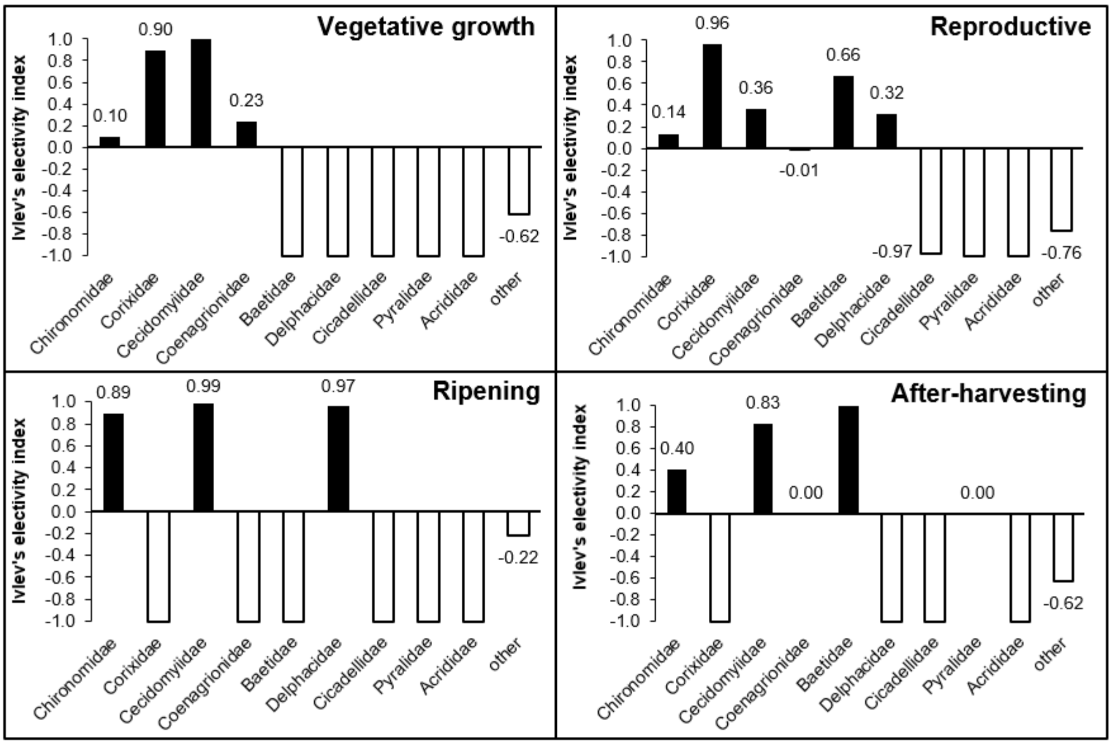

Figure 3. Ivlev's electivity index of main prey families in each stage of rice plant development.

