

## THE WEB STABILIMENTUM OF THE SPINY ORB-WEAVING SPIDER, *THELACANTHA BREVISPINA* (DOLESCHALL, 1857)

Timothy C. Hawes<sup>1</sup>

### ABSTRACT

The orb-weaving araneid, *Thelacantha brevispina*, spins webs ca. 1.0–2.5 m above the ground depending on environmental context and ontogenic stage. Its webs often incorporate a highly simplified stabilimentum into radial lines. The relationship between these silk decorations and wind exposure and contact was examined. Correspondence analysis of a matrix of web attributes found that both individual webs and categories of exposure were distributed on the basis of the presence of the stabilimentum. The presence of the stabilimentum was closely associated with web height and ventral shielding of the web by vegetation. In *T. brevispina*, the stabilimentum is considered to be part of a suite of web characteristics that contribute to web stability; it was found in webs with greater aerial exposure and with the co-occurrence of other stabilizing measures. Separate observations of web kinesis using macrophotography indicated that a localized increase in web rigidity may be conferred by the addition of supplementary silk to the web. Ancillary behavioral observations were also made of an adult holding the stabilimentum with Legs I and II during wind movements.

Keywords: orb-weaver, stabilimentum, *Thelacantha*, web decoration, wind

### INTRODUCTION

Many spiders decorate their webs with supplementary silk. The French arachnologist, Eugène Simon, introduced the term “stabilimentum” to describe these web accessories (SIMON, 1892). As the name suggests, he posited a structural function to these decorations; however, today the stability hypothesis has few adherents. For example, BLACKEDGE *ET AL.* (2011) recently noted that despite “...the name, little evidence supports the antiquated hypothesis that stabilimentum decorations somehow stabilize webs...”. The purpose of this paper is to present observations that recommend that examinations of the structural interactions between stabilimenta and webs are worth revisiting.

One reason there is no real evidence for a stability effect is because there have been so few attempts to explore and examine the hypothesis. COMSTOCK (1948) stated, “Some of the orb weavers strengthen their webs by spinning a zigzag ribbon across the centre or below the hub” (p. 203). However, no rationale for the attribution of strengthening properties was given. ROBINSON & ROBINSON (1970; 1973), probably the most quoted proponents, did not test for functions, but described the stabilimentum of the relevant spider and then ascribed a range of hypothetical uses. Of the few experimental studies that have considered web strengthening, all used coarse correlations between silk decorations and wind exposure to either disprove (LUBIN, 1975) or support the hypothesis (NEET, 1990).

<sup>1</sup> Akarn Teeranee, Soi 35, Pahonyothin Road, Khet Jatujak, Bangkok, Thailand.

E-mail: timothyhawes@hotmail.com

Received 19 February 2016; accepted 28 September 2018.

Hypothetical objections to a stabilizing effect are also often unsatisfactory because they are, like the early attributions of stability, either not based on any real evidence and/or use porous logic. For example, the looseness of stabilimenta has never been measured or demonstrated properly. Indeed, in the species considered here, the stabilimentum is visibly quite rigid. Likewise, even a potentially looser stabilimentum of the *Argiope* type might not necessarily detract from stability; stability does not necessarily mean an increase in web tension. Loose stabilimenta might, for example, stabilize webs in wind by reinforcement or increasing drag. The objection that nocturnal spiders lack stabilimenta has some logic, but our knowledge of nocturnal spiders' webs is currently too scant for it to be treated as a legitimate argument. Even presuming they are only employed by diurnal spiders, visually-oriented evolutionary functions of stabilimenta (EBERHARD, 1990; BLACKEDGE *ET AL.*, 2011) do not preclude structural interactions. In fact, structural interactions, are, to varying degrees, both implicit and explicit in the concept of silk addition.

