



A new view of orb webs: multiple trap designs in a single structure

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Spider orb webs are impressive for their apparently uniform geometric patterns. There are, however, consistent, substantial and taxonomically widespread periphery-to-hub differences in the distances between both adjacent radii and between sticky spiral lines. Radii in typical orbs were on average about 4–5 times farther apart at the outer edge than the inner edge of the area covered by sticky lines. Distances between sticky spiral loops were on average about two times larger near the outer edge than in more inner portions. This pattern in sticky spiral spacing was absent in the modified orbs of *Nephila clavipes*, in which distances between radii varied less. Thus, patterns in sticky spiral spacing may be related to inter-radial spacing; there is, however, probably no single explanation for all of the different patterns of sticky spiral spacing. The patterned differences in radius and sticky spiral spacing have important consequences for understanding orb function, because the lines in a prey's immediate vicinity largely determine whether it will be stopped and then retained, and elementary physics dictates that contact with more lines will tend to increase prey being stopped and retained. Rather than being a unit trap with a single set of prey capture properties, an orb has locally different trapping properties in different sectors. Abandoning the previous typological style of discussion of 'the' ability of a given design to stop and retain prey promises to lead to improved understanding of orb web designs. Published 2014. This article is a U.S. Government work and is in the public domain in the USA, *Biological Journal of the Linnean Society*, 2014, **111**, 437–449.

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The first impression of an orb web is usually one of geometric uniformity: to a first approximation, the radii are placed at similar angles, and the distances between the loops of the sticky spiral are also relatively uniform. Discussions of the functional significance of orb designs have long emphasized this uniformity and its probable advantages in terms of the optimal use of resources to make a structure that can survive stress and trap prey (Hingston, 1920; Savory, 1952; Witt, 1965; Denny, 1976; Chacón & Eberhard, 1980; Vollrath & Mohren, 1985; Eberhard, 1986; Craig, 2003; Cranford *et al.*, 2012). This paper points out that, in fact, the spacing of lines in orb webs is anything *but* uniform. Furthermore, this variation shows consistent intra-orb patterns, and these patterns are taxonomically widespread. This pat-

terned variation has important consequences for understanding how orbs function to stop and retain prey.

Three of the most basic prey capture functions of an orb web are to: (1) intercept prey flying through the air; (2) absorb the prey's momentum when it strikes the web (stop the prey without breaking); and then (3) retain the prey long enough for the spider to arrive to attack (Denny, 1976; Eberhard, 1986; Lin, Edmonds & Vollrath, 1995; Craig, 2003; Blackledge, Agnarsson & Kuntner, 2011; Herberstein & Tso, 2011). The stopping and retention functions are largely performed by different lines. The non-adhesive radii, because of the mechanical properties of the ampullate gland silk of which they are made, are much more important than the sticky spiral lines in stopping prey (Denny, 1976; Craig, 2003; Blackledge *et al.*, 2011; Cranford *et al.*, 2012) (some details are still under discussion – Lin *et al.*, 1995; Blackledge *et al.*, 2011; Sensenig *et al.*,

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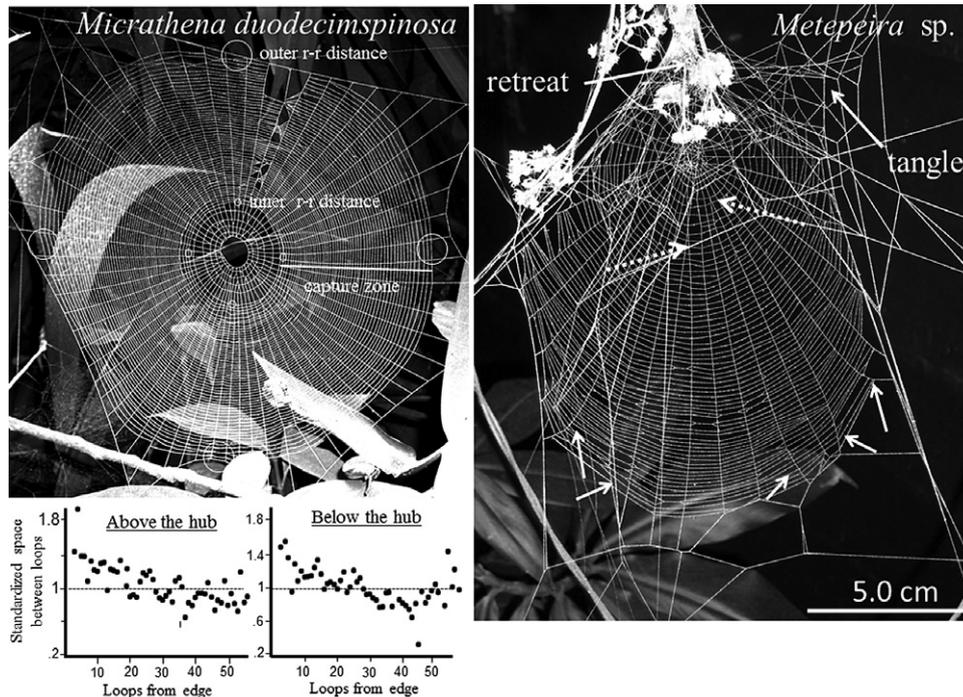


