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# Mass predicts web asymmetry in *Nephila* spiders

Matjaž Kuntner · Matjaž Gregorič · Daiqin Li

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**Abstract** The architecture of vertical aerial orb webs may be affected by spider size and gravity or by the available web space, in addition to phylogenetic and/or developmental factors. Vertical orb web asymmetry measured by hub displacement has been shown to increase in bigger and heavier spiders; however, previous studies have mostly focused on adult and subadult spiders or on several size classes with measured size parameters but no mass. Both estimations are suboptimal because (1) adult orb web spiders may not invest heavily in optimal web construction, whereas juveniles do; (2) size class/developmental stage is difficult to estimate in the field and is thus subjective, and (3) mass scales differently to size and is therefore more important in predicting aerial foraging success due to gravity. We studied vertical web asymmetry in a giant orb web spider, *Nephila pilipes*, across a wide range of size classes/developmental stages and tested the hypothesis that vertical web asymmetry (measured as hub displacement) is affected by gravity. On a sample of 100 webs, we found that hubs were more displaced in heavier and larger juveniles and that spider mass explained vertical web asymmetry better than other measures of spider size

(carapace and leg lengths, developmental stage). Quantifying web shape via the ladder index suggested that, unlike in other nephilid taxa, growing *Nephila* orbs do not become vertically elongated. We conclude that the ontogenetic pattern of progressive vertical web asymmetry in *Nephila* can be explained by optimal foraging due to gravity, to which the opposing selective force may be high web-building costs in the lower orb. Recent literature finds little support for alternative explanations of ontogenetic orb web allometry such as the size limitation hypothesis and the biogenetic law.

**Keywords** *Nephila pilipes* · Spider web architecture · Ontogeny · Biogenetic law · Size limitation hypothesis · Allometry · Nephilidae

## Introduction

Spider webs are increasingly becoming a focus of biological and interdisciplinary research (e.g., Swanson et al. 2007; Agnarsson et al. 2010), with web architecture and its changes through spider ontogeny and evolution as important topics (Hesselberg 2010; Kuntner et al. 2010). The architecture of vertical aerial orb webs may be affected by a mixture or proximate factors such as gravity (Masters and Moffat 1983; ap Rhisiart and Vollrath 1994; Herberstein and Heiling 1999; Nakata and Zschokke 2010; Zschokke and Nakata 2010), the available web space (Kuntner et al. 2008b; Harmer 2009; Harmer and Herberstein 2009; Kuntner and Agnarsson 2009), or prey specialization (Robinson and Robinson 1972; Eberhard 1975; Stowe 1978); however, it has been unclear how these factors influence ontogenetic allometric changes and whether or not phylogenetic and developmental factors play a role in

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architectural changes following a biogenetic law (Nelson 1985). In spider web biology, biogenetic law postulates that web features in young spiders will resemble those of phylogenetic ancestral taxa, whereas those in growing instars will add derived features to such ground plan (Eberhard et al. 2008; Hesselberg 2010).

Several studies have focused on a simple yet salient parameter in vertical orb webs, its vertical (a)symmetry where web hub is displaced towards the top of the web and how spider size/mass or ontogeny affects a shift from symmetric to asymmetric webs (Masters and Moffat 1983; ap Rhisiart and Vollrath 1994; Herberstein and Heiling 1999; Kuntner et al. 2008b; Kuntner and Agnarsson 2009). A good model of study are diverse webs ranging from small arboricolous ladder webs to gigantic aerial orbs in the spider family Nephilidae in which both the ontogenetic and evolutionary changes are becoming better understood (Kuntner et al. 2010); however, prior studies have used an array of approaches to quantify web allometry which, as we point out here, are suboptimal. As a measure of spider size, most prior studies have used field estimated size classes (Bleher 2000; Kuntner et al. 2008b; Kuntner and Agnarsson 2009), which is a quick but rather subjective technique that takes a trained researcher's guess. In addition to size/instar classes, other studies have used spider size data such as the length of the first patella+tibia or carapace length and these indeed all covary (Kuntner et al. 2010). Nevertheless, vertical hub asymmetry is believed to be influenced by gravity, not spider size per se; differences in upward and downward running speeds are logically affected by the spider's weight (Masters and Moffat 1983; ap Rhisiart and Vollrath 1994; Herberstein and Heiling 1999; Zschokke and Nakata 2010). Therefore, if foraging success is affected by gravity, correlating spider's mass, not size, with hub asymmetry should produce better results. Mass also scales differently to sizes and lengths and may therefore be more accurate in predicting web asymmetry and foraging success.