Stability is a web property that is conferred by an entire suite of factors ranging from choice of web location, to web orientation, to web architecture, etc. Web decorations and any contribution they make to stability necessarily need to be examined in a more holistic framework with regard to structural interactions. In this context, it should be noted that a number of investigators have started to revisit wind-web interactions. For example, recent research on wind interactions with ampullate silk is particularly intriguing in this regard (e.g. LIAO *ET AL.*, 2009; WU *ET AL.*, 2013).

Ultimately, whether or not different species have web decorations that contribute positively to stability, all web decorations merit greater structural consideration. Web decorations add silk and/or other materials (in some cases, profusely), which is an addition of mass and a structural modification. Whether or not they confer stability, they certainly interact with it; thus, their presence cannot be neutral. At a minimum, if they are just absorbed into pre-existing web loading thresholds, they increase the proximity of these thresholds to that of the actual web. In some cases, decorations may complement or add to stability. In other cases, perhaps there is an inverted-jigsaw effect in which all the other components of stability conferral are employed to counteract the effect of the stabilimentum itself. An adjusted approach to structural interactions may be useful with regard to both the resolution of studies and the definition of web stability itself. With regard to the former, this means considering the ways in which the web components behave in the environment (e.g. under destabilizing agents, such as wind). With regard to the latter, it may be that attempts to look for a perfect counterbalance to destabilization have obscured more subtle ameliorative benefits.

This paper presents observations that support the hypothesis that the stabilimentum might play a role in stabilizing the wind webs of *Thelacantha brevispina* (Doleschall, 1857). Additional functions of the stabilimentum in this species are not ruled out; for example, the tuft decorations on its barrier webs seem to have another function (TSENG *ET AL.*, 2007). Nonetheless, these observations support the view that, whether or not structural concerns are the basis for its functional evolution as a web modification, the orb-stabilimentum of this species contributes to web stability.

## METHODS

Fieldwork was carried out on webs in the central-eastern Thai province of Chonburi. Specimens of *T. brevispina* were identified initially with reference to KOH & MING (2014).

Identification was subsequently confirmed by an examination of the epigynum and palps in a female and male (TANIKAWA, 2009). Nomenclature follows the WORLD SPIDER CATALOG (2019). The biology of the species is poorly known (see TSENG *ET AL.*, 2007; HAWES, 2017). Although not rare, this species was not abundant in the area and individual spiders were encountered individually over a period of about 10 months in 2014 during surveys of fruit orchards and open tree clearings in the study area. The presence of various exposure-related web characteristics was recorded for 17 webs.

Web and wind exposure measures were either scored, or converted to scores, to provide comparable ordinal indices. A binary matrix was constructed with each variable scored as either 1 or 0. Comparisons on the same scale assume that each variable has an equal effect; however, the assumption of equal difference or lack of difference is consistent with a null hypothesis model. Likewise, the aim of the matrix is not to compare actual remediation of exposure, but the relative association of the elements that are involved.

Parameters compared were: presence of silk stabilimentum (1= present; 0= absent); web immediately under umbrella of tree or shrub canopy (1= yes; 0= no); web employs vegetation as dorsal backing (1 = yes; 0 = no); web situated in leeward situation (1 = yes; 0 = no); web height (cm) (1=>1.5; 0=<1.5); web plane oriented side-on (perpendicular) to the wind rather than face-on (1= yes; 0= no); interstices of backing allow wind through to the web (1= no; 0 = yes). The matrix was analyzed using Correspondence Analysis (Minitab 14.2). Parameters were examined for relationships with stabilimentum occurrence. The binary orientation of the matrix was determined on the basis of either presence (= 1) or absence (= 0) or relative magnitude (e.g. higher webs >1.5 m = 1; lower webs <1.5 m = 0). The presence or relative presence of a parameter may increase or mitigate exposure according to its own relative properties, not the value given to it. For example, ventral blocking (score = 1) reduces exposure, but greater wind height (score = 1) increases exposure. Thus the “correspondence” or association of variables is independent of the hypothesis that the stabilimentum mitigates exposure.