flowers. The flooded paddy provides a habitat for many species of aquatic insects such as midge flies and water bugs (Zhi-yu, Hong, Feng-xiang, Qing, & Yang, 2011) and rice flowers can be used as a food source for a wide range of insects (Wilson, Ramakrishnan, Pavaraj, & Sevarkodiyone, 2014). Therefore, many insects migrate into the rice field in the reproductive rice stage (Wilson *et al.,* 2014). Previous studies reported that the density and growth rate of *Tetragnatha* in rice fields had a significant positive correlation with the abundance of available dipterans (Takada, Takagi, Iwabuchi, Mineta, & Washitani, 2014; Tsutsui *et al.,* 2016). According to our results, the number of *Tetragnatha* spiders increased when the number of dipterous insects, especially insects in the families Chironomidae and Tipulidae, increased in the early growing season. The rice reproductive stage also offers an optimum rice stem complexity to support spider webs, as in this stage the rice plants are neither too sparse (as in the vegetative stage) nor too dense (as in the ripening stage). Spiders can therefore effectively attach their webs and build them to an appropriate size and move easily across them to catch their prey (Jayakumar & Sankari, 2010; Rypstra, Carter, Balfour, & Marshall, 1999). According to many previous studies, the availability of attachment substrates for the webs of web-building spiders was determined by vegetation complexity because the increasing complexity of the habitat offers more shelter, food, and microhabitats for the spiders (Langellotto & Denno, 2004; McNett & Rypstra, 2000; Öberg & Ekbom, 2006; Sudhikumar, Mathew, Sunish, & Sebastian, 2005). On the other hand, both the spider populations and species richness were low in the after-harvesting stage. At this stage, the habitat in a rice field changes due to the harvesting process of the rice. Only rice straw and a small amount of vegetation remain in the rice fields which may also cause physical factors in the change of a rice field leading to a reduction in the population of insect prey and microhabitats to support spider webs. When the habitat is not suitable, spiders in rice fields normally move to other habitats which provide more suitable conditions such as levees or ditches (Bambaradeniya & Edirisinghe, 2008; Miyashita, Yamanaka, Tsutsui, 2014; Tsutsui *et al.,* 2016; Yu *et al.,* 2002). Therefore, our findings support the hypothesis that the population dynamics of *Tetragnatha* spiders change with the progression of rice growth because of the temporal changes in the attachment substrate and the availability of insect prey.

4.2 Prey compositions

In this study, the captured prey of *Tetragnatha* was different in different stages of rice growth. Chironomidae and Corixidae were the main prey families in the vegetative and reproductive growth stages. This may be because high water levels in rice fields support an abundance of these detritus and plankton-feeding insects. This is consistent with Ishijima *et al.* (2006) who found that dipterous insects, including chironomids (Chironomimdae), were an important alternative prey for spiders in the early cropping season. This finding corresponds to previous studies which suggested that non-pest insects such as dipterans may sustain spider populations in early growing stage of rice and strengthen the top-down effect of subsequent spider predation on insect pests when the pest is blooming in the reproductive and the ripening stage (Bardwell & Averill, 1997; Ishijima *et al.,* 2006; Motobayashi *et al.,* 2006; Settle *et al.,* 1996). In the ripening stage, the main captured prey was Delphacidae (Hemiptera), common rice insect pests in southern Thailand (Rattanapun, 2012). An important finding of our study is that prey composition in *Tetragnatha* spider web and sweeping net was changed from detritivorous insects (Chironomimdae) to herbivorous insects (Delphacidae, Cicadellidae) along the rice growing season. This finding might be caused by flight activity of the insect. In the ripening stage, the rice plant is too hard and opaque for feeding by sucking insects (Delphacidae, Cicadellidae). This may induce the insects to move out to search for a new habitat which leads to an increased number of insects in the spider webs and net sweeping. (Hu *et al.,* 2014; Pender, 1994)

The main captured prey of *Tetragnatha* spiders in this study were similar to those in previous studies of Rapp (1978) and Yoshida (1987) which found that *Tetragnatha* spiders mainly feed on midge flies (Chironomidae), mayflies (Baetidae), and other nematocerous dipterans of small body size. A number of previous studies demonstrated that small insects with many appendages and poor flying ability, that are highly abundant at the same height as the spider webs, were easily caught in the webs. Examples of these insects are Chironomidae, Cecidomyidae, Tipulidae, some Hemiptera, and small Ephemeroptera (Craig, 1986; Ludy, 2007; Tahir & Butt, 2009). The reason for the abundance of family Corixidae in the spider webs is unclear. It is possible they were trapped during their migratory flight from the rice fields to another place nearby when the water in the rice fields was drained out in the late reproductive stage (around 70 days after planting). Dispersal of water bugs is driven by a number of physical, environmental, ecological, and physiological factors (Savage, 1989), including decreased water level, habitat deterioration, an abundance of predators, and a high density of aquatic insects (Boda & Csabai, 2009; Pajunen & Jansson, 1969). Csabai, Kálmán, Szivák, and Boda (2012) revealed that the peak dispersal flight of Corixidae began at 1900 h and reached its maximum at 2100 h which corresponds to the highest feeding activity of *Tetragnatha* spiders (Kiritani *et al.,* 1972). Our results were slightly in contrast to Butt and Tahir (2010) who studied the diet composition of *T. javana* in a rice ecosystem in Pakistan (observation time periods were 0630–0730 h and 1700–1800 h) and found that the main prey of *T. javana* were Lepidoptera, Diptera, and Hemiptera. In our study, the incidence of Pyralidae (Lepidoptera) was low in every stage of rice growth and Cicadellidae (Hemiptera) were abundant in the reproductive and ripening stages but proportionally low in the *Tetragnatha* webs. This difference may be due to the difference in the observation times, prey flight activity (Csabai *et al.,* 2012; Perfect & Cook, 1982), and the available prey composition in each location (McCoy, 1990). It would be interesting in the near future to study the diet composition of *Tetragnatha* in rice fields over an entire night (1800–0600h) to obtain a more precise evaluation of the role of spiders in rice fields because spiders stay with their web all night until they collect prey from the web at dawn the next day.

