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TREE TRUNK TOPOGRAPHY MODIFIES THE WEBS OF THE ARBORICOLE SPIDER, *HERENNIA MULTIPUNCTA* (DOLESCHALL, 1859) (ARANEAE: NEPHILIDAE)

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ABSTRACT

The arboricole spider, *Herennia multipuncta* (Doleschall, 1859), actively colonizes areas in which primary forest has been either lost or replaced by planted trees. The benefits of such plasticity for the survival of the species in modern Southeast Asia are transparent. However, niche plasticity is a generalist strategy that seems at odds with its status as a specialist that makes a highly derived web form (ladder webs). Although some colonized trees may offer equivalent or even better sites for web location, many may be predicted to provide less than ideal web substrates. Bark extrusion, in particular, can compromise web properties in numerous ways and fully realized ladder webs are optimally located on smooth substrates. In order to quantify what elements of specialization have been traded-off against the benefits of niche expansion, *H. multipuncta* ladder webs on secondarily planted trees of *Acacia mangium* Willd. with rough, sub-optimal trunk surfaces were examined for lost and retained characteristics. Only the derived hub-cup was universally kept in these "no frills" ladder webs. Observed modifications that compensated for degradation of the *Herennia* archetypal web template included plastic, site-specific adjustments of the hub-cup to tree microtopography and alternative web forms.

Keywords: *Acacia mangium*, arboricole, *Herennia multipuncta*, ladder web, plasticity

INTRODUCTION

In "The Comity of Spiders," Bristowe (1941) fondly recalled that *Herennia* spiders "were common in southern Siam" and that he often "marvelled" at them "pressed flat against the silvery grey trunks of the Kapok trees." Today, as a result of its relatively large size (adult females reach a length of ca. 10–14 mm), its tree-living habits, and its beautifully ornate webs, *Herennia multipuncta* (Fig. 1) is still one of Thailand's signature spiders. However, in the over half century since Bristowe's (1941) reminiscences the habitat potentially available to the spiders has shrunk considerably in absolute terms, in particular as a result of the period from 1976–1989 when 28% of forest cover in Thailand was permanently lost (Cropper *et al.*, 1999).

Deforestation is an endemic problem in Southeast Asia and Thailand is no exception to the rule, although the greatest losses are not contemporary but occurred during the excesses of development in the second half of the 20th century before "green" thinking had achieved any degree of mainstream presence. Greater prioritization of the environment is reflected in recent assessments. For example, Thailand showed the lowest permanent losses in forest cover

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(0.2%) among the Mekong Basin countries in the first decade of the 21st century (LEINENKUGEL *ET AL*., 2015). Nonetheless, despite an impressive system of national parks and reserves, the contraction of Thailand's available primary and secondary forest habitats outside of protected areas has had a largely unknown impact on large swathes of its original flora and fauna (e.g. DEELEMAN-RHEINOLD, 2001).

In this context, *H. multipuncta* is an interesting study model. It is an obligate arboricole because it is obliged to live on tree trunks as a result of evolutionary specialization, although occasionally it can also utilize alternative habitats that offer analogous structural opportunities. The main basis for this continued dependence on trees has been the evolution of its ancestral orb web into a "ladder web" (Fig. 2).

Ladder webs are elongated webs in which the vertical dimension exceeds the horizontal dimension to the extent that their shape resembles a ladder. The first description of this web-type has been traditionally attributed to ROBINSON & ROBINSON (1972). Since their use of the term, ladder webs have been identified in a number of unrelated families and genera (EBERHARD, 1975; STOWE, 1978; ROBINSON & LUBIN, 1979; FORSTER & FORSTER, 1985; KUNTNER *ET AL*., 2008, 2010; HARMER & FRAMENAU, 2008; HARMER, 2009). They are of particular interest because of their unusual architecture (e.g. EBERHARD, 1975; ROBINSON & LUBIN, 1979; FORSTER & FORSTER, 1985), interactions with substrate (e.g. KUNTNER *ET AL*., 2010) and/or prey specialization (e.g. EBERHARD, 1975; STOWE, 1978), and as a model for the plasticity of the web template (e.g. HARMER & FRAMENAU, 2008; HARMER, 2009; HARMER & HERBERSTEIN, 2009).