Figure 1. The spaces between loops of sticky spiral are larger in the outer portion of this orb of *Micrathena duodecimspinosa* (left) than near the hub. The thick white line marks the width of the catching zone, while the large and small circles mark the distances between adjacent radii at the inner and outer edges of the capture zone. In contrast, distances between sticky spiral lines near the outer edge below the hub of the web of *Metepeira* sp. (right) are smaller than those nearer the hub. The longer radii in the lower portion of the orb of *Metepeira* sp. are bent (solid arrows) toward especially large spaces between radii; some radii ‘split’ where tertiary radii originate (dotted arrows).

2012). In contrast, the adhesive properties and great extensibility of sticky spiral lines (and the non-sticky nature of the radii) make the sticky spiral much more important than radii in retaining prey. The area where sticky lines are present determines the ‘capture zone’ where prey are most likely to be captured (Fig. 1).

Both stopping and retaining prey are complex functions that are likely to be affected by multiple variables that include the presence of both types of line at the point of impact (Denny, 1976; Blackledge *et al.*, 2011; Eberhard, 2013). To a first approximation, basic physics dictates that contact with a greater number of lines of a given type will tend to increase the probability that the major function of that type of line will be performed successfully (e.g. a prey that encounters two radii in an orb will be more likely to be stopped than if it encounters only one). Experimental impacts of objects with more kinetic energy than an orb is able to absorb have also shown the particular importance of local as opposed to web-wide properties, because only the lines that are contacted directly tend to break (Cranford *et al.*, 2012). Whether a prey with a particular amount of momentum (determined by its mass and velocity) will be stopped by a given orb is

thus largely determined by how many radial lines it encounters directly, not by the orb as a whole (Sensenig *et al.*, 2012).

The effects of the densities of radii and sticky spiral lines on their abilities to stop and retain faster and larger prey (which on average are nutritionally more profitable – Venner & Casas, 2005) result in a basic design trade-off: the larger the area that is covered by the capture zone, the more prey it is likely to intercept; but, given that a spider has only a finite supply of silk, larger webs will have radial and sticky lines that are farther apart (or thinner), and will thus have reduced abilities to stop and to retain prey.

PREVIOUS HYPOTHESES TO EXPLAIN NON-UNIFORM SPACING

Neither the distances between radii nor those between loops of sticky spiral are uniform in the orb webs of spiders (Fig. 1). The radial arrangement of the radii is, in fact, the epitome of a pattern of non-uniform spacing; the density of radii at the inner edge of the capture zone of a typical orb is greater than the density of radii near its outer edge. Geom-

etry dictates that the distance between adjacent radii (a) that are separated by angle α increases monotonically with increasing distance from the hub (c): $a = c/\sin(\alpha/2)$. This relationship has important consequences for prey capture: a prey striking the capture zone near its inner edge is likely to encounter more radii, and is thus more likely to be stopped than if it strikes the same orb near its outer edge. Previous models of how orbs absorb the momentum of prey impact have failed to analyse the importance of this variation in different parts of the web and its consequences (Witt, 1965; Eberhard, 1986; Craig, 1987; Sensenig, Agnarsson & Blackledge, 2010).

The distances between loops of sticky spiral within some orbs are also known to show patterned intra-orb variation in some species. Systematic edge-to-hub differences in spacing have been noted in the araneids *Araneus diadematus* (Peters, 1939; ap Rhihiart & Vollrath, 1994), *Zygiella x-notata* (LeGuelte, 1966) and *Larinioides sclopetarius* (Heiling & Herberstein, 1999) (also Zschokke, 2002; Sensenig *et al.*, 2010). In these species, sticky spiral loops near the outer edge of the capture zone are generally farther apart than those closer to the hub. In addition, the distances between sticky spiral loops tend to be larger above than below the hub (Peters, 1939; LeGuelte, 1966; but see Zschokke, 2011). The effects of these patterns have not been analysed in previous models of orb function.