The calculated Ivlev's electivity indices indicated that prey compositions in *Tetragnatha* webs did not simply represent insect availability in the rice fields. Some groups of insects were caught in webs disproportionately more than would be expected from their estimated availability based on sweep netting. These insects included Corixidae, Cecidomyidae, Delphacidae, and Baetidae. The over-representation of Corixidae which are aquatic insects, in the webs in the vegetative and reproductive growth stages might be due to flight activity of these insects and the observation time period by the sweeping method possibly did not correspond with flight activity. Consequently such insects were proportionally fewer in the sweeping net (Csabai *et al.,* 2012; Savage, 1989). On the other hand, some main groups of available prey, including Acrididae (Orthoptera), Cicadellidae, Miridae (Hemiptera), and Pyralidae (Lepidoptera), were represented less in the *Tetragnatha* webs than their estimated availability in the rice fields indicated. The under-representation of these groups in the spider webs was possibly due to their ability to avoid spider webs (Nentwig, 1980). Two reasons for this under-representation in spider webs are considered here. The first is the flight behavior or the flight activity of particular insects. They fly less for daily dispersal except for searching new habitats or migration such as sap sucking insects (Cicadellidae) (Hu *et al.*, 2014; Perfect & Cook, 1982). The second reason is to avoid or escape from spider webs thanks to morphological or physiological features such as large body size, strong mandibles, good flying ability, or streamlined shape (Nentwig, 1987; Turnbull, 1973). For example, insects in the order Orthoptera have large bodies and strong mandibles and can escape quickly when they are trapped in webs.

This study found that the main groups in the prey spectrum of *Tetragnatha* spiders were detritus feeding, plankton feeding, and sap-sucking insects (insect pests), which were trapped in webs in different proportions along the rice growing season. It was shown that *Tetragnatha* spiders feed on a diverse and a broad range of prey types which may explain their potential survival and occurrence along a rice growing season. This information is important for the understanding of this spider which might play an important role in the biological control in some stages of the rice plant. Moreover, effective management of a natural control strategy across the rice growing season in a rice ecosystem will demand an understanding of changes in the density and composition of prey species of which *Tetragnatha* spiders are the main natural enemy.

5. Conclusions

This present study showed that the population of *Tetragnatha* spiders fluctuated along the rice growing season in response to the changing availability of insect prey and sites for web attachment. The prey composition of this spider also changed with the growth and development of the rice crop. The findings also highlight the existence of stable relationships between *Tetragnatha* spiders and their preys. The populations of this spider in rice fields can be conserved and enhanced through the non-use of chemical agents. Biological control which maintains a high diversity and long-term sustainability of a rice ecosystem should be the focus in effective management strategies and deciding what is environmentally safe.