SIMON (1894) described *Herennia* webs in Sri Lanka as stretched, orbicular webs. However, although SIMON (1894) was the first to emphasize the ornateness of *Herennia* webs, the first description of ladder webs as we know them today came from Oates (in THORELL [1895]). Eugene W. Oates collected the Burmese spiders that formed the basis of Thorell's "Descriptive Catalogue of the Spiders of Burma" (1895). Oates also provided Thorell with some observations on the spiders in the collection, some of which Thorell included with his species descriptions. THORELL's (1895) catalogue of Burmese spiders is one of the founding texts on the systematics of Southeast Asian spiders. Although the descriptions were accessible to his contemporaries, they remain largely inaccessible to readers now due to their use of Latin and lack of figures. However, on page 163 in his description of *H. multipuncta*, he quoted Oates's description of the web in English:

> "Rangoon 8/8/87. Makes a web about 3 feet (91.4 cm) long on a smooth tree trunk. Width ⅓ or ¼ of girth of tree. All the lines are vertical, forming *a perfect rope ladder*. The web follows the convexity of the trunk, and is everywhere about ½ inch (1.27 cm) from it. Verticals about 1 inch (2.54 cm) apart, horizontals about ¼ inch (0.64cm) apart." [Metric conversions added in brackets; italics added for emphasis.]

Thus the first appellation of "ladder" may be attributed to Oates's observations and indeed, so may the first accurate description of the web of *H. multipuncta*. That ROBINSON & ROBINSON (1972) later used the same appellation nearly a century later is testimony to the suitability of the term. In fact, Oates' "rope ladder" is perhaps an even more apposite term given the analogous properties of spider silk.

From an architectural perspective, *Herennia* webs may be considered the exemplar of the ladder form *par excellence* as a result of a number of unique web elements that complement elongation; web curvature and the hub-cup are of particular note, the former enabling the spider's web to achieve the seemingly impossible engineering feat of curving its web plane around a tree trunk.

Figure 1. A female arboricole spider, *Herennia multipuncta,* (body length 14 mm) at its web hub on a tree-trunk, Huai Yai, Bang Lamung, Chonburi, Thailand: (a) dorsal aspect; and (b) lateral aspect with prey.

However, these unique traits of *H. multipuncta's* ladder web template mean that its webs are architecturally best suited to trees in which the topography of the tree trunk is sufficiently streamlined (relatively smooth surface) to facilitate their expression. This study tests the hypothesis that niche expansion onto tree trunks with rough, extrusive topographies leads to a degradation of the archetypal *Herennia* web template (modification and/or loss of derived web elements). A field study was carried out on a colonizing population of *H. multipuncta* on *Acacia mangium* trees, which have a more rugose surface topography. *A. mangium* is a particularly relevant test of the stated hypothesis because this species, which originated from Australia and Papua New Guinea, is now secondarily planted throughout Southeast Asia, particularly in areas that have been subject to roadside development and at sites where land is being reclaimed after clearance for construction.

METHODS

Acacia mangium Willd. were identified with reference to Jensen (1999). Spider systematic nomenclature follows the World Spider Catalog (2015). A copse of ca. 150 planted *A. mangium* trees was surveyed in February 2014 in the central eastern province of Chonburi, Thailand, for webs of *H. multipuncta*. Including previous pilot observations, the total number of *H. multipuncta* found occupying the copse was 27. At the start of the study, eight individuals were found to have either relocated or been predated, so parameters for 19 webs were collected during the study period and are used here.

The following measures were made: spider body length (mm), height of hub above ground (cm); compass orientation of web plane as determined from hub-cup; tree circumference (cm); width and length of sticky capture area (cm); distance of hub to top of sticky capture area (cm); distance of left side-frame to hub (cm); distance of web plane to bark from hub (cm); and presence and ratio of frame side-attachments.