A few studies that did use spider mass as predictor of web allometry focused either on adult web architectures or juveniles of an unspecified stage (Masters and Moffat 1983; ap Rhisiart and Vollrath 1994; Nakata and Zschokke 2010; Herberstein and Heiling 1999) and thus ignored potential ontogenetic factors. This is again a suboptimal estimation of real developmental shifts because spiders at various stages differ in their foraging investment. For example, adult females rarely invest full resources in foraging (and thus optimal web size) but rather more in reproduction (Higgins 2006). It is possible that web size alone, if dramatically different in gravid females compared to juveniles, may affect web proportions. Thus, it may be argued that juvenile spiders are better suited for testing the interplay between spider mass, its optimal web design, and

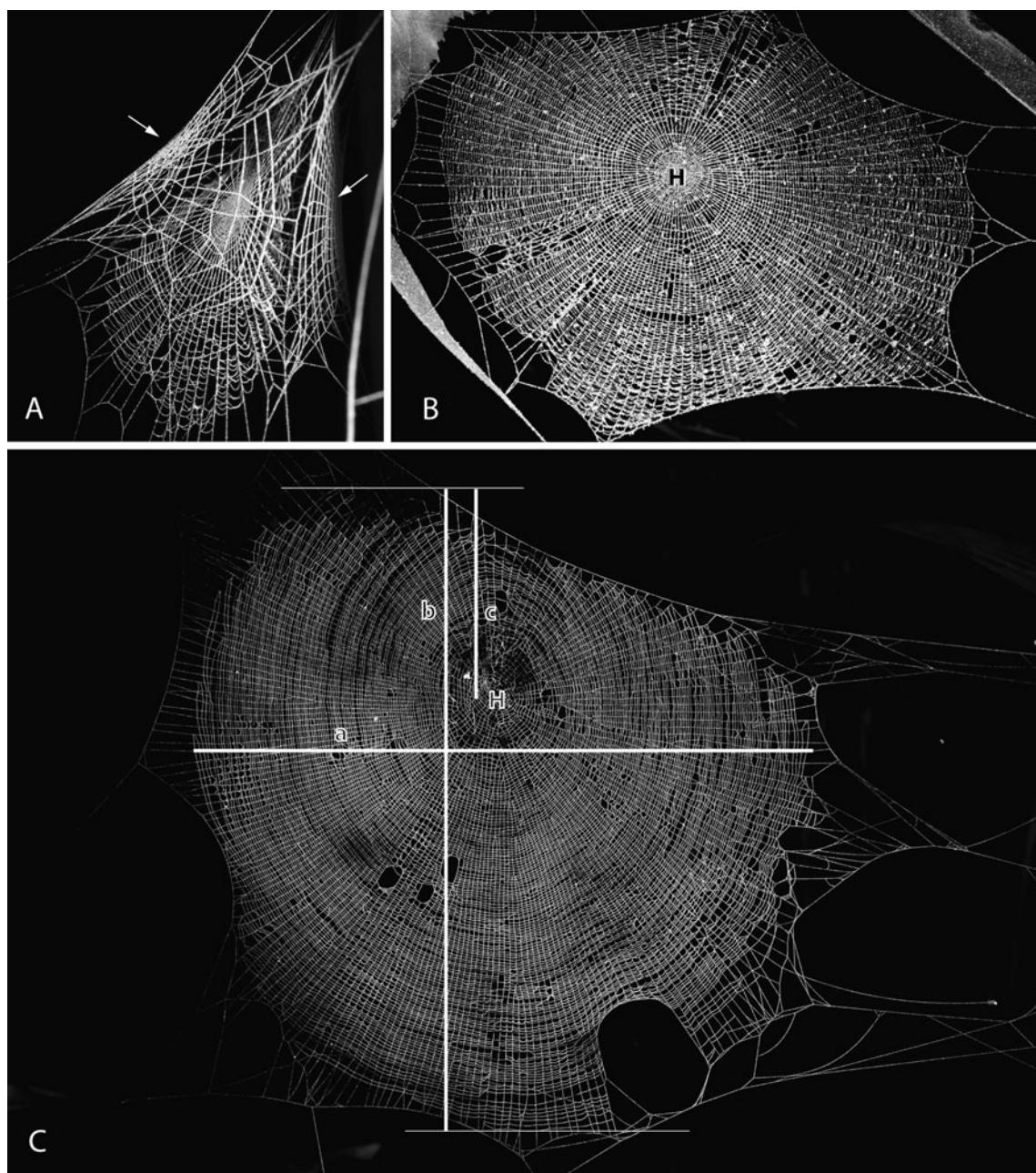
ontogeny. Therefore, a study on orb web changes through an entire ontogenetic range from small to large juveniles using their mass is clearly desired, especially on a relatively big and heavy species. To our knowledge, this has not been done.

Here, we used such an approach to study the webs of the common Southeast Asian nephilid spider *Nephila pilipes*, whose females reach gigantic proportions being close to the largest orb web spiders (Kuntner and Coddington 2009; but see Kuntner and Agnarsson 2010). *Nephila* comprises 15 species distributed globally, but their web architecture is uniform (Kuntner et al. 2008a) and therefore *N. pilipes* can be considered as a representative of the genus. *Nephila* webs change through ontogeny from small round orbs with extensive additional three-dimensional feature termed the barrier web to giant two-dimensional orbs with dozens of radii and with an asymmetrically positioned hub towards the top web frame (Fig. 1; Bleher 2000; Higgins 1992; Kuntner et al. 2008a). We tested the effect of gravity on *Nephila* web architecture by documenting juvenile web architectures in natural habitat and measuring spider size and mass in the laboratory. We excluded adult females from the analyses because adult web architecture in *Nephila* is sometimes simplified and ceases to function as prey catching device (own data).