To examine the behavior of webs under destabilizing aerial conditions in a *in situ* environment, longitudinal observations were made of two spiders. Macrophotography and attendant observations of kinetic webs were carried out on one adult and one juvenile over a 13 day period, visiting each web 2–3 times a day (=13 webs for each individual) (Rebuilt webs utilize the same frame and hub position but the sticky spiral and radii are renewed, and it is these elements that are subject to exposure effects). “Kinetic webs” refers to webs in aerial motion via wind. Static webs were photographed face-on for identification purposes and to document the general morphology of the stabilimentum. Kinetic webs were photographed from a range of angles as they were blown by the wind. Given the micro-gravimetric distortions produced by artificially increasing silk line visibility through either cornstarch or water-misting, webs and silk lines were photographed in their natural state. Focusing on this kind of movement with its irregular velocity and multiple depths of field of view, and given the relative invisibility of silk lines, is complicated. More than 200 photographic images were taken of these webs interacting with the wind, the most in-focus and representative are presented here to provide qualitative descriptions of the character of wind-web interactions in the presence of stabilimenta. Angles of silk lines were measured using ImageJ 1.49 for Windows bundled with Java 1.8.0\_60 (<http://imagej.nih.gov/ij>). These angles were measured relative to spider body plane (Fig. 2) or two points or trajectories on the same silk line for bending lines (Fig. 3). The difficulties of photographing kinetic webs made a standardized viewing angle impractical.

## RESULTS

### Association of Web Parameters with Web Stabilimentum

The presence of the stabilimentum was found to determine the distribution of individual webs on the correspondence axes. Individual webs were found to clearly cluster on either one or the other side of Component 1, with webs #1–10 on one side and webs #11–17 on the opposite side (Table 1; Fig. 1A). This distribution was identical to the observed presence (webs #1–10) or absence (webs #11–17) of stabilimenta (Fig. 1A). Exploration of the association among web parameters found that stabilimenta were closely associated with both ventral-backing and web height (Table 1; Fig. 1B), with the former associated with amelioration of exposure and latter with increased exposure. The stabilimentum showed least association with web characteristics considered to provide shelter from exposure: web orientation, leeward situation, and a close canopy.

### Adult Web Kinesis

The adult web was located in an exposed situation (hub height: 166 cm) with bridge line and anchor threads strung from a bush to a tree branch across a clearing. The main observations reported here were made with the spider's dorsum orientated face-on to a northerly wind (Fig. 2). The stabilimentum was a thin band of silk that stretched down the lower central radius spanning most of the free sector between the hub and capture spiral. The ratio of spider body length to stabilimentum length was 1:2.6. Web deformation shows that wind gusts were concentrated on the central lower half of the web. The stabilimentum retained rigidity in the face of the wind (Fig. 2), even when the lower hemisphere of the web was blown upwards to an almost 90° angle (Fig. 2). Reinforcement of the perpendicular plane of the web during kinesis was demonstrated by examination of magnified close-up images, which showed neighboring radii, unlike the stabilimentum, bending during kinesis (Fig. 3). This was most prominent at a point along the radii that corresponds to the terminus of the stabilimentum. The conferred rigidity to neighboring radii extended along the horizontal plane of the web for a length equivalent to its own extension and for a width of at least 2 radii (Fig. 3). The angles delineated refer to the inclination of lines as considered from the web plane's vertical axis (top to bottom). The fact that these lines and their bending can be seen indicates that they have been displaced across their horizontal axis (side to side) by wind movement to a greater degree than was the stabilimentum. If they were not, they would have to be in line with or slightly behind the stabilimentum rather than pushed forward. Magnification of the images of the raised stabilimentum also revealed a behavioral component to web-stabilimentum-wind interactions. The spider was clearly holding the hub-end of the stabilimentum with both left and right Legs I and II (Fig. 4). Wind contact angle (center of web) and stabilimentum orientation agree (Fig. 5A, B) (see also observations of juvenile web below [Fig. 5C, D] for comparison).