Two types of hypotheses have been proposed to explain the differences in sticky spiral spacing. One class of explanation supposes that they are incidental, possibly non-adaptive consequences of constraints imposed during sticky spiral construction. Peters (1939, 1954) argued that the geometric relations between the cues that are used by spiders to build an orb-like pattern of lines incidentally result in changes in sticky spiral spacing. He found that in *A. diadematus* the relationship between the length of a segment of sticky spiral and the distance between sticky spiral loops is relatively constant. He argued that the gradual decrease in the distances between loops of sticky spiral nearer the hub is a result of the spider adjusting sticky spiral spacing on the basis of the distance between adjacent radii. Herberstein & Heiling (1999) proposed a second 'energetic constraint' hypothesis: the larger distances between sticky spiral loops near the upper edge of the web in heavier individuals of the araneids *Larinioides* (= *Nuctenea*) *sclopetarius* and *Argiope keyserlingi* are adjustments that result from energetic constraints that are imposed during sticky spiral construction by the cost of lifting the spider's abdomen to make attachments above the hub.

Two other hypotheses propose adaptive explanations. Heiling & Herberstein (1998) proposed an

adaptive hypothesis to explain edge-to-hub differences in sticky spiral spacing in *L. sclopetarius*. Rephrasing their argument slightly, investment in sticky silk to retain prey that strike the orb nearer rather than farther from the hub is likely to yield a larger payoff to the spider, because spider attacks on prey are more rapid (and thus would be more likely to be successful) when the prey are closer to the hub (Masters & Moffat, 1983). Thus, an investment of additional sticky silk nearer the hub would be more likely to yield increased captures than would a similar investment in additional sticky silk far from the hub. This hypothesis could justify a major change of focus in discussions of orb web function. It suggests that within a single orb-like structure, different portions of the web have different designs that result in different prey-capturing properties ('multiple traps'), rather than the orb constituting a single prey-capture unit.

A second adaptive hypothesis to explain edge-to-hub differences in sticky spiral spacing was proposed by Zschokke (2002). Because of the greater density of radii in the inner portion of the capture zone, prey that strike an orb in this area are more likely to be stopped. The 'radius density' hypothesis proposes that orb weavers can gain greater payoffs by improving retention in this area, via closer spacing of the sticky spiral lines, than by investing the same amount of silk in the outer portion of the capture zone. An improvement in the stopping function via a greater density of radii is likely to be especially important for larger prey, for two reasons. The greater cross-sectional area of larger prey would make them more likely to encounter multiple radii on impact; in addition, larger prey would often (but not always – Eberhard, 2013) have greater momentum when they encounter the web, and would thus be more likely to be stopped if they encounter multiple radii. Larger prey are likely to be especially important biologically, because of their greater nutritional value (Venner & Casas, 2005; Blackledge, 2011). Expressed in terms of the possible ways that a spider that has enough silk to extend the borders of its catching zone and increase interception of prey can invest its silk, the spider will be best served by not spacing the sticky lines in this extension too closely together, as the prey that are large enough to require larger numbers of more closely spaced sticky lines for retention will tend not to be stopped in this area, due to the radii there being relatively far apart. Note that the larger cross-sectional area of larger prey will make them likely to contact more sticky lines as well as more radii. But if the number of sticky lines that are needed to retain larger and larger prey rises more rapidly than do the numbers of radii needed to stop the same prey (data are lacking on this point), then decreased sticky

spiral spacing at higher radius densities will be advantageous.

The likely importance of collisions with multiple radii is greater than might be supposed by comparing prey diameters with the direct distances between radii (e.g. Eberhard, 1986). This is because many (probably most) prey will strike webs at acute angles, rather than perpendicular to the web plane (see Fig. 6). When the angle between a prey's path and the plane of the orb is acute, the likelihood that it will encounter multiple radii increases. If one assumes, as seems reasonable, that a prey's first contact with the web in such acute-angle collisions (e.g. with the prey's wing tip) will often cause it to veer toward the web's plane. The tendency of the first radius to extend under impact will also allow the prey to strike additional radii. The likelihood that acute-angle impacts will result in contact with multiple radii reinforces Zschokke's radius density hypothesis. This hypothesis could justify a major change of focus in discussions of orb web function. This hypothesis also suggests the need for a 'multiple trap' view of orb web function.

The present paper demonstrates that patterned edge-to-hub variations in both radius and sticky spiral spacing is more general than previously appreciated, and includes species in three additional families that make horizontal as well as vertical orbs (thus contradicting the energetic constraint argument). In addition, sticky spiral spacing often shows complex, non-linear changes with distance from the hub (thus contradicting the geometrical constraint argument). I discuss three additional possible functions for these edge-to-hub sticky spiral patterns, one of which is also related to the uneven spacing of radii. I test these new and old ideas, and find some support for the uneven radius spacing hypotheses, but conclude that no single hypothesis is likely to explain the documented patterns in sticky spiral spacing. These patterned spacing differences support the multiple trap change in focus that follows from the ideas proposed by Heiling & Herberstein (1998) and Zschokke (2002).