We first documented how the shape of *Nephila* web changes through ontogeny. Prior work suggests that first instars construct a symmetrical orb (Bleher 2000; own data), but larger instars construct increasingly vertically asymmetrical webs (Fig. 1), which are not increasingly elongated as in other nephilid genera (*Clitaetra*, *Herennia*, *Nephilengys*, see Kuntner et al. 2008b, 2010). Our hypothesis was that hub displacement (a measure of vertical web asymmetry) is affected by gravity. If so, we predicted that (1) hubs will be more displaced in heavier spiders and (2) measures of spider size (carapace and leg lengths, developmental stage) and mass will covary, but spider mass will better predict hub displacement compared with spider size. Finally, we were interested to what extent gravity predicts vertical orb web architecture (as measured by the ladder index) and whether or not there is evidence for explanations of ontogenetic orb web allometry alternative to the effects of gravity, e.g., phylogenetic constraints as exemplified by the biogenetic law (Benjamin and Zschokke 2004; Eberhard et al. 2008; Hesselberg 2010).

## Methods

We measured a randomly encountered sample of 100 juvenile webs of *N. pilipes* on Pulau Ubin, Singapore, on 2 January 2010. We used a detailed knowledge of *Nephila* taxonomy to identify juvenile *N. pilipes* from the syntopic



**Fig. 1** *N. pilipes* web architecture. **a** Second juvenile instar web from the side (note extensive barrier web on each side of orb), **b** another second juvenile instar web frontally (note relatively central hub)

position (*H*), **c** fifth juvenile instar web (note relatively displaced hub (*H*). Parameters measured, *a*=web width, *b*=web height, *c*=top to hub distance (see [Methods](#))

congeneric *Nephila antipodiana* and to estimate their size class (or stage) in the field. After measurements, we captured all spiders and brought them to the laboratory where we temporarily anesthetized them with CO<sub>2</sub>, weighed them to the nearest 0.0001 g, measured their first leg patella+tibia length and carapace length to the nearest 0.01 mm, then left them to recover. We subsequently released all spiders back into the wild.

In the field, we measured the following parameters on every web (Fig. 1c): *a*=web width between the outermost

sticky spirals (centimeters), *b*=web height between the top and lowest sticky spirals (centimeters), *c*=top sticky spiral to hub distance (centimeters). We then calculated the following web architecture measures, hub displacement ( $HD=(b-c)/b$ ) as used in Kuntner et al. (2008b), Kuntner and Agnarsson (2009), and Gregorić et al. (2010), similar to hub asymmetry sensu Blackledge and Gillespie (2002) and asymmetry index sensu Nakata and Zschokke (2010). A web with the hub in the geometric center thus has an *HD* value of 0.5 and *HD* increases with the hub being displaced

towards the top frame, ladder index ( $LI=b/a$ ) as used in Kuntner et al. (2008b) and Kuntner and Agnarsson (2009), equivalent to web elongation sensu Harmer (2009), and similar to web shape sensu Zschokke (1993) and web asymmetry sensu Blackledge and Gillespie (2002).  $LI$  defines the web capture area departure from a circular shape. This value increases as the web becomes vertically elongated.

We checked all data for normality using the Kolmogorov-Smirnov test. Because mass was not distributed normally, we performed square root transformation. To test if the measures of spider body size and mass correlate, we used Pearson's correlation. As spider body size (first leg patella+tibia length and carapace length) and mass were linearly related (see Results), we then performed backward linear regression to test which measures of body size and mass were better predictors of HD and LI. The first leg patella+tibia length, carapace length, and mass were entered as independent variables while HD or LI were entered as dependent variables. Only the factors showing significant effects were retained in the final model. We performed all analyses in PASW version 18 for PC.

## Results

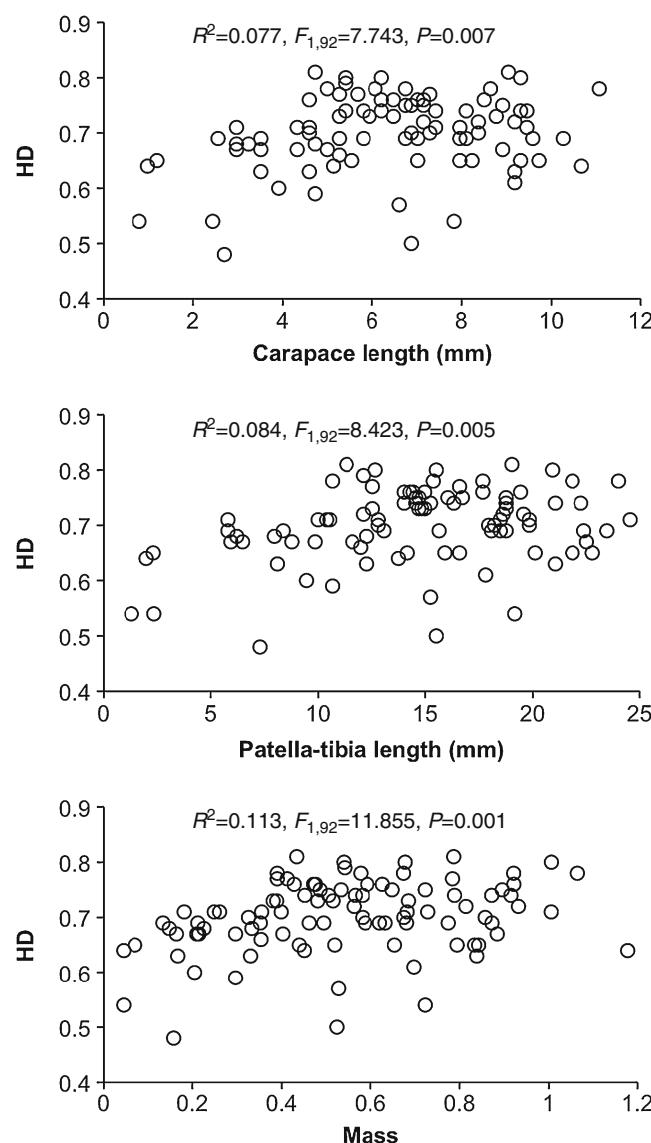
The ontogeny of the *N. pilipes* web progressed from small, close to symmetrical orb with extensive barrier web on each side (Fig. 1a, b) towards larger vertical orbs with a gradually increasing vertical hub asymmetry (Fig. 1c; Appendix). All measures of spider size and mass were correlated (Table 1), and carapace length, leg length, and mass significantly correlated with HD (Fig. 2); however, linear regression revealed that mass was the best predictor of HD in the final model ( $y=0.65+0.09 \times \text{mass}$ ;  $R^2=0.119$ ,  $F_{1,92}=12.451$ ,  $P=0.001$ ) (Fig. 2). Heavier spiders exhibited a higher hub displacement. None of the spider size and mass parameters could predict changes in LI ( $R^2=0$ ) meaning, the larger spiders do not elongate their webs.