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References

Alderweireldt, M. (1994). Prey selection and prey capture strategies of linyphiid spiders. *Bulletin of the British Arachnological Society, 9*(9), 300-308. Retrieved from https://www.researchgate.net/publication/281325455

Bambaradeniya, C. N., & Edirisinghe, J. P. (2008). Composition, structure and dynamics of arthropod communities in rice agroecosystem. *Ceylon Journal of Science (Biological Sciences), 37*(1), 23-48. Retrieved from https://cjsbs.sljol.info/articles/10.4038/cjsbs.v37i1.494/

Bardwell, C. J., & Averill, L. (1997). Spiders and their prey in Massachusetts cranberry bogs. *Journal of Arachnology, 25*(1), 31-41. Retrieved from http://www.jstor.org/stable/3705525

Barrion, A. T., & Litsinger, J. A. (1995). *Riceland Spiders of South and Southeast Asia*. Oxfordshire, England: CAB International.

Boda, P., & Csabai, Z. (2009). Seasonal and diel dispersal activity characteristics of *Sigara lateralis* (Leach, 1817) (Heteroptera: Corixidae) with special emphasis on possible environmental factors and breeding state. *Aquatic Insects, 31*(4), 301-314. doi:10.1080/01650420903110519

Butt, A., & Tahir, H. M. (2010). Resource partitioning among five agrobiont spiders of a rice ecosystem. *Zoological Studies, 49*(4), 470-480. Retrieved from zoolstud.sinica.edu.tw/Journals/49.4/470.pdf

Corcuera, P., Jiménez, M. J., & Valverde, P. L. (2008). Does the microarchitecture of Mexican dry forest foliage influence spider distribution. *Journal of Arachnology, 36*, 552–556. Retrieved from http://www.bioone.org/doi/pdf/10.1636/T05-20.1

Cotes, B., González, M., Benítez, E., De-Mas, E., Clemente-Orta, G., Campos, M., & Rodríguez, E. (2018). Spider Communities and Biological Control in Native Habitats Surrounding Greenhouses. *Insects, 9*(33), 1-12. Doi:10.3390/ insects9010033

Craig, C. L. (1986). Orb-web visibility: the influence of insect flight behavior and visual physiology on the evolution of web designs within the Araneoidea. *Animal Behaviour, 34*, 54-68. doi:10.1016/0003-3472(86)90006-0

Csabai, Z., Kálmán, Z., Szivák, I., & Boda, P. (2012). Diel flight behaviour and dispersal patterns of aquatic Coleoptera and Heteroptera species with special emphasis on the importance of seasons. *The Science of Nature, 99*(9), 751-65. Doi: 10.1007/s00114-012-0957-6

Diehl, E., Mader, V. L., Wolters, V., & Birkhofer, K. (2013). Management intensity and vegetation complexity affect web-building spiders and their prey. *Oecologia, 173*(2), 579-589. doi:10.1007/s00442-013-2634-7

Hassell, M. P. (1978). *The Dynamics of Arthropod Predator–Prey Systems*. Princeton, NJ: Princeton University Press.

Hu, G., Lu, F., Zhai, B. P., Lu, M. H., Liu, W. C., Zhu, F., . . . Zhang, X. X. (2014). Outbreaks of the brown planthopper *Nilaparvata lugens* (Stål) in the Yangtze River Delta: Immigration or local reproduction. *PLoS ONE, 9*(2). doi:10.1371/journal.pone.0088973

International Rice Research Institute. (2010). *Arthropod Biodiversity, Taxonomy and Identification*. Los Banos, Laguna, Philippines.

Ishijima, C., Taguchi, A., Takagi, M., Motobayashi, T., Nakai, M., & Kunimi, Y. (2006). Observational evidence that the diet of wolf spiders (Araneae: Lycosidae) in paddies temporarily depends on dipterous insects. *Applied Entomology and Zoology, 41*(2), 195-200. doi:10.1303/aez.2006.195

Ivlev, V. (1961). *Experimental ecology of the feeding of fishes*. New Haven, CT: Yale University Press.