The ladder web template of *H. multipuncta* is summarized in Figure 1. *Herennia* web elements that were either retained or modified were noted for each individual web. Their presence in the *A. mangium* population was compared in terms of percentage occurrence. The following web elements were recorded: (1) hub-cup, (2) vertical asymmetry, (3) parallel side-frames, (4) pseudo-radii, (5) contact with bark, (6) curvature around the tree trunk surface, (7) retention of within-frame-template surface area, and (8) use of trunk microtopographic

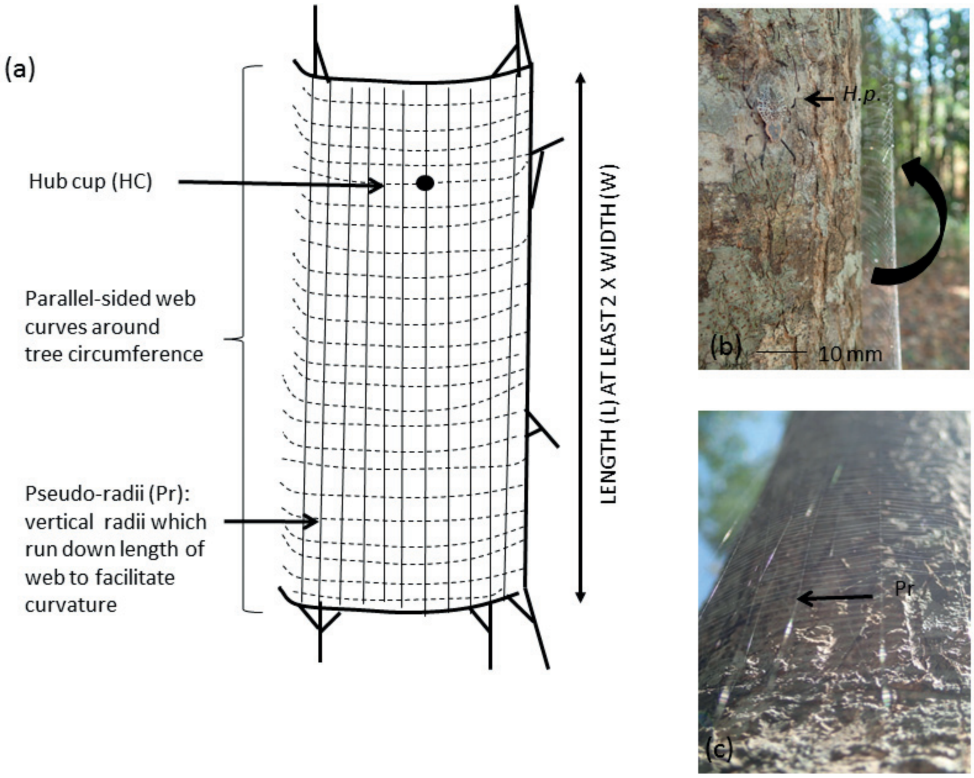


Figure 2. Ladder web template of *Herennia multipuncta* on smooth tree surface: (a) idealized representation showing general architecture and derived elements (straight lines represent pseudo-radii; dashed lines represent sticky silk); (b) photograph of adult female sitting in hub cup with web plane curving around *Senna siamea* (Lam.) Irwin & Barneby tree trunk (*H. p.* indicates female sitting at hub; curved arrow denotes web curvature); (c) photograph of web mesh looking up *S. siamea* tree trunk (Pr denotes representative pseudo-radius).

depressions and undulations to situate the hub-cup deeper and further away from the web plane. Elements 1 and 4 follow the nomenclature introduced by ROBINSON & LUBIN (1979). Hub-cups are so called because the hub has been turned into a sunken funnel or "cup" which sits below the web plane and in all but the earliest instars, attaches to the bark; pseudo-radii do not radiate from the hub as "true" radii do in orb webs, but run vertically down the ladder (ROBINSON & LUBIN, 1979).

