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Relationships Between Morphology and Web Characteristics of Four Spider Species (Araneae: Tetragnathidae) in Malaysia

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Abstract. Approximately 34 tetragnathid species have been recorded in Malaysia. These orb-web spiders start building their first webs in early juvenile stages. The relationships between the morphology and the web characteristics of four tetragnathid species (*Leucauge argentina, L. celebesiana, Mesida gemmea* and *Tylorida ventralis*) were presented in this paper. The morphology was represented by eight morphological variables interpreted through first principal component analysis. The correlations between the morphology and each web characteristic were tested. The results showed that while there was a correlation between the principle component and the web size, there was no significant correlation in the number of spirals, number of radii, web-sites and web-angles in the four tetragnathid species. Factors that affect web characteristics in different body sizes were likely influenced by environmental factors. Changes of web characteristics could have corresponded to the condition at different habitats types. The information obtained from this study could provide a better insight for other arachnids study particularly in Malaysia.

Key words: Relationships, morphology, web characteristics, Tetragnathidae, Malaysia

Introduction

The long-jawed orb-weaver spiders from the family Tetragnathidae contain at least 967 species from 47 genera worldwide (Platnick, 2014) where the members of this family are very diverse in morphology and behavioral characteristics. According to Dzulhelmi (2016), at least 34 tetragnathid species have been recorded in Malaysia. Orb-web spiders foraging strategies have highly depended on the web selection, in which they have first started building since juvenile stage. The orb-webs must be built before foraging success could be assessed (Higgins, 1995). They also being known as 'sit-and-wait' predators that employ a homogeneous foraging strategy across their life stages (Sensenig et al., 2011) and highly dependent on the webs they construct at strategically chosen microhabitats. Minimizing energy cost for building webs was important for maximizing the prey-capture efficiency (Blamires et al., 2010). Orb-web spiders usually improve the performances of their web structures by altering a few web parameters (i.e. web area, mesh size, number of spirals and number of radii) that have direct impact on the costs and benefits of building the webs (Liao et al., 2009; Wu et al., 2013 but see Zschokke & Nakata, 2010). While the type of silk and structures of orb-webs from juvenile to the adult stage had remained relatively constant, the silk amount and quality differed, as large size spiders tend to target larger prey (Sensenig et al., 2010). For instance, intercepting, stopping and retention potential of adult Neoscona arabesca orb-webs were sturdier compared to that of juvenile spiders although there were no changes in the mesh-size of the two stages (Sensenig et al., 2011). On the other hand, juvenile Nephila clavipes and N. maculata would alter their web characters by either increasing or decreasing the web sizes in response to the level of decrement in prey capture (Higgins, 1995) which they had learned through experience.

Some spiders changed their web-sites and microhabitats to achieve a higher rate of prey captures (Moore, 1977; Wise, 1993). For example, *Argiope aurantia* shifts from forest edges to open fields as they reach adulthood (Enders, 1973), because of the significant differences in the variety and abundance of prey in open fields compared to the forest edges (McReynolds, 2000). This foraging investment corresponded with the spiders' response to resource availability. Although the natural history and ecology of other arthropod species remained unknown, previous studies that investigated spiders at species-level had mostly been conducted in other geographical regions (i.e. Enders, 1974; Higgins, 1995; Kuntner et al., 2008) while studies that had taken place within the Southeast Asian region were very scarce (i.e. Dzulhelmi et al., 2017). During our field samplings for tetragnathid species that build orb-webs, four common species, *Leucauge argentina, L. celebesiana, Mesida gemmea* and *Tylorida ventralis* were identified

at various locations in Malaysia (Norma-Rashid & Li, 2009; Koh et al., 2013; Dzulhelmi et al., 2014a; Dzulhelmi et al., 2014b), and their wide distribution was the evidence of their successful ecological adaptation. Unfortunately, very little is known about the relationship between the life stages and the web characteristics of these four species.

Although orb-web spiders of any stage would initially build webs typical to that of adult spiders, they would subsequently alter their web structures throughout their lives to adapt to biotic and abiotic conditions. This study aimed to determine whether there were relationships between the morphology and the web characteristics of these tetragnathid species. This study hypothesized that if the morphology and web characteristics were not correlated, the variability of web characteristics were probably influenced by environmental factors instead of life stages.