Jayakumar, S., & Sankari, A. (2010). Spider population and their predatory efficiency in different rice establishment techniques in Aduthurai, Tamil Nadu. *Journal of Biopesticides, 3*(1 Special issue), 20-27. Retrieved from www.jbiopest.com/ users/lw8/efiles/ jeya_kumar_s.pdf

Kiritani, K. S., Kawahara, S., Sasaba, T., & Nakasuji, F. (1972). Quantitative evaluation of predation by spiders on the green rice leafhopper. *Nephotettix cincticeps* Uhler, by a sight-count method. *Researches on Population Ecology, 13*(2), 187-200. doi:10.1007/BF02521977

Landis, D. A., Wratten, S. D., & Gurr, G. M. (2000). Habitat management to conserve natural enemies of arthropod pests in agriculture. *Annual Review of Entomology, 45*, 175-201. doi:10.1146/annurev.ento.45.1.175

Langellotto, G. A., & Denno, R. F. (2004). Responses of invertebrate natural enemies to complex-structured habitats: a meta-analytical synthesis. *Oecologia, 139* (1), 1–10. doi:10.1007/s00442-004-1497-3

Ludy, C. (2007). Prey selection of orb-web spiders (Araneidae) on field margins. *Agriculture, Ecosystems and Environment, 119*(3-4), 368-372. doi:10.1016/j.agee.2006.08.005

McCoy, E. D. (1990). The distribution of insects along elevational gradients. *Oikos, 58*(3), 313-322. Retrieved from https://www.jstor.org/stable/pdf/3545222.pdf

McNett, B. J., & Rypstra, A. L. (2000). Habitat selection in a large orb- weaving spider: vegetation complexity determines site selection and distribution. *Ecological Entomology, 25*(4), 423-432. Retrieved from https://onlinelibrary.wiley.com/doi/abs/10.1046/j.1365-2311.2000.00279.x

Meteorological Department. (2016). Rainfall accumulation from the weather data of the Weather Station, Meteorology Department (Monthly rainfall during dry season). Retrieved from http://www.thaiwater.net/current/2016/drought59/body.html

Miyashita, T., Yamanaka, M., & Tsutsui, H. M. (2014). Distribution and abundance of organisms in paddy-dominated landscapes with implication for wildlife-friendly farming. In T. Miyashita & U. Nishikawa (Eds.). *Social-ecological restoration in paddy-dominated landscapes* (pp. 45-65). Tokyo, Japan: Springer.

Motobayashi, T., Ishijima, C., Takaji, M., Murakami, M., Taguchi, A., & Hidaka, K. (2006). Effects of tillage practices on spider assemblage in rice paddy fields. *Applied Entomology and Zoology, 41*(2), 371-381. doi:10.1303/aez.2006.371

Nentwig, W. (1980). The selective prey of Linyphiid-like spiders and of their space webs. *Oecologia, 45*(2), 236-243. doi:10.1007/BF00346464

Nentwig, W. (1985). Prey analysis of four species of tropical orb-weaving spiders (Araneae: Araneidae) and a comparison with araneids of the temperate zone. *Oecologia, 66*(4), 580-594. Retrieved from http://www.jstor.org/stable/4217674

Nentwig, W. (1987). *The ecophysiology of spiders*. Berlin, Germany: Springer.

Nyffeler, M. (2000). Ecological impact of spider predation: A critical assessment of Bristowe's and Turnbull's estimates. *Bulletin of the British Arachnological Society, 11*(9), 367-373. Retrieved from https:// www.conservation.unibas.ch/team/nyffeler/pdf/nyffeler2000bas.pdf

Nyffeler, M., & Sunderland, K. D. (2003). Composition, abundance and pest control potential of spider communities in agroecosystems: a comparison of European and US studies. *Agriculture, Ecosystems and Environment, 95(*2-3), 579-612. doi:10.1016/S0167-8809(02)00181-0

Öberg, S., & Ekbom, B. (2006). Recolonisation and distribution of spiders and carabids in cereal fields after spring sowing. *Annals of Applied Biology, 149*, 203-211. doi:10.1111/j.1744-7348.2006.00088