METHODS

Webs of adult females of species in five major families of orb-weaving spiders, *Leucauge mariana* (Tetragnathidae) ($N = 22$), *Zosis geniculata* (Uloboridae) ($N = 15$), *Nephila clavipes* (Nephilidae) ($N = 13$), *Anapisona simoni* (Anapidae) ($N = 21$), and *Micrathena duodecimspinosa* ($N = 15$) and *Metepeira* sp. ($N = 25$) (Araneidae) were photographed after being coated with white powder (corn starch or talcum powder). The webs of *M. duodecimspinosa* and *N. clavipes* were photographed in the field, the others in captivity. Each web was of a different mature

female spider, except in *Metepeira* sp. in which five webs from each of five adult females were used. The webs of *Z. geniculata* were built in 50-cm-diameter plastic containers, and were all within 10° of horizontal). Those of *A. simoni* were built in wire cubes, and were more or less horizontal, but with the hub pulled upward to form a shallow cone (Eberhard, 2007). The orbs of *L. mariana* were built in approximately 50-cm-diameter wire hoops; the hoop was hung so that it was either nearly perfectly horizontal, or at 45° to the horizontal (Eberhard, 1987).

I measured the distances between sticky spiral lines on selected radii and between adjacent radii at the inner and outer edges of the capture zone (Fig. 1) from digital photographs using the program ImageJ (National Institutes of Health). I calculated the mean of the ratio of the distances between adjacent radii at the inner and outer edge of the capture zone between four pairs of radii, at approximately 90° to each other for each web (in the highly asymmetrical webs of *N. clavipes*, I measured the separation between three pairs of adjacent radii: at 90° to the horizontal; and 30° on either side). Tertiary radii that were added by *Metepeira* sp. and *N. clavipes* during temporary spiral construction, after primary and secondary radii and hub construction had ended, were identified by branching points (Figs 1, 2).

In the 45° orbs of *L. mariana* and the more nearly vertical webs of *Metepeira* sp. (about 60–70°), *N. clavipes* (about 60–75°) and *M. duodecimspinosa* (mean 75 ± 7°), I measured the distances between the attachments of all adjacent sticky spiral loops on the most nearly vertical radii below and above the hub (in *Metepeira* sp. and *N. clavipes*, in which there were relatively few loops above the hub, I measured only the distances on the longest radius, which was always below the hub). In horizontal orbs I measured the distances on the longest radius in the web. Because *Z. geniculata* does not attach the sticky spiral to all the radii it crosses in the inner portion of the orb, I measured some distances between attachments to nearby radii (Fig. 3). In *N. clavipes*, I included only distances between adjacent sticky lines, and excluded the distances between sticky spiral and temporary spiral loops.

Several variables such as spider size, feeding history and web size are known to influence sticky spiral spacing, so I standardized the measurements of distances between sticky spiral loops on a radius by dividing each measurement by the median space on that radius; this gave dimensionless 'standardized distance' values. To compare the edge-to-hub patterns in the standardized spacing in different webs and in different species, I plotted the standardized spacing against the 'relative distance to the hub' (the fraction of the total number of spaces between loops attached