### Juvenile Web Kinesis

Reflective of its relative size and strength in comparison to the adult, the juvenile's web was located in a more sheltered condition within the canopy of a small tree (hub height: 210 cm). However, while the adult's web was oriented directly into the wind, the nature of the interstitial gaps in the canopy and the way that wind passed around the leaves to the web, meant that not only did the juvenile's web receive wind, but it did so in a less optimal loca-

Table 1. Correspondence analysis of the webs of *Thelacantha brevispina* by individual web and web parameters (Q = Quality; M = Mass; I = Inertia; Coord. = Coordinates; Corr. = Correspondence; Contrib. = Contribution).

Webs and parameters	Q	M	I	Component 1		Component 2	
				Coord.	Corr.	Coord.	Contrib.
<i>Individual webs</i>							
1	0.184	0.060	0.026	-0.174	0.058	0.003	0.126
2	0.184	0.060	0.026	-0.174	0.058	0.003	0.126
3	0.914	0.060	0.032	-0.751	0.888	0.059	0.026
4	0.914	0.060	0.032	-0.751	0.888	0.059	0.026
5	0.914	0.060	0.032	-0.751	0.888	0.059	0.026
6	0.914	0.060	0.032	-0.751	0.888	0.059	0.026
7	0.914	0.060	0.032	-0.751	0.888	0.059	0.026
8	0.805	0.080	0.014	-0.370	0.671	0.019	0.134
9	0.597	0.040	0.055	-0.989	0.596	0.068	0.001
10	0.447	0.060	0.034	-0.401	0.238	0.017	0.210
11	0.868	0.040	0.110	1.338	0.549	0.124	0.319
12	0.868	0.040	0.110	1.338	0.549	0.124	0.319
13	0.478	0.020	0.060	0.773	0.169	0.021	0.310
14	0.857	0.100	0.211	1.147	0.523	0.229	0.334
15	0.124	0.040	0.040	0.248	0.052	0.004	0.071
16	0.461	0.100	0.062	0.557	0.420	0.054	0.040
17	0.393	0.060	0.092	0.613	0.206	0.039	0.186
<i>Web parameters</i>							
Stabilimentum	0.856	0.200	0.119	-0.773	0.844	0.208	0.012
Close canopy	0.759	0.060	0.155	1.018	0.337	0.108	0.422
Ventral blocking	0.646	0.180	0.124	-0.727	0.643	0.165	0.003
Leeward situation	0.687	0.080	0.227	1.443	0.617	0.290	0.070
Web height	0.297	0.240	0.066	-0.210	0.136	0.018	0.161
Web orientation	0.644	0.020	0.151	1.512	0.254	0.079	0.390
Interstitial effect	0.712	0.220	0.158	0.586	0.403	0.132	0.308