**Table 1** Pearson correlations among spider mass (Mass), patella-tibia I length (PaTi), carapace length (CL) and estimated developmental stages (Stage)

	PaTi	CL	Mass	Stage
PaTi	1	0.957*	0.941*	0.894*
CL		1	0.946*	0.906*
Mass			1	0.956*
Stage				1

$N=95$

\* $P<0.001$



**Fig. 2** Correlations between measures of spider size (carapace length, patella+tibia I length) and mass (square root transformed) with HD as a measure of vertical web asymmetry. Although all measures of size correlate with mass (Table 1), backward linear regression showed the mass to be the best predictor of HD ( $y=0.65+0.09 \times \text{Mass}$ ;  $R^2=0.119$ ,  $F_{1,92}=12.451$ ,  $P=0.001$ )

## Discussion

We studied vertical asymmetry and web shape in juveniles of all size classes in the giant orb web spider *N. pilipes*. The ontogeny of *N. pilipes* web progresses from small, nearly symmetrical orb with extensive barrier web on each side towards large vertically asymmetric orb with little or no barrier web (Fig. 1). As predicted, hubs were more displaced in heavier and larger juveniles (Fig. 2), but spider mass was a better predictor of vertical web asymmetry than measures of spider size (carapace and leg lengths, developmental stage; Fig. 2). *Nephila* webs do not become

vertically elongated (ladderized) as the webs of other nephilids (Kuntner 2005, 2006, 2007). Building on published (Higgins 1992; Bleher 2000; Hesselberg 2010) and our own unpublished field data from other *Nephila* species, such ontogenetic web changes in *N. pilipes* are representative of the genus *Nephila*.

The fact that all measures of spider size (size class, carapace length, first patella+tibia length) highly correlated with spider mass (Table 1) and with HD (Fig. 2) gives credibility to previous studies that only used size classes or size measurements in quantifying orb web allometry (Kuntner et al. 2008b, 2010; Kuntner and Agnarsson 2009). Nevertheless, linear regression retained mass as the only predictor of hub displacement (not in the case of ladder index), which supports our a priori predictions. Thus, if feasible, future studies should use spider mass rather than size for discovering orb web allometric patterns.

The detected ontogenetic pattern of progressive vertical web asymmetry in *Nephila* may best be explained by optimal foraging due to gravity because spider downward running speed is greater compared with upward speed (Nakata and Zschokke 2010; Zschokke and Nakata 2010). Heavier instars have significantly displaced hubs towards the top web frame, an ontogenetic trend present in most nephilids studied (Japyassu and Ades 1998; Kuntner et al. 2008b, 2010; Kuntner and Agnarsson 2009). An exception may be *Nephila clavipes*, but the study that failed to detect this pattern only used two juvenile stages and adults (Hesselberg 2010), otherwise *N. clavipes* webs are as in other *Nephila* (Higgins 1992; Kuntner et al. 2008a). Such “gravity explanation” (Masters and Moffat 1983) does not in itself invalidate the biogenetic law (Nelson 1985), which postulates that later instars add to web allometry and that such trend would replicate the phylogenetic pattern; however, the currently understood macroevolutionary pattern in Nephilidae suggests that the ancestral web architecture was a small ladder web, which evolved into a highly specialized arboricolous ladder, into a large semiladder and into a secondarily derived aerial orb as found in *Nephila* (Kuntner et al. 2010). Although the ancestral web architecture at a more inclusive phylogenetic scale might well be a perfectly round orb (Blackledge et al. 2009), this is not the case in the common ancestor of *Nephila*, which probably built a ladder web against substrate (Kuntner et al. 2010). The ontogenetic changes in the *Nephila* web architecture therefore do not resemble the currently understood macroevolutionary patterns. As also concluded by Hesselberg (2010), biogenetic law is not a valid explanation for *Nephila* ontogenetic web asymmetry changes.

Although there is preliminary evidence for biogenetic law in other spider groups such as sheet web-building spiders (Benjamin and Zschokke 2004; Eberhard et al.