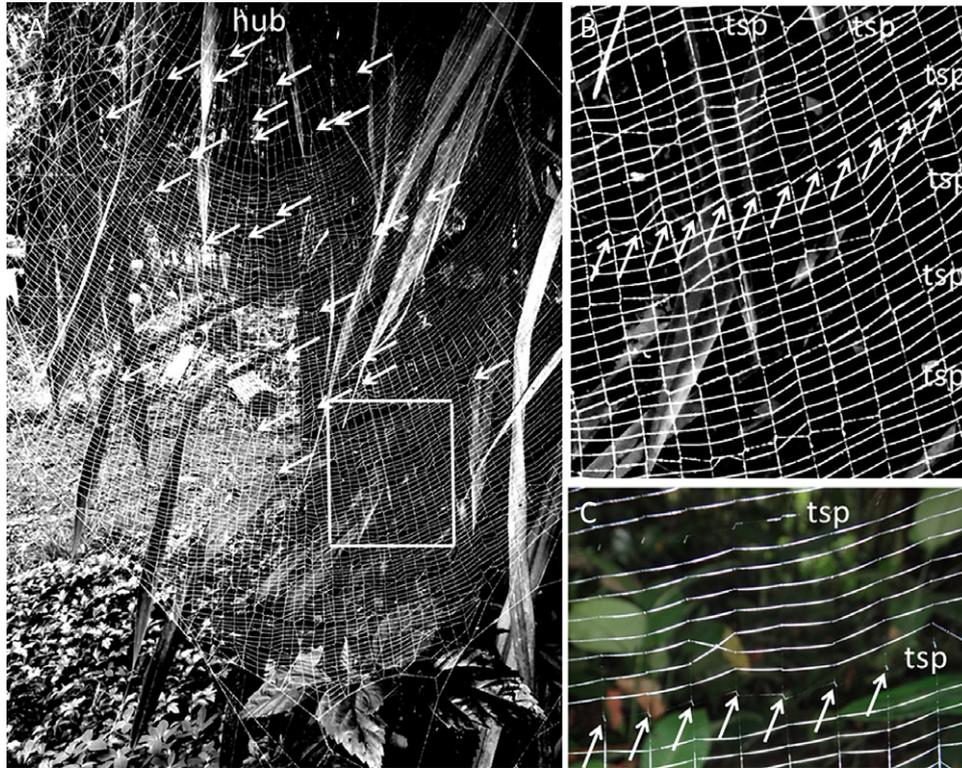


Figure 2. The modified orb webs of adult *Nephila clavipes*. A, Most of an orb; the arrows mark divided radii that were added during temporary spiral construction. B, close-up view of the sector marked in A; C, close up of a small section of an unpowdered orb (of a different female); the sticky spiral lines are much more visible than the non-sticky radial and temporary spiral lines. The arrows in B and C mark double attachments of the non-sticky temporary spiral to the non-sticky radii; the temporary spiral pulls the radius out of line at these sites.

to that radius; 1.0 corresponded to the space nearest the hub). Means are given \pm 1SD.

The webs of *N. clavipes* are derived from typical orbs (Kuntner, Coddington & Hormiga, 2008), but are so highly modified that they are discussed separately. The orbs of mature females are very asymmetrical, with the hub at or very near the upper margin of the web (Kuntner *et al.*, 2008; Hesselberg, 2010); they often have a sparse protective tangle of lines near the hub (Higgins, 1992; Kuntner *et al.*, 2008), but often most of the orb has no nearby tangle (Fig. 2). The non-sticky spiral that corresponds to the temporary spiral of other orb weavers is left intact in the finished web, and the many additional pairs of radii (divided radii; arrows in Fig. 2A) added during temporary spiral construction are pulled apart from each other by the first subsequent loop of the relatively tense temporary spiral; they are then held apart at nearly constant distances by additional loops of temporary spiral farther from the hub (Peters, 1953, 1954; Eberhard, 1982, 1990; Zschokke & Vollrath, 1995; Hesselberg & Vollrath, 2012; see also Hingston, 1922; Wiehle, 1931; and Shinkai, 1982 on other *Nephila* species). In any given area of the web, most

adjacent radii are thus usually nearly parallel to each other (Fig. 2).

RESULTS

TYPICAL ORBS

The ratio of the distance between adjacent radii at the outer edge vs. the inner edge of the capture zone varied substantially within an orb. The means for the five species showed similar values: 4.44 ± 3.74 in *A. simoni*, 4.63 ± 0.82 in *L. mariana* at 0° , 4.80 ± 1.08 in *L. mariana* at 45° , 4.86 ± 1.27 in *M. duodecimspinosa*, 5.18 ± 1.78 in *Metepeira* sp. and 5.37 ± 1.96 in *Z. geniculata*. The standardized distances between sticky spirals also varied substantially: the median standardized distance in the tenth of the capture zone in which the sticky lines were farthest apart was between 123 and 241% that of the tenth in which the sticky lines were closest together (Figs 4, 5). All species showed substantial variation, with the largest differences near the outer and inner edges of the capture zone (Figs 4, 5).