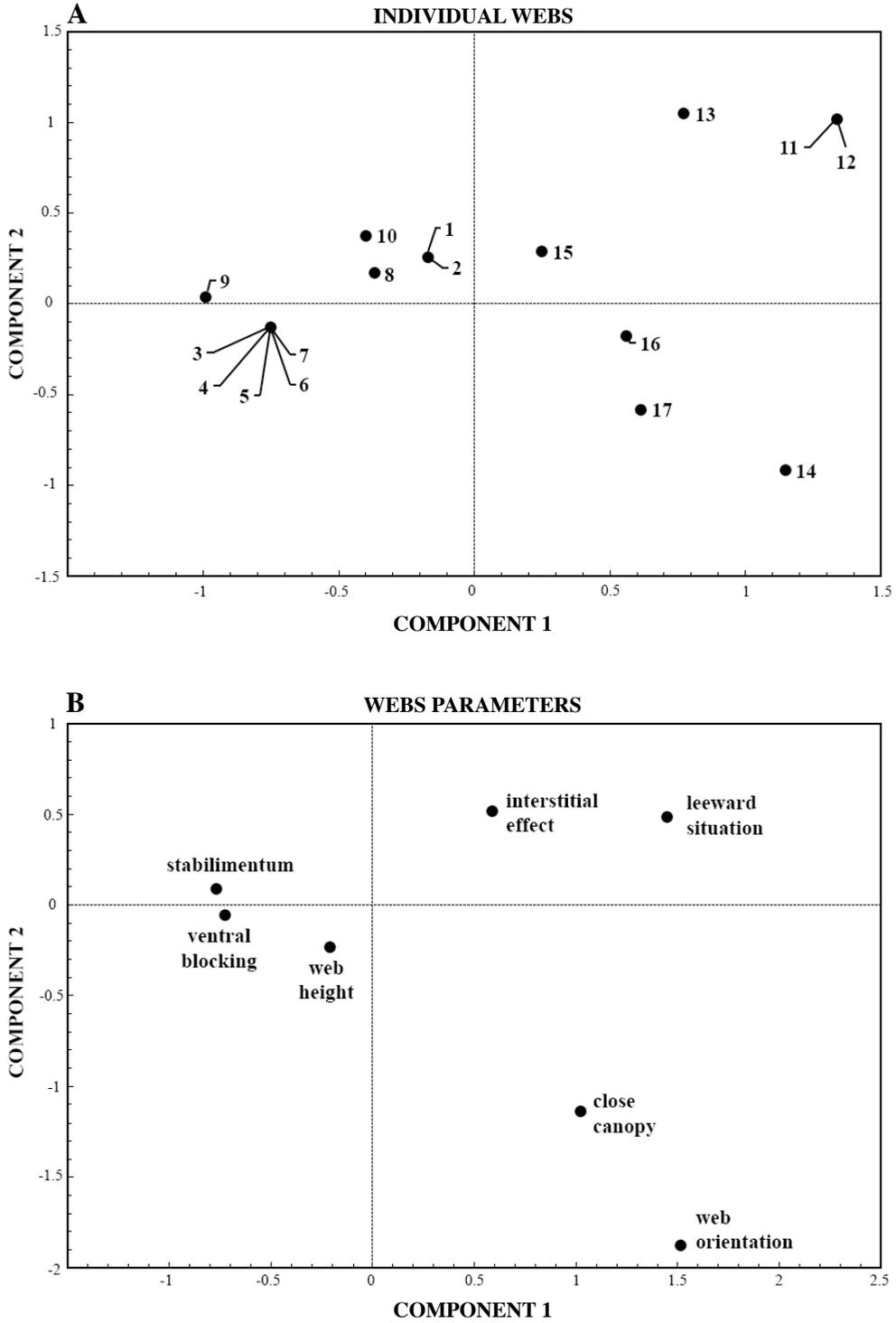


Figure 1. Correspondence analysis of webs of *Thelacantha brevispina* with (A) association of individual webs and (B) association of web parameters.



Figure 2. Kinesis of adult *Thelacantha brevispina* web with rigidity of stabilimentum maintained during wind contact, with angles of stabilimentum delineated (A–D) (where 180° corresponds to undisturbed web plane). Note the maintenance of the line of stabilimentum in contrast to deformation of the web. Photographs by Timothy C. Hawes.



Figure 3. Stabilimentum and neighboring radii during wind-contact of adult *Thelacantha brevispina*: (A) normal view without annotation; (B) close-up with neighboring radii highlighted with arrows; and (C) close-up with dashed lines and angles delineated to indicate relative curvature of different radii during contact. Angles calculated from the inclination of each line at the point corresponding to the terminus of the stabilimentum. Photographs by Timothy C. Hawes.