Material and methods

Data collection

Field surveys for tetragnathid spiders orb-webs were conducted from April 2013 and June 2013 in six locations in Malaysia (Table 1). Searching of orb-webs was done during daytime (1000–1400 hours) and night time (2000–0000 hours) for three consecutive days in each site. The web orientations or angular tilts were measured using a protractor by placing the straight edge of the protractor in parallel to the bases of the slanted webs (Ramirez et al., 2003). Meanwhile, the vertical distances of the webs from ground (web-sites) were measured using a measuring tape. The webs were dusted with powder to increase visual contrast for photography. Collected spider specimens were stored in 75% ethanol solution for species identification. Absence of pedipalp (male) was ensured so that only female spiders were used for web characteristics analysis. The female genitalia were dissected and cleaned using potassium hydroxide (KOH) before examination under a 50× dissecting microscope (AmScope, USA). The spiders' morphological measurements were obtained based on the: total lengths (TL), carapace lengths (CL), carapace widths (CW), abdomen lengths (AL), the lengths of leg I-III-III-IV. Likewise, the web characteristics measured were: web areas, free-zone areas, hub areas, mesh-sizes, number of spirals, number of radii, angles and web-sites. The measurements for both spider specimens and web characteristics were measured were:

Location	GPS	Forest types
Kuala Selangor Nature Park, Selangor	3°20'16" N, 101°14'56" E	Mangrove forest
Ulu Gombak Field Study Centre, Selangor	3°22'60" N, 101°47'20" E	Secondary forest
Kubah National Park, Sarawak	1°36'41"N, 110°11'44"E	Heath forest
Gunung Gading National Park, Sarawak	1°41'27''N, 109°50'45''E	Dipterocarp forest
Bako National Park, Sarawak	1º41'8"N, 110º26'10"E	Peat swamp forest
Mesilau National Park, Sabah	6°02'5"N, 116°54'1"E	Montane oak forest

Table 1. The forest types and GPS coordinates of each location surveyed for tetragnathid spider species.

Data analyses

One hundred individuals belonging to four tetragnathid spider species were collected throughout the field sampling. The spider specimens collected were consisted of *L. argentina* (14 individuals from Gunung Gading National Park and 11 individuals from Kubah National Park), *L. celebesiana* (29 individuals from Mesilau Nature Park), *M. gemmea* (12 individuals from Gunung Gading National Park and nine individuals from Ulu Gombak Field Study Centre) and *T. ventralis* (19 individuals from Kuala Selangor Nature Park and six individuals from Bako National Park).

L. argentina, *M. gemmea* and *T. ventralis* were found in more than one site. Therefore, the Welch t-test was performed to compare the same web variables in the two sites where the same species were found. Modification was made to the degrees of freedom in the Welch t-test to determine whether all the individuals of the same species from different sites could be pooled. Other web character variables with no significant difference in the mean values were also pooled for further analyses. The same analysis was also used to analyze the web characteristic variables that were not influenced by the habitat type. The average measurement values (mean with standard deviation) of the morphological and web characteristics of the four selected female tetragnathid spider species used were summarised (Table 2 and Table 3).

Instead of using a single proxy variable for the spider size, the morphological variables were log normalized $[\log (x+1)]$ (Table 4). The eight morphological variables were then converted into principal components. Since there was a very high covariance

between the morphological variables, the first principle component was able to summarize more than 80% of the variance in the tetragnathid species: *L. argentina* (84%), *L. celebesiana* (86%), *M. gemmea* (87%) and T. *ventralis* (91%) (Table 5). Spearman Rank Correlation was used to detect any correlation of the first principle component and each of the web characteristics. The analysis was performed using R 3.1.0 (R Core Team, 2015).

Results

The Welch t-test analysis showed no significant difference in web characteristic of *L. argentina*, *M. gemmea* and *T. ventralis* among different populations and habitats except for the hub-area of *L. argentina* (data not shown). The scatter plots between the morphological characters (PC1) and each web character variable for *L. argentina* (Fig. 1), *L. celebesiana* (Fig. 2), *M. gemmea* (Fig. 3) and *T. ventralis* (Fig. 4) were as presented. For all the plots, there are few indications of trends in for variables number of radii, number of spirals, web-angle and web-sites. However, there is an obvious correlation between PC1 and the variables Meshsize, Web-area, Freezone and Hub-area. Spearman Rank Correlation showed strong correlations between the web-area, freezone-area, hub-area and mesh-size (except for *M. gemmea*) and the spider size, represented as PC1 (Table 6). Other web features that showed no correlation with the spider size were the number of radii, number of spirals, web-angle and web-sites would remain constant as the spiders grew as they develop into maturity. It also reflected the stability of environmental conditions throughout the life stages of the spiders within the habitat.