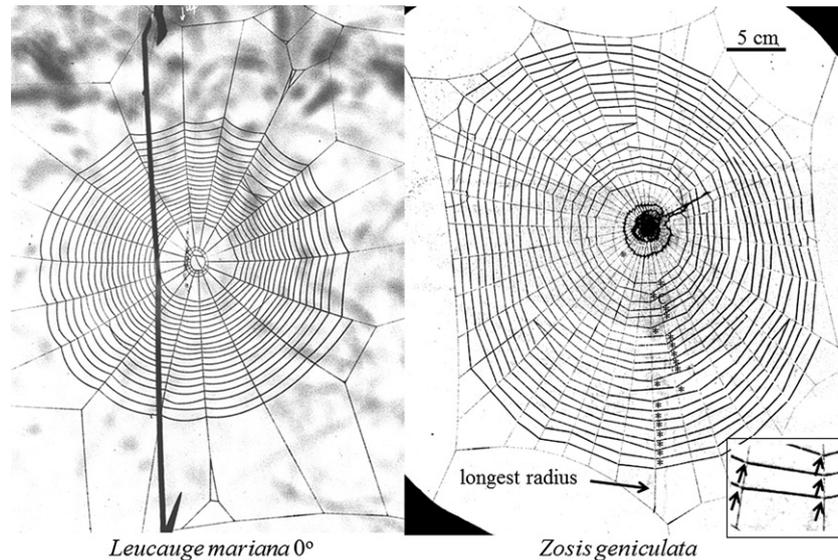


Figure 3. Horizontal orbs of the tetragnathid *Leucauge mariana* and the uloborid *Zosis geniculata* that show clear edge-to-hub differences in sticky spiral spacing. The asterisks in the *Z. geniculata* web mark sites where the sticky spiral was attached to the longest radius or to adjacent radii, and thus where sticky spiral spacing was measured. The insert shows a magnified portion of this web, with arrows indicating the small gaps in the thick mat of sticky cribellum lines that the spider left just after making each attachment; these gaps were used to discriminate points where the sticky spiral was attached to a radius rather than simply crossing it.

Setting aside for a moment *Metepeira* sp., the standardized distances between loops near the outer edge were significantly greater than those in the middle and inner portions of the web in all four species (Tables 1, 2). In *A. simoni* and in the lower portion of *M. duodecimspinosa* orbs, the standardized spacing also rose near the hub (a pattern found previously below the hub in the araneid *Zygiella x-notata*) (LeGuelte, 1966). This pattern did not occur, however, in the upper portion of *M. duodecimspinosa* orbs, nor above or below the hub in *L. mariana* 45° orbs. Edge-to-hub differences persisted even after removing data from the outermost 20% and the innermost 20% of the capture zone, where standardized spacing varied most (Figs 4, 5). There were highly significant negative linear correlations between the standardized distance and the relative distance to the hub when data from the middle portions of different webs and individuals were combined (Table 1). The median spaces between the loops in the outer 20%, the inner 20% and the middle 60% of the capture zone also showed similar, significant differences in many species when the data were analysed web-by-web (Table 2).

The pattern of standardized distances in *Metepeira* sp. webs (Fig. 1) differed from the patterns in the other species. The smallest distances were near the outer edge of the orb, and the distances increased

monotonically closer to the hub (Figs 4, 5). In the middle portion of the capture zone, there was a highly significant positive relationship between standardized sticky spiral spacing and the relative distance from the edge to the hub (Table 1).

There were also differences in the absolute distances between the sticky spiral loops above and below the hub in *M. duodecimspinosa* webs: the median distances in the upper portion were greater in each of 14 webs ($\chi^2 = 9.33$, d.f. = 1, $P = 0.003$), and the above–below differences were statistically significant with Mann–Whitney U tests in 12 of the 14 webs. In contrast, the differences in the absolute values above and below the hub were reversed in the *L. mariana* 45° webs: the mean spacing on the upward radius was less than that on the lower radius of the same web in 20 of 24 orbs ($\chi^2 = 6.0$, d.f. = 1, $P = 0.014$).

MODIFIED ORBS OF *NEPHILA CLAVIPES*

The mean ratio of the distance between radii at the outer versus the inner edges of the capture zone was less than half those in other species (2.23 ± 0.88). The standardized distances between loops of sticky spiral of *N. clavipes* also showed weaker edge-to-hub trends that were positive rather than negative, and were weaker than those of the other species (Fig. 4, Table 1).