2008), other recent studies on orb webs also failed to find support for such hypothesis (but see Hesselberg 2010). Nakata (2010) recognized that in order to distinguish between the predictions of the biogenetic law versus the gravity effects, one would need to study the ontogeny of vertical webs with inverse asymmetry, a relatively rare phenomenon where orbs are larger above, rather than below, the hub (Kuntner et al. 2008a; Nakata and Zschokke 2010). Nakata (2010) studied such webs of *Eriophora sagana* and found that webs of heavier adults were less vertically asymmetric compared with lighter subadult webs. Assuming that the ancestral state was a symmetrical orb, these results invalidated the biogenetic law and supported the optimal foraging hypothesis, which is in accordance with the conclusions from our *Nephila* study.

In addition to biogenetic law, other alternatives have been sought to explain the relatively straightforward problem of vertical orb web asymmetry. Hesselberg (2010) tested the size limitation hypothesis in *N. clavipes*, predicting that small spiders make more web-building mistakes being limited in their central nervous system size and ability but found no support for it. Coslovsky and Zschokke (2009) tested another alternative hypothesis stating that many webs are asymmetrical due to higher building costs above versus below the hub (Herberstein and Heiling 1999), but also failed to find support for it. Rather, their results suggested that lower orb building was more costly, which might suggest that vertical webs would be even more asymmetric than they are, should web-building costs be equal above and below the hub. If so, optimal foraging area is a stronger selective agent for higher displaced orbs compared with the opposing selective agent (higher web-building costs in lower web). Thus, it is logical that in order to explain increased hub displacement in larger spiders, most recent literature converges on the central foraging theory, which predicts that gravity will affect hub displacement in vertical, but not horizontal orb webs (Zschokke and Nakata 2010). Our empirical data on *Nephila* webs support the theoretical model, which postulates that spiders maximize their foraging success if sitting head down in a vertically asymmetric web (Maciejewski 2010), and this asymmetry increases with the spider mass.

## Conclusions

Our hypothesis that hub displacement would be affected by gravity is supported. Hubs were more displaced in heavier spiders, all the measures of spider size (carapace and leg lengths, developmental stage) and mass covaried, but spider mass was the best predictor of hub displacement. The

detected ontogenetic changes in the ladder index suggest that *Nephila* webs do not become ladderized in larger and heavier spiders.

Evidence from orb web spider ontogeny suggests that a typical allometric shift from vertically symmetric towards increasingly asymmetric webs in larger and heavier spiders is due to gravity. Spider mass critically affects its optimal foraging area and perhaps, to some extent, web-building costs (Herberstein and Heiling 1999; Coslovsky and Zschokke 2009). In fact, optimal foraging area and web-building costs may represent opposing selective agents, and

the progressively asymmetric web is the resulting trade-off. Little to no support exists in the literature for alternatives to the gravity explanation, such as the size limitation hypothesis or biogenetic law.

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## Appendix

Measured and derived parameters

Stage	Web width (cm)	Web height (cm)	Top to hub (cm)	Live mass (g)	Patella–tibia length (mm)	Carapace length (mm)	Hub displacement (HD)	Ladder index (LJ)	Transformed mass
2	9	13	6	0.002	1.31	0.8	0.54	1.44	0.0447
2	11	14	5	0.002	2	0.99	0.64	1.27	0.0447
2	8	8	3.7	0.002	2.36	2.44	0.54	1	0.0447
3	15	17	6	0.005	2.33	1.2	0.65	1.13	0.0707
4	20	24	7.5	0.018	5.8	2.56	0.69	1.2	0.1342
4	28	30	9.5	0.022	6.21	2.97	0.68	1.07	0.1483
4	4.8	5	2.6	0.025	7.29	2.7	0.48	1.04	0.1581
4	6	4	1.5	0.028	8.1	3.51	0.63	0.67	0.1673
5	29	21	7	0.027	6.48	2.97	0.67	0.72	0.1643
5	28	24	7	0.033	5.8	2.97	0.71	0.86	0.1817
5	6.5	7.5	3	0.042	9.45	3.91	0.6	1.15	0.2049
5	23.5	21.5	7	0.044	5.94	3.51	0.67	0.91	0.2098
5	28	29	9	0.045	8.37	3.51	0.69	1.04	0.2121
5	24	30	10	0.046	8.77	3.51	0.67	1.25	0.2145
5	35	38	12	0.051	7.96	3.24	0.68	1.09	0.2258
5	15	19	5.5	0.062	9.99	4.32	0.71	1.27	0.249
5	29	31	9	0.068	10.53	4.32	0.71	1.07	0.2608
5	13.5	18	6	0.088	9.85	4.32	0.67	1.33	0.2966
5	33	36	11	0.124	13.09	5.26	0.69	1.09	0.3521
5	38	35	10	0.126	12.82	4.59	0.71	0.92	0.355
6	26	27	11	0.088	10.66	4.72	0.59	1.04	0.2966
6	32	37	11	0.106	12.82	4.59	0.7	1.16	0.3256
6	35	31	11.5	0.109	12.28	4.59	0.63	0.89	0.3302
6	32	36	11.5	0.111	12.28	4.72	0.68	1.13	0.3332
6	33	37	12.5	0.125	12.01	5.26	0.66	1.12	0.3536
6	43	42	11.5	0.145	12.55	5.26	0.73	0.98	0.3808
6	27	28	7.5	0.151	14.71	6.48	0.73	1.04	0.3886
6	33	27	6	0.152	10.66	4.99	0.78	0.82	0.3899
6	37	39	9	0.152		5.67	0.77	1.05	0.3899
6	30	35	10	0.159	10.39	4.59	0.71	1.17	0.3987
6	15.5	15	5	0.162	11.6	4.99	0.67	0.97	0.4025