Species	N	TL	CL	CW	AL	Leg I	Leg II	Leg III	Leg IV
L. argentina	25	3.28±0.76	1.51±0.26	1.22±0.28	2.22±0.69	6.59±1.51	4.91±1.05	2.96±0.57	4.26±0.88
L. celebesiana	29	6.78±2.31	2.61±0.74	1.96 ± 0.50	$4.40{\pm}1.65$	18.29±7.07	12.69±4.79	6.14 ± 2.05	10.89±3.99
M. gemmea	21	3.44±0.99	1.42 ± 0.42	1.05±0.23	2.16±0.59	9.29±3.26	$5.98{\pm}1.86$	2.99 ± 0.73	4.92±1.33
T. ventralis	25	4.81±1.21	1.86±0.49	1.38±0.35	2.95±0.79	12.84 ± 4.12	7.43 ± 2.34	3.79±0.99	6.11±1.79

Table 2. The mean values with standard deviation in centimeters of the morphological characters of the four female tetragnathid spider species.

Species	Ν	Radii (n)	Spirals (n)	Mesh-size	Web-area (cm ²)	Freezone-	Hub-area	Web-angle	Web-sites
				(cm ²)		area (cm ²)	(cm ²)	(cm ²)	(cm ²)
L. argentina	25	26.64±4.80	30.84±8.92	0.24 ± 0.07	145.83 ± 68.92	7.79±4.11	0.60 ± 0.36	39.60±20.86	43.80±32.12
L. celebesiana	29	20.17±3.51	24.01±5.43	0.39±0.13	264.96 ± 145.94	19.33±9.53	2.22 ± 1.37	63.28 ± 7.82	66.72±34.36
M. gemmea	21	17.24±3.10	28.48±8.10	0.38±0.16	262.88±267.16	11.42 ± 8.67	0.80 ± 0.51	41.43 ± 27.98	152.62 ± 55.70
T. ventralis	25	18.32±2.01	28.07±6.89	0.40 ± 0.14	338.44±181.65	18.90±11.55	1.20 ± 0.72	57.20±17.39	153.40±54.50

Table 3. The mean values with standard deviation of the web characteristics of the four female tetragnathid spider species.

Variables	L. argentina	L. celebesiana	M. gemmea	T. ventralis	
TL	1.116	0.916	1.050	0.891	
CL	0.586	0.663	0.609	0.720	
CW	0.743	0.572	0.488	0.632	
AL	1.271	0.859	0.864	0.840	
Leg I	1.252	1.272	1.528	1.398	
Leg II	1.026	1.2151	1.229	1.271	
Leg III	0.819	1.010	0.852	0.896	
Leg IV	0.969	1.237	0.981	1.092	

Table 4. Loadings of the first principle component (PCA) for each morphological variable.

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	Principal compone	Principal component (PC1)					
Species	L. argentina	L. celebesiana	M. gemmea	T. ventralis			
Standard Deviation	0.44	0.76	0.61	0.61			
Proportion of variance	0.84	0.86	0.87	0.91			

Table 5. The proportion of variance morphological principle component for each species.



Figure 1. Scatter plots between morphological characters (PC1) and each web characteristic variable of *L. argentina* (abbreviations: NoRad = radii; MeshH = mesh-size; Freezone = freezone-area; WebDeg = angles; HGround = web-sites).



Figure 2. Scatter plots between morphological characters (PC1) and each web characteristic variable of *L. celebesiana* (abbreviations: NoRad = radii; MeshH = mesh-size; Freezone = freezone-area; WebDeg = angles; HGround = web-sites).



Figure 3. Scatter plots between morphological characters (PC1) and each web characteristic variable of *M. gemmea* (abbreviations: NoRad = radii; MeshH = mesh-size; Freezone = freezone-area; WebDeg = angles; HGround = web-sites).



Figure 4. Scatter plots between morphological characters (PC1) and each web characteristic variable of *T. ventralis* (abbreviations: NoRad = radii; MeshH = mesh-size; Freezone = freezone-area; WebDeg = angles; HGround = web-sites).