Parameters best summarized in terms of presence and absence were hub-cup, curvature, parallel-side frames, pseudo-radii, use of microtopography, and web contact. Reductions to within-frame-template capture surface area were too context-specific to quantify beyond presence-absence, but representative descriptions of some instances of these are described and presented. Within-frame-template reductions in surface area refer to losses of capture area that are not described by length-width measures—i.e., where the web's length and width remain ladder-like but morphological alterations have been made to the actual capture-area template (see Results).

Quantitative comparisons were made of the two factors with greatest influence on prey capture efficiency: (1) Reduction or loss of vertical asymmetry reduces the sticky capture area potentially, and archetypically, available for capturing prey. Ladders were defined as webs in which the length was at least twice the width. (2) Hub vertical asymmetry is understood to represent an optimal foraging model of web construction in which unequal distributions of energetic expenditure or web stress are brought about by vertically-oriented webs and compensated for by displacing the hub above the central line of the web. Perhaps the most popular explanation of this model is that the hub is displaced to compensate for the differential running speeds of spiders moving either up or down a web (MASTERS & MOFFAT, 1983; ZSCHOKKE & NAKATA, 2010, 2015). Hub upward displacement in sampled webs was identified as a ratio (hub distance from top : total length of sticky capture area) <0.5, where 0.5 represents hub vertical symmetry. Both of these indices of vertical asymmetry should be related to the substrate characteristic to which they are supposed to be a response: tree circumference (see HARMER, 2009; KUNTNER *ET AL.*, 2010). Linear regression was used to test for evidence of such a relationship in the sample population on *A. mangium* trees. In the context of this study, significant relationships were interpreted as architectural *status quo* and lack of such significant relationships as a further indicator of the degradation of the archetypal web template.

One factor that might confound the results presented here is ontogenic differences in web architecture. The sample population was a colonizing population and was therefore relatively small and dominated by intermediate-to-late instars. It was therefore necessary to collate, rather than partition, web data. Using body length (BL) as a correlate for ontogenic stage, no significant correlation was found between BL and vertical elongation of webs (Pearson's correlation coefficient = 0.262; $p = 0.279$). Thus, the variations in web elements and forms in this study are attributed to habitat.

RESULTS

Parameters of 19 webs located on *A. mangium* trees were recorded (Table 1). All webs had complete canopy cover; however, because the copse is an artificial plantation, trees occurred in regularly spaced rows 2–5 m apart and with a relatively open sub-canopy light environment due to the regular management of all non-tree vegetation beneath. The percentage

Table 1. Parameters for *Herennia multipuncta* webs on *Acacia mangium* trees.

#	Spider body length (mm)	Height (cm)	Orienta-tion	Tree circum-ference (cm)	Width sticky capture area (cm)	Length sticky capture area (cm)	Top to hub (cm)	Side to hub-cup (L to R) (cm)	Web plane to bark from hub (cm)	Frame side attachments (L:R) (#)
1	5.45	181	SW	119	9.5	38.4	8.8	4.6	0.7	1:1
2	10.41	137	NE	105	11.6	33	13	4.1	0.8	1:1
3	6.13	179	NE	111	8.3	38.5	14.6	5.1	2.8	2:0
4	8.94	235	S	116	23.3	54.5	10.8	10.1	1.8	1:1
5	4.73	227	S	103	10.2	24.6	11.1	5.4	0.9	1:1
6	4.77	189	S	102	7.4	25.6	14.5	4.4	1.6	1:1
7	3.86	207	NE	109	7.2	18	6.2	3.2	0.6	1:1
8	4.8	144	SE	97	11.1	23.1	16	6.2	0.5	1:1
9	6.39	115	SE	93	12.4	28	10.5	6.8	1.1	2:0
10	3.21	45	S	87	7.6	7.7	3.4	3.2	0.5	2:0
11	3.95	78	S	84	8.2	22.7	12.5	3.9	0.7	1:1
12	4.35	36	SE	79	13.3	38.1	16.1	11.3	1.2	1:1
13	2.02	157	W	78	6.8	9.2	5.8	3.2	0.9	1:1
14	2.98	235	S	67	5.1	12.1	5.1	2.5	1.1	1:1
15	1.2	185	S	105	4.2	11.5	5.1	1.9	0.8	1:1
16	3.5	162	S	98	6.3	12.9	4.6	2.1	1.1	2:2
17	5.97	85	NE	92	17	31	16	7.9	0.6	5:5
18	5.25	117	W	81	8.5	27.8	12.3	4.4	1.2	1:1
19	4.72	210	N	88	6.6	8.6	4.5	3.5	0.5	0:1