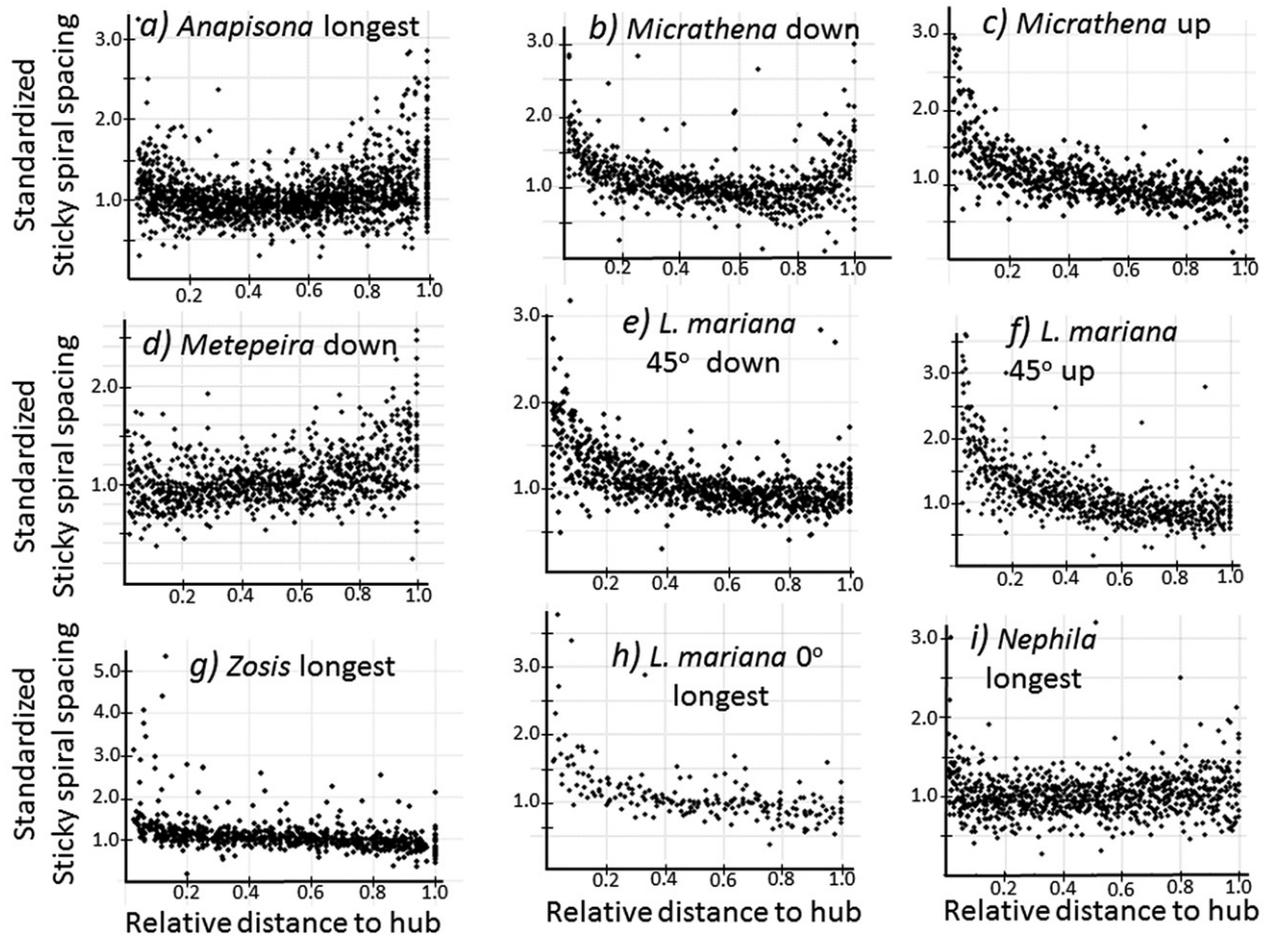


Figure 4. Edge-to-hub patterns of relative sticky spiral spacing in the orbs of six species in five families of orb weavers; all but *N. clavipes* build typical orb webs. 'Relative distance to the hub' = X/Y , where X is the number of sticky loops between the site in the orb and the outer edge of the capture zone, and Y is the total number of sticky spiral loops from the outer edge to the hub. Regression analyses for the central portions (distance to hub 0.2–0.8) were all highly significant (Table 1).

DISCUSSION

All six species in the five families in this study showed significant edge-to-hub differences in both radius and sticky spiral spacing. In four of the five species that build typical orbs, the standardized distances between loops were greater near the outer edge of the capture zone than those in its inner portion. These observations extend the pattern of wider spacing of sticky spiral loops farther from the hub that was noted by previous authors in Araneidae (Peters, 1939; LeGuelte, 1966; Heiling & Herberstein, 1999) to Anapidae, Uloboridae and Tetragnathidae. Photographs of four webs of the theridiosomatid *Epeirotypus chavarría* (W. Eberhard, unpubl. data) indicate that a similar pattern of larger spaces

near the edge may also occur in the family Theridiosomatidae, at least in the upper portion of the orb. A sample of published photographs of orbs suggests that the pattern of greater sticky spiral spacing in the outer portions of the capture zone (especially on longer radii in the upper portion of orbs in which the outer loop of sticky spiral does not approach the frame line closely) occurs in many other genera, including the araneids *Acacesia*, *Acanthepeira*, *Alpaida*, *Argiope*, *Cyclosa*, *Deliochis*, *Eustala*, *Eriophora*, *Gasteracantha*, *Hypophthalma*, *Neoscona*, *Spilasma* and *Wixia*, the tetragnathids *Chrysometa*, *Dolichognatha* and *Tetragnatha*, the uloborids *Philoponella* and *Uloborus*, and the anapid *Anapis* (Kaston, 1948; Witt, Reed & Peakall, 1968; Carico, 1986; Coddington, 1986a, b; Eberhard, 1986;

Lubin, 1986; Kuntner *et al.*, 2008) (*U. barbipes* is an apparent exception – see Lubin, 1986). Generally only a single photograph is available for each species, however, so further documentation will be needed to confirm the generality of this trend.