(continued)

Stage	Web width (cm)	Web height (cm)	Top to hub (cm)	Live mass (g)	Patella–tibia length (mm)	Carapace length (mm)	Hub displacement (HD)	Ladder index (LJ)	Transformed mass
6	41	41	9.5	0.17	12.55	5.26	0.77	1	0.4123
6	29	29	7	0.183	14.44	4.59	0.76	1	0.4278
6	30	32	6	0.188	11.33	4.72	0.81	1.07	0.4336
6	14	21	5	0.222	14.3	6.48	0.76	1.5	0.4712
6	41	41	11	0.265	14.98	6.48	0.73	1	0.5148
7	31	34	12	0.193	14.17	5.53	0.65	1.1	0.4393
7	43	44	16	0.203	13.76	5.13	0.64	1.02	0.4506
7	45	43	11	0.204	15.25	5.8	0.74	0.96	0.4517
7	31	35	11	0.213	15.65	7.96	0.69	1.13	0.4615
7	22	38	9	0.226	14.03	6.21	0.76	1.73	0.4754
7	45	44	12	0.231	14.84	5.94	0.73	0.98	0.4806
7	43	48	12	0.236	16.73	7.15	0.75	1.12	0.4858
7	13	16	5	0.244	13.09	5.8	0.69	1.23	0.494
7	46	50	13	0.255	14.57	5.4	0.74	1.09	0.505
7	11	10	3.5	0.269	16.6	7.96	0.65	0.91	0.5187
7	29	28	14	0.274	15.52	6.88	0.5	0.97	0.5235
7	30	46	20	0.278	15.25	6.61	0.57	1.53	0.5273
7	35	40	10	0.284	14.71	6.75	0.75	1.14	0.5329
7	23	23	4.5	0.291	12.68	5.4	0.8	1	0.5394
7	35	34	7	0.293	12.14	5.4	0.79	0.97	0.5413
7	49	51	14.5	0.316	12.14	7.15	0.72	1.04	0.5621
7	52	41	9	0.333	15.38	6.07	0.78	0.79	0.5771
7	40	38	10	0.338	14.03	6.21	0.74	0.95	0.5814
7	47	50	15	0.338	18.22	7.29	0.7	1.06	0.5814
7	35	45	14	0.345	15.65	7.02	0.69	1.29	0.5874
7	38	41.5	13	0.385	18.49	7.02	0.69	1.09	0.6205
7	59	61	19	0.401	18.76	6.75	0.69	1.03	0.6332
7	49	60	15	0.421	16.06	6.88	0.75	1.22	0.6488
7	38	35	10	0.466	19.84	7.42	0.71	0.92	0.6826
7	39	45	13	0.531	18.49	7.96	0.71	1.15	0.7287
7	55	65	20	0.6	22.4	9.58	0.69	1.18	0.7746
8	40	46	12	0.319	16.33	7.42	0.74	1.15	0.5648
8	47	45	11	0.351	17.68	7.02	0.76	0.96	0.5925
8	41	42	10	0.393	14.98	7.15	0.76	1.02	0.6269
8	54	50	17.5	0.428	15.92	7.02	0.65	0.93	0.6542
8	40	49	11	0.455	17.68	6.75	0.78	1.23	0.6745
8	42	46	14	0.456	17.95	6.88	0.7	1.1	0.6753
8	50	50	10	0.46	15.52	6.21	0.8	1	0.6782
8	52	65	20	0.464	18.08	8.1	0.69	1.25	0.6812
8	38	41	11	0.47	18.76	8.77	0.73	1.08	0.6856
8	43	57	22	0.487	17.81	9.18	0.61	1.33	0.6979
8	31	31.5	8	0.523	14.57	6.75	0.75	1.02	0.7232
8	47	37	17	0.523	19.16	7.83	0.54	0.79	0.7232
8	43	48	11	0.615	16.6	7.29	0.77	1.12	0.7842
8	47	35	9	0.622	22.26	9.31	0.74	0.74	0.7887
8	66	65	18	0.663	19.57	8.37	0.72	0.98	0.8142
8	52	52	18	0.695	22.8	9.31	0.65	1	0.8337
8	58	60	22	0.703	21.05	9.18	0.63	1.03	0.8385

(continued)