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Species	Variables	rho	t	df	р	Sig.
L. argentina	Radii	-0.314	-1.585	23	0.127	NS
	Spirals	0.060	0.289	23	0.774	NS
	Mesh-size	0.469	2.544	23	0.018	*
	Web-area	0.628	3.870	23	0.001	*
	Freezone	0.647	4.073	23	0.001	*
	Hub-area	0.499	2.761	23	0.011	*
	Web-angle	-0.012	-0.056	23	0.956	NS
	Web-sites	-0.074	-0.354	23	0.726	NS
L. celebesiana	Radii	0 125	0.656	27	0.517	NS
21 00100 0510110	Spirals	0.015	0.079	2.7	0.937	NS
	Mesh-size	0.394	2.225	27	0.034	*
	Web-area	0.468	2.754	27	0.010	*
	Freezone	0.669	4.681	27	0.0001	*
	Hub-area	0.483	2.873	27	0.008	*
	Web-angle	-0.124	-0.649	27	0.521	NS
	Web-sites	0.115	0.600	27	0.553	NS
M. gemmea	Radii	-0.268	-1.214	19	0.240	NS
	Spirals	0.400	1.902	19	0.072	NS
	Mesh-size	0.215	0.960	19	0.349	NS
	Web-area	0.777	5.385	19	0.0001	*
	Freezone	0.709	4.383	19	0.0001	*
	Hub-area	0.781	5.460	19	0.0001	*
	Web-angle	-0.191	-0.847	19	0.408	NS
	Web-sites	-0.153	-0.677	19	0.506	NS
T. ventralis	Radii	-0.260	-1.294	23	0.208	NS
	Spirals	0.068	0.330	23	0.745	NS
	Mesh-size	0.554	3.189	23	0.004	*
	Web-area	0.655	4.163	23	0.001	*
	Freezone	0.719	4.963	23	0.0001	*
	Hub-area	0.641	4.009	23	0.001	*
	Web-angle	0.059	0.281	23	0.781	NS
	Web-sites	0.272	1.356	23	0.188	NS

*Significant to 0.05; NS Not significant

Table 6. Correlation between morphological principle component and web characteristic variables.

Discussion

In general, the freezone-area and hub-area of a web increase proportionately to the web-area as these web characteristics were inter-related. Adult spiders with larger body sizes would construct larger web sizes than the juvenile spiders with smaller body sizes to sustain their own body weights (Sensenig et al., 2011). This is in consistence with the present results where the body sizes were observed positively correlated with the web-area, freezone-area and hub-area of these spiders' webs. The web materials improved significantly as the spiders developed into adulthood (Sensenig et al., 2011), corresponding to captured prey variation (Richardson & Hanks, 2009) during different life stages. Regarding to Tahir et al. (2010), the bigger bodied orb-web spiders are

known to capture larger prey at higher web-sites and reduce competition with smaller size spiders. Yet, larger and faster prey usually has higher kinetic energy and larger spiders tend to invest in more and higher quality silk to achieve better performance (Sensenig et al., 2011). Nonetheless, web-site height does not always correlate to spider size (Richardson & Hanks, 2009). Comparably, this study has identified the correlations between the spider body size and mesh-size, which were in concordance with previous studies (i.e. Eberhard, 1988; Herberstein et al., 2000a, but see Tahir et al., 2010). Additionally, most orb-web spiders are able to capture a diverse and profitable array of prey types depending on the web-sites. For example, Diptera, Hymenoptera and Lepidoptera were the main prey captured in the colonial webs of *Leucauge* sp. (Salomon et al., 2010).

Although numerous field studies have failed to find a consistent relationship between the mesh-size and prey size (Herberstein & Heiling, 1998), several studies have suggested otherwise. In some instance, the spider *Argiope keyserlingi* did not alter their mesh sizes (Herberstein et al., 2000b; Blamires, 2010; Blamires et al., 2017) despite the availability of a diverse prey of different sizes. On the other hand, Some spider species such as *Leucauge mariana* increased their web-areas but reduced the mesh-sizes (Eberhard, 1988) as they developed into maturity. This study had not determined the relationships between the web mesh-size and the prey size among spiders of different sizes due to lack of prey specimen collected from the spiders' webs.

Analysis on all four tetragnathids have found no correlation between the body size and the number of radii. Witt et al. (1972) found that the juveniles had more number of radii than adult spiders of *Araneus diadematus*. Spiders were able to save more energy and maintain the same web effectiveness, stiffness and function even if they reduced the number of radii (Sensenig et al., 2010). In contrast, other orb-web spider species such as *Nephila, Nephilengys* and *Herennia* species increased the number of radii as the spider size increased (see Kuntner et al., 2008). More number of radii proportionate to the spider size resulted in stronger webs (e.g. Blamires et al., 2011). This allowed effective capturing of faster and heavier prey because of the increment in kinetic energy absorption from the impact (Eberhard, 1990; Wise, 1993). Too much tension on the web might permit the prey to fly through or bounce off depending on the size and velocity of the prey, a phenomenon known as the 'trampoline effect' (Sensenig et al., 2011).