occurrence of *Herennia* web elements on *A. mangium* trees was compared to their probability of occurrence on ideal web substrates (Table 2). Only hub-cups were present in all webs. The two web elements that showed greatest degradation of the web archetype were web displacement from the tree trunk surface (so that there is no contact between the web plane and tree bark) and web curvature. Five of the 11 contact-webs had sticky capture areas with multiple points of bark contact distributed across at least half of the entire web, as if the web had been laid across the bark surface rather than suspended away from it. Figure 3 shows two examples of bark-web contact: (a) a major bark extrusion which locally compromises web tension; and (b) multiple points of contact in which the web has been laid over the bark. Note the uninterrupted web plane in Figure 2c, for comparison.

Three alternative web forms were observed (Fig. 4). These instances of within-frame-template modification emphasize the extent to which length-breadth measures may, on a context-specific basis, prove to be inadequate for some webs and require supplementary qualification. All three forms were responses to tree trunk topography. The half-orb-half-ladder web ($n = 1$) was found on a tree where the orb half of the web had to traverse a large, deep dip in the trunk's vertical contour. The fork-tail webs ($n = 4$) (including the melanic adult female described in Hawes [2015]) and the hexagon ($n = 1$) were responses to bark extrusion. One web had tapering termini; however, I considered that to be sufficiently close to the parallel/sub-parallel web form to discount it as a new form.

The ranked distributions of (a) vertical asymmetry in web area, and (b) hub top displacement in the sampled population, are shown in Figure 5. Mean vertical asymmetry was 2.53 (± 0.21) with elongation of web area normally distributed (Anderson-Darling

Table 2. Ranked percentage (%) occurrence of *Herennia multipuncta* web elements on *Acacia mangium* trees. Statistical comparison of observed occurrence with probability of occurrence in archetypal web template using different thresholds for archetype (Body of table shows significance levels for signicant differences [$p<0.05$] between observed occurrences and four different percentage archetype template thresholds)*.

	Observed occurrence (%)	Percentage thresholds for archetype web template			
		50%	75%	90%	95%
Hub-cup	100	-	-	-	-
Parallel side-frames	89.47	-	-	-	-
Ladders	78.95	-	-	-	0.013
Pseudo-radii	73.68	-	-	0.035	0.002
Within-frame surface area	73.68	-	-	0.035	<0.001
Hub top displacement	68.42	-	-	0.009	<0.001
Use of micro-topography	47.37	-	0.009	<0.001	<0.001
No contact with bark	42.11	-	0.002	<0.001	<0.001
Curvature	15.79	0.002	<0.001	<0.001	<0.001

* Although these elements define the archetypal web template, in real webs, even in optimal habitat, their occurrence may be mediated to some extent by context. Archetype thresholds: >90% are diagnostic of ordinary web-habitat-interactions; 75% represents a partially degraded template; the 50% threshold indicates an unambiguously degraded template.

Figure 3. Examples of bark-web contact in *Herennia multipuncta* webs constructed on *Acacia mangium* trees: (a) major localized bark extrusion (indicated by arrow) into web plane that is otherwise stretched without interruption away from the tree trunk; and (b) multiple bark-web contacts in which the space between the tree trunk and the web plane has been almost completely compromised.