Stage	Web width (cm)	Web height (cm)	Top to hub (cm)	Live mass (g)	Patella–tibia length (mm)	Carapace length (mm)	Hub displacement (HD)	Ladder index (LJ)	Transformed mass
8	60	57	20	0.71	20.11	9.72	0.65	0.95	0.8426
8	52	68	18	0.76	21.05	9.45	0.74	1.31	0.8718
8	53	62	19	0.761	23.48	10.26	0.69	1.17	0.8724
9	63	66	12.5	0.619	19.03	9.04	0.81	1.05	0.7868
9	47	63	22	0.631	21.86	8.23	0.65	1.34	0.7944
9	50	80	24	0.735	19.84	8.37	0.7	1.6	0.8573
9	58	63	21	0.782	22.53	8.91	0.67	1.09	0.8843
9	60	57	14	0.802	18.76	8.91	0.75	0.95	0.8955
9	46	46	12	0.837	18.76	8.1	0.74	1	0.9149
9	46	63	14	0.848	21.86	8.64	0.78	1.37	0.9209
9	50	54	13	0.849	19.43	8.5	0.76	1.08	0.9214
9	33	61	17	0.868	18.62	9.18	0.72	1.85	0.9317
9	51	51	15	1.01	24.56	9.45	0.71	1	1.005
9	67	90	18	1.011	20.92	9.31	0.8	1.34	1.0055
9	40	40	9	1.131	24.02	11.06	0.78	1	1.0635
9	93	86	31	1.388	25.5	10.66	0.64	0.92	1.1781

## References

- Agnarsson I, Kuntner M, Blackledge TA (2010) Bioprospecting finds the toughest biological material: extraordinary silk from a giant riverine orb spider. *PLoS ONE* 5(9):e11234. doi:[10.1371/journal.pone.0011234](https://doi.org/10.1371/journal.pone.0011234)
- ap Rhisiart A, Vollrath F (1994) Design features of the orb web of the spider, *Araneus diadematus*. *Behav Ecol* 5:280–287. doi:[10.1093/beheco/5.3.280](https://doi.org/10.1093/beheco/5.3.280)
- Benjamin SP, Zschokke S (2004) Homology, behaviour and spider webs: web construction behavior of *Linyphia hortensis* and *L. triangulalis* (Araneae: Linyphiidae) and its evolutionary significance. *J Evol Biol* 17:120–130. doi:[10.1046/j.1420-9101.2004.00667.x](https://doi.org/10.1046/j.1420-9101.2004.00667.x)
- Blackledge TA, Gillespie RG (2002) Estimation of capture areas of spider orb webs in relation to asymmetry. *J Arachnol* 30:70–77
- Blackledge TA, Scharff N, Coddington JA, Szűts T, Wenzel JW, Hayashi CY, Agnarsson I (2009) Spider web evolution and diversification in the molecular era. *PNAS* 106:5229–5234. doi:[10.1073/pnas.0901377106](https://doi.org/10.1073/pnas.0901377106)
- Bleher B (2000) Development of web-building and spinning apparatus in the early ontogeny of *Nephila madagascariensis* (Vinson, 1863) (Araneae: Tetragnathidae). *Bull Br arachnol Soc* 11 (7):275–283
- Coslovsky M, Zschokke S (2009) Asymmetry in orb-webs: an adaptation to web building costs? *J Insect Behav* 22:29–38. doi:[10.1007/s10905-008-9151-2](https://doi.org/10.1007/s10905-008-9151-2)
- Eberhard WG (1975) The ‘inverted ladder’ orb web of *Scoloderus* sp. and the intermediate orb of *Eustala* (?) sp. (Araneae: Araneidae). *J Nat Hist* 9:93–106. doi:[10.1080/00222937500770071](https://doi.org/10.1080/00222937500770071)
- Eberhard WG, Barrantes G, Madrigal-Brenes R (2008) Vestiges of an orb-weaving ancestor? The “biogenetic law” and ontogenetic changes in the webs and building behavior of the black widow spider *Latrodectus geometricus* (Araneae: Theridiidae). *Ecol Evol* 20:211–244. doi:[10.1080/08927014.2008.9522523](https://doi.org/10.1080/08927014.2008.9522523)
- Gregorič M, Kostanjšek R, Kuntner M (2010) Orb web features as taxonomic characters in *Zygiella* s.l. (Araneae: Araneidae). *J Arachnol* 38:319–327
- Harmer AMT (2009) Elongated orb-webs of Australian ladder-web spiders (Araneidae: *Telaproceria*) and the significance of orb-web elongation. *J Ethol* 27:453–460. doi:[10.1007/s10164-008-0142-8](https://doi.org/10.1007/s10164-008-0142-8)
- Harmer AMT, Herberstein ME (2009) Taking it to extremes: what drives extreme web elongation in Australian ladder web spiders (Araneidae: *Telaproceria maudae*)? *Anim Behav* 78:499–504. doi:[10.1016/j.anbehav.2009.05.023](https://doi.org/10.1016/j.anbehav.2009.05.023)
- Herberstein ME, Heiling AM (1999) Asymmetry in spider orb webs: a result of physical constraints? *Anim Behav* 58:1241–1246. doi:[10.1006/anbe.1999.1255](https://doi.org/10.1006/anbe.1999.1255)
- Hesselberg T (2010) Ontogenetic changes in web design in two orb-web spiders. *Ethology* 116:535–545. doi:[10.1111/j.1439-0310.2010.01760.x](https://doi.org/10.1111/j.1439-0310.2010.01760.x)
- Higgins L (1992) Developmental changes in barrier web structure under different levels of predation risk in *Nephila clavipes* (Araneae, Tetragnathidae). *J Insect Behav* 5:635–655. doi:[10.1007/BF01048010](https://doi.org/10.1007/BF01048010)
- Higgins L (2006) Quantitative shifts in orb-web investment during development in *Nephila clavipes* (Araneae, Nephilidae). *J Arachnol* 34:374–386
- Japyassu HF, Ades C (1998) From complete orb to semi-orb webs: developmental transitions in the web of *Nephilengys cruentata* (Araneae: Tetragnathidae). *Behaviour* 135:931–956
- Kuntner M (2005) A revision of *Herennia* (Araneae: Nephilidae: Nephilinae), the Australasian ‘coin spiders’. *Invertebr Syst* 19:391–436. doi:[10.1071/IS05024](https://doi.org/10.1071/IS05024)
- Kuntner M (2006) Phylogenetic systematics of the *Gondwanan nephilid* spider lineage Clitaetinae (Araneae, Nephilidae). *Zool Scr* 35:19–62. doi:[10.1111/j.1463-6409.2006.00220.x](https://doi.org/10.1111/j.1463-6409.2006.00220.x)
- Kuntner M (2007) A monograph of *Nephilengys*, the pantropical ‘hermit spiders’ (Araneae, Nephilidae, Nephilinae). *Syst Entomol* 32:95–135. doi:[10.1111/j.1365-3113.2006.00348.x](https://doi.org/10.1111/j.1365-3113.2006.00348.x)
- Kuntner M, Agnarsson I (2009) Phylogeny accurately predicts behaviour in Indian Ocean Clitaetra spiders (Araneae: Nephilidae). *Invertebr Syst* 23:193–204. doi:[10.1071/IS09002](https://doi.org/10.1071/IS09002)