Figure 4. Adult *Thelacantha brevispina* holding silk stabilimentum during wind contact: (A) normal view; and (B) magnified close-up. Photographs by Timothy C. Hawes.

tion. The wind came through the canopy from behind the spider (spider's ventrum) at an angle of incidence such that the left side, rather than the center of the web, was the primary contact surface (Fig. 6C, D). It would be logical for wind-web orb spiders to construct the plane of the web so that air movements are evenly distributed. Optimization of the web plane in this respect might have an ontogenetic (i.e. experiential) component. Alternatively, this problem may simply be the result of a specific circumstance in which the complexities of airflow around and between leaves increased the angle of incidence of the wind. The ratio of spider body length to stabilimentum size was lower than that of the adult, 1: 1.7. Also, the stabilimentum was not placed on the lower central radius but on the first radius to the left of the central radius, corresponding to the region of greatest wind interaction (Fig. 5C, D). Because the wind hit the side rather than the center of the web, there was relatively minor deformation of the web along its perpendicular plane and side-flap of the web was delimited by the stabilimentum to the sticky capture spiral area outside the free sector and beyond the terminus of the stabilimentum (Fig. 6).

As with the adult, the stabilimentum showed greater rigidity than radii during web kinesis, although it was not as rigid as that of the adult (Figs. 2, 6). Examination of the sticky capture spiral clearly shows that web damage was limited to areas that were not in close proximity to the stabilimentum (Fig. 6C, D). However, it can only be inferred that this damage was the result of wind.

During the set of observations represented in Figure 6, the spider climbed up the central radius to the bridge line and remained there. In addition to the stabilimentum, further minor



Figure 5. Comparison of stabilimenta orientation and wind contact angle in adult and juvenile webs of *Thelacantha brevispina*: (A) adult with centrally-oriented linear stabilimentum; (B) central contact of wind on adult web; (C) juvenile with side-oriented linear stabilimentum; and (D) side-on contact of wind (notice the prominent side-flap of right side of web). Filled arrows highlight stabilimenta orientation; dashed arrows highlight wind-web contact. Photographs by Timothy C. Hawes.



Figure 6. Kinesis of juvenile *Thelacantha brevispina* web with stabilimentum. Note that rigidity is primarily conferring stability across the side of the web, with the web's right side clearly flapping, but the stabilimentum rigid: (A) side-on view with stabilimentum slightly bending perpendicular to the web plane and extending more rigidly across the right side; (B) side-on view with spider retreated to bridge line and stabilimentum conspicuously rigid (C) frontal view of web stretched by wind and with damage evident; and (D) the same with zones of damage indicated by dashed circles and silk doubling-up of radii indicated by arrows (note also the integrity of the sticky capture spiral in the area surrounding the stabilimentum). Photographs by Timothy C. Hawes.

silk reinforcements of web radial structure were observed with a doubling-up or overlaying of additional silk line alongside the radii to strengthen the inner frame. These radii were observed as more prominent and thicker than neighboring radii (Fig. 5C, D). “Doubling-up” refers generally to the laying of extra line—it was not possible to determine how many times extra line was laid). The spider was observed laying down these extra lines by shuttling movements between the hub and web frame along the radii.

## DISCUSSION

These observations support the hypothesis that silk reinforcement has a role in stabilizing the aerial webs of *T. brevispina*. Both the association of web parameters in relation to the stabilimentum, and the visualization of web kinesis indicate that silk reinforcements of radii are involved in wind-web interactions by locally strengthening web structure. The stability conferred is probably subtle; it is spatially specialized, and its benefits are probably felt in the web as a graded remediation of silk stresses to immediate and neighboring radii, not a whole sale management or removal of them. These reinforcements certainly do not provide absolute rigidity because the central radii bend; however, they bend *less* than do radii without the stabilimentum. In other words, there is a *relative* increase in rigidity.

The behavioral note of one of the spiders holding a stabilimentum during web-deforming wind was an isolated observation, but still remarkable. The basis of this action was not determined but the parsimonious explanations are: that either it was providing additional reinforcement to the stabilimentum’s rigidity by holding it in place, or it was trying to brace its own position on the hub by grasping the stabilimentum. Both explanations rely on the proposition that silk reinforcement is involved in web stability in some way.