None of the four tetragnathid species showed correlation between the body size and the number of spirals. This was consistent with the finding by Tahir et al. (2010) which stated that the spider body size is not correlated to the number of spirals. In contrast, Henaut et al. (2006) identified that the number of spirals differed between individuals at different web-sites. The abdomen width is also correlated to the number of spirals which is related to maturity (Henaut et al., 2006). However, Eberhard (1988) suggested that a broader abdomen and a heavier weight showed the sign of greater feeding success, and are also associated with the developmental stage of the eggs it carries. Web-sites selection appeared to be related to the sexual development of the spiders, and larger size spiders chose higher web-sites compared to smaller size spiders of conspecifics (Enders, 1974; Henaut et al., 2006). This was probably due to prey availability at different web-sites (Moore, 1977; Blackledge et al., 2003), and spiders might relocate their web-sites in response to the prey types (Moore, 1977; McReynolds, 2000; Henaut et al., 2006). Some studies had found correlation between the body sizes and the web-sites (e.g. Henaut et al., 2006). Current results demonstrated that the spider body size did not correlate with the web-sites in any of the four species.

There was however an alternative interpretation for this result; different tetragnathid species of different sizes might respond to the vegetation structure. For instance, larger spiders would construct larger webs at higher web-sites where there was more open space rather than at lower web-sites where space was limited by shrubs and grasses (McReynolds, 2000). If there was enough space to construct the webs, it would be preferable to maintain the web at these web-sites, where there is constant access of food supplies and less competition. Repairing, abandoning or reconstructing webs in other web-sites would be a waste of energy (Biere & Uetz, 1981; Sensenig et al., 2010). Therefore, the four tetragnathid species might have maintained their web-sites at certain height from the ground as they grew from juvenile into adult.

Orb-weavers have the capability to orient their planar webs in response to climatic factors and prey flight paths (Biere & Uetz, 1981). They would choose web-sites that provide desirable prey types and microhabitat structures, depending on their web characteristics (Herberstein, 1997; McReynolds, 2000). This study have identified that the four tetragnathid species constructed horizontal orb-webs, and have tilted the web angle more vertically as they grow into maturity. However, this study found no correlation between the body size and the web angle. Nonetheless, horizontal orb-webs have the disadvantages of reduced web capture by about 70%, lower retention of prey capture by 20%, and increased damage from rain drops and falling debris (Eberhard, 1990). Hence, the web angle was tilted in accordance to the condition of available space along with the fulfillment of other requirements.

Conclusions

Many biotic and abiotic factors were taken into consideration when determining the variations in web characteristics of each tetragnathid species. The four tetragnathid species in this study had produced a comparable number of spirals and radii at different body sizes. Other factors that reflect web characteristics of different body sizes were likely to be influenced by maturity. Similarly, changes of other web characteristics could be responding to the requirements of circumstances within the habitat type. The information on tetragnathid species obtained from this study could benefit researchers, particularly in Malaysia.

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馬來西亞產四種蜘蛛形態與織網特徵之關聯性研究 (蜘蛛目:長腳蛛科)

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摘要: 馬來西亞約紀錄有 34 種長腳蛛科物種,這些結圓網的蜘蛛在他們若蛛階段初期便會開始第一次結網,而本文即探討 4 種長腳蛛 (雪銀腹蛛 Leucauge argentina、西里伯銀腹蛛 L. celebesiana、裝飾天星蛛 Mesida gemmea 和橫帶高腹蛛 Tylorida ventralis)的形態與織網特徵之關聯性,形態特徵部分以 8 個形態變數作為代表並透過主成分分析方法 (Principal component analysis) 進行解析,測試形態與各織網特徵的相關性。結果顯示在這四種長腳蛛裡,結網尺寸與形態特徵具 有相關性,然而橫絲數 (Spirals)、縱絲數 (Radii)、結網位置和結網角度則與形態特徵無顯著關聯。影響不同體型尺寸長 腳蛛織網特徵的因子可能為環境因素所影響,織網特徵的改變則相應自不同棲地類型的狀況。本研究提供特別是馬來西 亞產的蛛形類研究一個嶄新的視野。

關鍵詞: 關聯性、形態、織網特徵、長腳蛛科、馬來西亞