- Kuntner M, Agnarsson I (2010) Web gigantism in Darwin's bark spider, a new species from Madagascar (Araneidae: *Caerostris*). *J Arachnol* 38:346–356
- Kuntner M, Coddington JA (2009) Discovery of the largest orb-weaving spider species: the evolution of gigantism in *Nephila*. *PLoS ONE* 4(10):e7516. doi:[10.1371/journal.pone.0007516](https://doi.org/10.1371/journal.pone.0007516)
- Kuntner M, Coddington JA, Hormiga G (2008a) Phylogeny of extant nephilid orb-weaving spiders (Araneae, Nephilidae): testing morphological and ethological homologies. *Cladistics* 24:147–217. doi:[10.1111/j.1096-0031.2007.00176.x](https://doi.org/10.1111/j.1096-0031.2007.00176.x)
- Kuntner M, Haddad CR, Aljančič G, Blejec A (2008b) Ecology and web allometry of *Clitaetra irenae*, an arboricolous African orb-weaving spider (Araneae, Araneoidea, Nephilidae). *J Arachnol* 36:583–594
- Kuntner M, Kralj-Fišer S, Gregorič M (2010) Ladder webs in orb-web spiders: ontogenetic and evolutionary patterns in Nephilidae. *Biol J Linn Soc* 99:849–866. doi:[10.1111/j.1095-8312.2010.01414.x](https://doi.org/10.1111/j.1095-8312.2010.01414.x)
- Maciejewski W (2010) An analysis of the orientation of an orb-web spider. *J Theor Biol* 265:604–608. doi:[10.1016/j.jtbi.2010.05.025](https://doi.org/10.1016/j.jtbi.2010.05.025)
- Masters WM, Moffat AJM (1983) A functional explanation of top-bottom asymmetry in vertical orbwebs. *Anim Behav* 31:1043–1046. doi:[10.1016/S0003-3472\(83\)80010-4](https://doi.org/10.1016/S0003-3472(83)80010-4)
- Nakata K (2010) Does ontogenetic change in orb web asymmetry reflect biogenetic law? *Naturwissenschaften* 97:1029–1032. doi:[10.1007/s00114-010-0719-2](https://doi.org/10.1007/s00114-010-0719-2)
- Nakata K, Zschokke S (2010) Upside-down spiders build upside-down orb webs: web asymmetry, spider orientation and running speed in *Cyclosa*. *Proc R Soc B* 277:3019–3025. doi:[10.1098/rspb.2010.0729](https://doi.org/10.1098/rspb.2010.0729)
- Nelson G (1985) Ontogeny, phylogeny, paleontology, and the biogenetic law. *Syst Zool* 27:324–345. doi:[10.2307/2412883](https://doi.org/10.2307/2412883)
- Robinson MH, Robinson B (1972) The structure, possible function and origin of the remarkable ladder-web built by a New Guinea orb-web spider. *J Nat Hist* 6:687–694. doi:[10.1080/00222937200770631](https://doi.org/10.1080/00222937200770631)
- Stowe MK (1978) Observations of two nocturnal orbweavers that build specialized webs: *Scoloderus cordatus* and *Wixia ectypa* (Araneae: Araneidae). *J Arachnol* 6:141–146
- Swanson BO, Blackledge TA, Hayashi CY (2007) Spider capture silk: performance implications of variation in an exceptional biomaterial. *J Exp Zool* 307A:654–666. doi:[10.1002/jez](https://doi.org/10.1002/jez)
- Zschokke S (1993) The influence of the auxiliary spiral on the capture spiral in *Araneus diadematus* Clerck (Araneidae). *Bull Br Arachnol Soc* 9:169–173
- Zschokke S, Nakata K (2010) Spider orientation and hub position in orb webs. *Naturwissenschaften* 97:43–52. doi:[10.1007/s00114-009-0609-7](https://doi.org/10.1007/s00114-009-0609-7)