Wind-web interactions are a complicated phenomenon from a behavioral point of view in that they require that spiders respond to an environmental variable that is fundamentally unpredictable in magnitude and origin. In such scenarios, probably the most pragmatic mitigating behaviors are energetically economical adjustments that may not remove web stresses, but which assist in their remediation. Laying a thin stabilimentum on a web spoke and doubling-up of lines on more stressed radii may both serve such functions for webs of *T. brevispina*. The latter action, in particular, emphasizes how web-decorating, in this species at least, may be expressed as a continuum of silk additions that culminates in the stabilimentum but that is supported by the ancillary laying down of extra silk line elsewhere.

It is hoped that these minor observations reveal the potential for a more resolved examination of interactions between stabilimenta and web structure. There is considerable scope for a more integrated perspective of the interactions between web structure and web decorations. Although this paper concentrates on how stability is increased by web decoration, it also emphasizes how stability is a holistic product of a diverse suite of environmental variables, web parameters and spider behavior.

## ACKNOWLEDGEMENTS

I am grateful to two anonymous referees for their comments on the manuscript.

## REFERENCES

- BLACKEDGE, T. A., M. KUNTNER, AND I. AGNARSSON. 2011. The Form and Function of Spider Orb Webs: Evolution from Silk to Ecosystems. Pages 175–262 in J Casas (ed.), *Advances in Insect Physiology*. Vol. 41. Academic Press, Burlington.
- COMSTOCK, J. H. 1948. *The Spider Book*. Ithaca: Cornell Univ. 729 pp.
- EBERHARD, W. G. 1990. Function and phylogeny of spider webs. *Ann Rev. Ecol. Syst.* 21: 341–372.
- HAWES, T. C. 2017. A bridge line web-pulling maneuver by the spiny orb-weaving spider, *Thelacantha brevispina* (Doleschall, 1857). *Thai. Nat. Hist. Mus. J.* 11: 91–8.
- KOH, J. K. H., AND L. T. MING. 2014. *Spiders of Borneo*. Opus Publications. Kota Kinabalu. 357 pp.
- LIAO, C., K. CHI, AND I. TSO. 2009. The effects of wind on trap structural and material properties of a sit-and-wait predator. *Behav Ecol.* 20: 1194–120.
- LUBIN, Y. D. 1975. Stabilimenta and barrier webs in the orb webs of *Argiope argentata* (Araneae, Araneidae) on Daphne and Santa Cruz Islands, Galapagos. *J. Arach nol.* 2: 119–126.
- NEET, C. R. 1990. Function and structural variability of the stabilimenta of *Cyclosa insulana* (Costa) (Araneae, Araneidae) *Bull. Brit. Arch. Soc.* 8: 161–164.
- ROBINSON, M. H., AND B. ROBINSON. 1970. The stabilimentum of the orb web spider, *Argiope argentata*: an improbable defence against predators. *Can. Entomol.* 102: 641–655.
- ROBINSON, M. H., AND B. ROBINSON. 1973. The stabilimenta of *Nephila clavipes* and the origins of stabilimentum-building in araneids. *Psyche* 80: 277–288.
- SIMON, E. 1892. *Histoire naturelle des Araignées*. Librairie Encyclopédique de Roret. Vol. 1. Paris. 1084 pp.
- TANIKAWA, A. 2009. Hersiliidae, Nephilidae, Tetragnathidae, Araneidae. Pages 403–463 in H. Ono (ed.), *The Spiders of Japan with keys to the families and genera and illustrations of the species*. Tokai University Press, Kanagawa, 149 pp.
- TSENG, H. J., R. C. CHENG, S. H. WU, S. BLAMIRE, AND I. M. TSO. 2011. Trap barricading and decorating by a well-armored sit-and-wait predator: extra protection or prey attraction? *Behav. Ecol. Sociobiol.* 65: 2351–2359.
- WORLD SPIDER CATALOG. 2019. World Spider Catalog. Version 20. Natural History Museum Bern. Available from: <http://wsc.nmbe.ch> (accessed 20 Jan. 2019)
- WU, S., S. J. BLAMIRE, C. WU, AND I. TSO. 2013. Wind induces variations in spider web geometry and sticky spiral droplet volume. *J. Exp. Biol.* 216: 3342–3349.