Pajunen, V. I., & Jansson, A. (1969). Dispersal of the rock pool corixids *Arctocorisa carinata* (Sahlb.) and *Callicorixa producta* (Reut.) (Heteroptera, Corixidae). *Annales Zoologici Fennici, 6*(4), 391-427. Retrieved from https://www.jstor.org/stable/23731568

Pender, J. (1994). Migration of the brown planthopper, *Nilapawata lugens* (Stal.) with special reference to synoptic meteorology. *Grana, 33*, 112-115. doi:10.1080/00173139409427843

Perfect, T. J., & Cook, A. G. (1982). Diurnal periodicity of fight in some Delphacidae and Cicadellidae associated with rice. *Ecological Entomology, 7*(3), 317-326. doi:10.1111/j.1365-2311.1982.tb00672.x

Rapp, W. F. (1978). Preliminary studies of *Tetragnatha* (Araneida) as predators of mosquitoes. *Mosquito News, 38*(4), 506-507. Retrieved from https://archive.org/

details/cbarchive_117261_preliminarystudiesoftetra gnath1978

Rattanapun, W. (2012). Diversity and population dynamics of pests and predators in irrigated rice fields with treated and untreated pesticide. *Communications in Agricultural and Applied Biological Sciences, 77*(4), 601-609. Retrieved from https://www.ncbi.nlm.nih.gov/pubmed/23885426

Rypstra, A. L., Carter, P. E., Balfour, R. A., & Marshall, S. D. (1999). Architectural features of agricultural habitats and their impact on the spider inhabitants. *Journal of Arachnology, 27*, 371–377. Retrieved from http://www.jstor.org/ stable/3706009

Savage, A. A. (1989). *Adults of the British Aquatic Hemiptera Heteroptera: Key with ecological notes*. University of Minnesota, Minneapolis, MN.

Sebastian, A. P., Mathew, J. M., Pathummal, B. S., Joseph, J., & Biju, R. C. (2005). The spider fauna of the irrigated rice ecosystem in the central Kerala, India. *Journal of Arachnology, 33*(2), 247-255. doi:10.1636/05-08.1

Settle, W. H., Ariawan, H., Astuti, E. T., Cahyana, W., Hakim, A. L., & Hindayana, D. (1996). Managing tropical rice pests through conservation of generalist natural enemies and alternative prey. *Ecology,77* (7), 1975-1988. doi:10.2307/2265694

Shepard, B. M., Banion, A. T., & Litsinger, J. A. (1995). *Rice-Feeding insects of Tropical Asia.* Manila, Philippines: International Rice Research Institute.

Sigsgaard, L. (2000). Early season natural biological control of insect pests in rice by spiders - and some factors in the management of the cropping system that may affect this control. *European Arachnology 2000*, 57-64. Retrieved from http://www.european-arachnology.org/wdp/wp-content/uploads/2015/08/057-064_Sigsgaard.pdf

Sudhikumar, A. V., Mathew, M. J., Sunish, E., & Sebastian, P. A. (2005). Seasonal variation in spider abundance in Kuttanad rice agroecosystem, Kerala, India (Ara neae). *Acta Zoologica Bulgarica, 1*, 181-190. Retrieved from https://www.researchgate.net/publication/303400781

Tahir, H. M., & Butt, A. (2008). Activities of spiders in rice fields of central Punjab, Pakistan. *Acta Zoologica Sinica, 54*(4), 701-711. Retrieved from http://www.actazool.org/temp/%7BB8400287-5393-423C-8CA3-968804BFAAA2%7D.pdf

Tahir, H. M., & Butt, A. (2009). Predatory potential of three hunting spiders inhabiting the rice ecosystems. *Journal of Pest Science, 82*(3), 217-225. doi:10.1007/s10340-008-0242-9

Tahir, H. M., Butt, A., & Sherawat, S. M. (2009). Foraging strategies and diet composition of two orb web spiders in rice ecosystems. *Journal of Arachnology, 37*(3), 357-362. doi:10.1636/P08-89.1