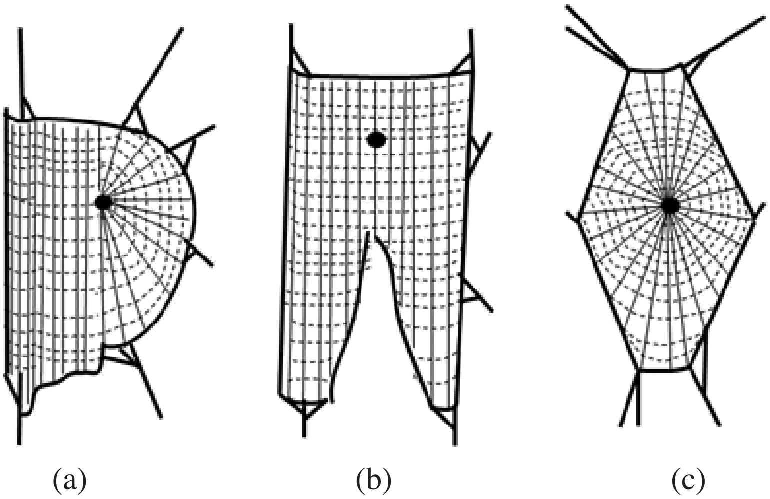
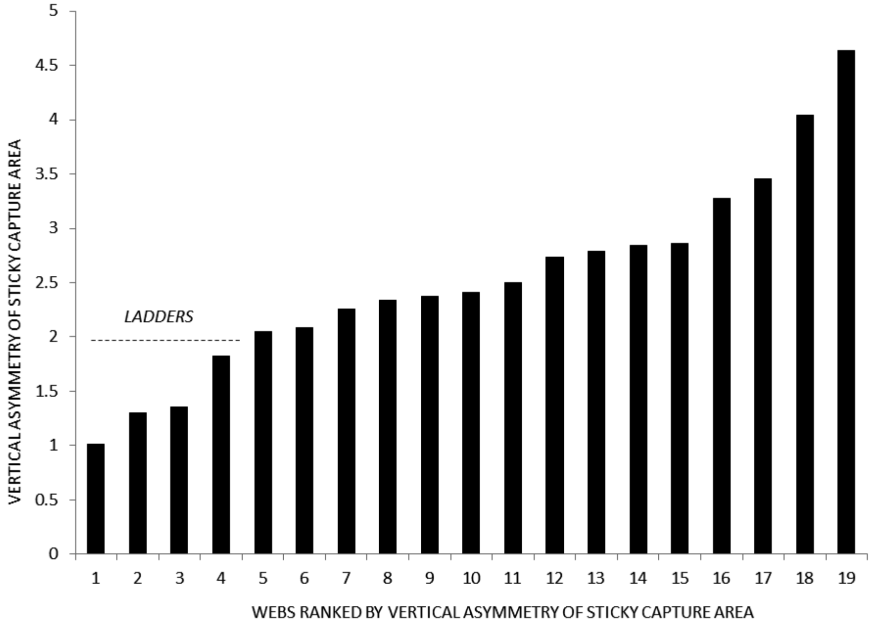


Figure 4. Schematic representation of alternative web-forms of *Herennia multipuncta* on *Acacia mangium* trees: (a) half-ladder-half-orb; (b) forktail web; and (c) hexagon web (black circles represent hubs; straight lines represent pseudo-radii; dashed lines represent sticky silk).

(a)



(b)