Takada, M. B., Kobayashi, T., Yoshioka, A., Takagi, S., & Washitani, I. (2013). Facilitation of ground-dwelling wolf spider predation on mirid bugs by horizontal webs built by *Tetragnatha* spiders in organic paddy fields. *Journal of Arachnology, 41*(1), 31–35. Retrieved from http://www.bioone.org/doi /full/10.1636/P12-30.1

Takada, M. B., Takagi, S., Iwabuchi, S., Mineta, T., & Washitani, I. (2014). Comparison of generalist predators in winter-flooded and conventionally managed rice paddies and identification of their limiting factors. *Springerplus, 3*, 1-7. doi:10.1186/2193-1801-3-418

Tsutsui, M. H., Tanaka, K., Baba, Y. G., & Miyashita, T. (2016). Spatio-temporal dynamics of generalist predators (*Tetragnatha* spider) in environmentally friendly paddy fields. *Applied Entomology and Zoology, 51*(4), 631-640. doi:10.1007/s13355-016-0440-5

Turnbull, A. L. (1973). Ecology of the true spiders (Araneomorphae). *Annual Review of Entomology*, *18*(1), 305-348. doi:10.1146/annurev.en.18.010173.001513

Venturino, E., Isaia, M., Bona, F., Chatterjee, S., & Badino, G. (2008). Biological controls of intensive agroecosystems: wanderer spiders in the Langa Astigiana. *Ecological Complexity, 5*(2), 157-164. doi:10.1016/j.ecocom.2007.10.003

Wang, Z., Yuan, Z., Song, D., & Zhu, M. (2004). Analysis on the dynamics of spatial distribution pattern of mixed spider population in rice field. *Insect Science, 11*(4), 257-265. doi:10.1111/j.1744-79172004.tb00422.x

Wilson, J. J., Ramakrishnan, R., Pavaraj, M., & Sevarkodiyone, S. P. (2014). A Study on the Age-Wise and Seasonal Distribution of Spider Fauna in the Paddy and Maize Field. (Athikulam, Virudhunagar District, Tamil Nadu, India). *World Journal of Zoology, 9*(1), 13-18. doi:10.5829/idosi.wjz.2014.9.1.82266

Yoshida, M. (1987). Predatory behavior of *Tetragnatha praedonia* (Araneae: Tetragnathidae). *ACTA Arachnology, 35*(2), 57-75. doi:10.2476/asjaa.35.57

Yu, X. P., Zheng, X. S., Xu, H. X., Lu, Z. X., Chen, J. M., & Tao, L. Y. (2002). A study on the dispersal of lycosid spider, Pirata subpiraticus between rice and Zizania fields (in Chinese with English abstract). *Acta Entomol Sin, 45*(5), 636–640.

Yu, X. P., Zheng, X. S., Xu, H. X., Lu, Z. X., Chen, J. M., & Tao, L. Y. (2002). A study on the dispersal of lycosid spider, Pirata subpiraticus between rice and Zizania fields (in Chinese with English abstract). *Acta Entomol Sin, 45*(5), 636–640.

Yu, X. P., Zheng, X. S., Xu, H. X., Lu, Z. X., Chen, J. M., & Tao, L. Y. (2002). A study on the dispersal of lycosid spider, Pirata subpiraticus between rice and Zizania fields (in Chinese with English abstract). *Acta Entomol Sin, 45*(5), 636–640.

Yu, X. P., Zheng, X. S., Xu, H. X., Lu, Z. X., Chen, J. M., & Tao, L. Y. (2002). A study on the dispersal of lycosid spider, *Pirata subpiraticus* between rice and *Zizania* fields (in Chinese with English abstract). *Acta Entomologica Sinica, 45*(5), 636–640. Retrieved from http://www.insect.org.cn/EN/Y2002/V45/I5/636

Zhi-yu, L., Hong, Y., Feng-xiang, L., Qing, F., & Yang, H. (2011). Occurrence and population dynamics of chironomids in early-season rice fields. *Rice Science, 18*(2), 136-141. doi:10.1016/S1672-6308(11)60019-X