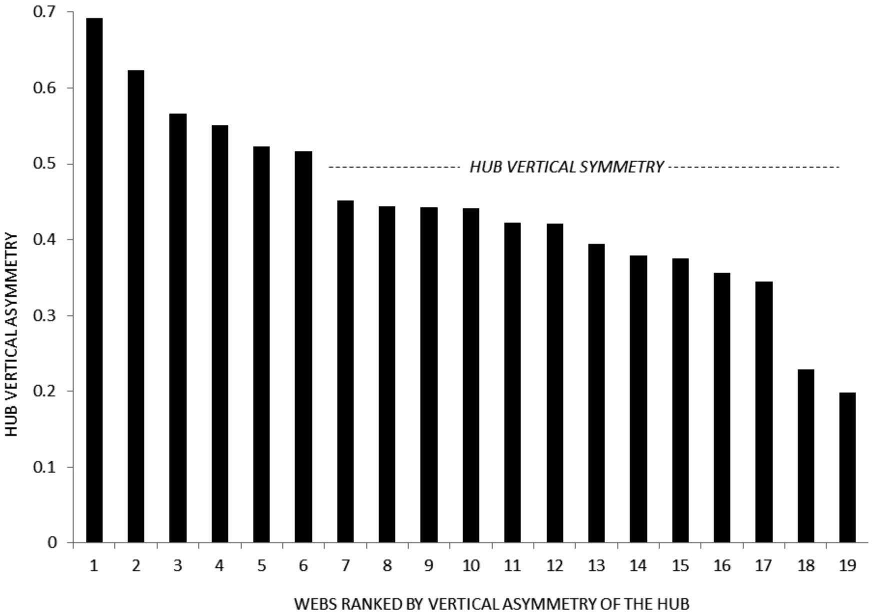


Figure 5. Ranked distributions of: (a) vertical asymmetry in web area; and (b) hub top displacement in the sampled population of *Herennia multipuncta* webs on *Acacia mangium* trees.

statistic = 0.28; $p = 0.594$). Linear regression found no significant relationship between web area elongation and tree circumference. Mean hub top displacement was 0.44 (± 0.03) with measures normally distributed (Anderson-Darling statistic = 0.29; $p = 0.578$). However, there was a significant negative linear relationship between hub top displacement and tree circumference ($df = 1$; $F = 6.13$; $p = 0.024$).

DISCUSSION

Perhaps the best way to describe many *H. multipuncta* webs on *A. mangium* tree trunks is "functional". They are "no frills" ladder webs, either with or without context-modified architectural embellishments. Excluding the hub-cup, the degradation of the *Herennia* web archetype was expressed in all web elements. The web template on *A. mangium* trees was particularly prone to the loss of two of the spider's greatest engineering feats: suspension of the web away from the tree trunk surface and curvature of the web around the circumference of the tree. The principle trade-off for niche expansion can therefore be understood to be the muted expression of the web archetype. The gain may be readily noted in terms of new habitat and the survival of at least a few colonizers into reproductive adulthood (e.g. Hawes, 2015).

The lack of significant linear relationship between vertical asymmetry and tree circumference provides additional evidence for the degradation of the archetypal web template. However, although significant linear relationships were found by Harmer (2009) and Kuntner *et al*. (2010), in the former the relationship was less significantly pronounced in some instars, and in the latter it was not a universal predictor, but significant only for some instar classes. Thus, although a lack of such relations adds to the argument along with other evidence for web-habitat interactions presented in this study, it is not considered definitive in its own right. On the other hand, the presence of a significant relationship between hub vertical asymmetry and tree circumference connects to the retention of the hub in all webs. This makes sense because as a single point within the web, the hub and its preferred position are much easier to retain than the shape (see Figs. 2, 4) or vertical dimensions (Fig. 5a) of the web, which are much more susceptible to the spatial circumscription and/or other modifications demanded by a suboptimal substrate.

This study has particular relevance to the emergent properties of contemporary Southeast Asia's tree-scape, but its findings also have some application to areas of contracted primary forest; such habitats are by definition heterogeneous in composition in which optimal tree surfaces also may be uncommon. In addition it also provides the first evidence of plasticity in *Herennia* webs. This was most evident in: a) the use of suboptimal new habitat; b) the use of microtopography; and c) alternative web forms. Linking this study's evidence with that of *Telaprocera* spp. (Harmer, 2009) shows that the ladder-web form, at least in two unrelated families, is fundamentally plastic in response to ecological drivers. The presence of such plasticity probably has some connection to the evolutionary success of these ladder webs.

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