The substantial magnitudes of the differences in standardized sticky spiral spacing, combined with their consistent edge-to-hub patterns, indicate that within-orb variation in sticky spiral spacing is a design trait that requires an explanation, and is not simply the result of errors by the spiders during sticky spiral construction.

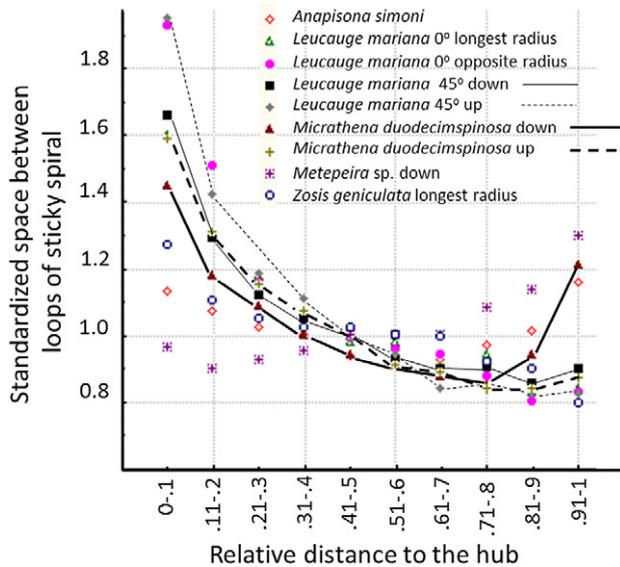


Figure 5. Edge-to-hub patterns of mean standardized spaces between loops of sticky spiral for each tenth of the distance from the outer to the inner edge of the capture zone in five species in four families that build typical orbs. ‘Relative distance to the hub’ = X/Y , where X is the number of sticky loops between the site in the orb and the outer edge of the capture zone, and Y is the total number of sticky spiral loops from the outer edge to the hub.

EVALUATING PREVIOUS HYPOTHESES

EXPLAINING VARIATION IN RADIUS SPACING

The edge-to-hub differences in the spaces between radii result from radii converging on a central area. Radial patterns of lines probably arose early in the evolution of prey capture webs around the mouths of burrows (Shear, 1986; Vollrath & Selden, 2007). There are several advantages of radial arrangements that may have contributed to the maintenance and to subsequent convergences on this pattern (Coyle, 1986; Blackledge, Scharff & Coddington, 2009): effective transmission of vibrations from the prey to the spider; provision of direct paths for the spider to reach prey; increased area that the spider can monitor for prey; and possibly balancing tensions and stresses to make the web more stable in the face of generalized mechanical stress such as wind (Witt, 1965).

EXPLAINING PATTERNS IN STICKY SPIRAL SPACING

The geometric constraint hypothesis of Peters (1939) for the differences in sticky spiral spacing is contradicted by several patterns: the increase in the standardized sticky spiral spacing in the innermost portion of the capture zone in *M. duodecimspinosa* and *A. simoni*; a similar increase found previously (LeGuelte, 1966) below the hub in the orbs of *Zygiella x-notata*; the larger absolute spaces above than below the hub in *M. duodecimspinosa* but not in *L. mariana* 45° webs; and the inverse edge-to-hub pattern of smaller standardized spacing near the edges of the capture zone in *Metepeira* sp. and *N. clavipes* webs.

The energetic constraint idea (Herberstein & Heiling, 1999) also fails to explain some patterns found here, including the edge-to-hub patterns of standardized sticky spiral spacing on radii below the hub in *M. duodecimspinosa*, *Metepeira* sp., *N. clavipes* and *L. mariana* 45° webs, where the spider did not

Table 1. Regression analyses of standardized space between loops of sticky spiral and the relative distance from edge to the hub in the central portion of the capture zone (between 0.2 and 0.8)

Spider	R	R ²	F	d.f.	Slope	P of slope
<i>Anapisona simoni</i> (Anapidae) longest	0.17	0.029	30.64	1, 1034	-0.17	< 0.00001
<i>Leucauge mariana</i> (Tetragnathidae) 0° longest	0.32	0.10	14.4	1, 127	-0.32	0.00023
<i>Leucauge mariana</i> (Tetragnathidae) 45° below	0.44	0.196	124.1	1, 509	-0.44	< 0.00001
<i>Leucauge mariana</i> (Tetragnathidae) 45° above	0.52	0.265	176.3	1, 488	-0.52	< 0.00001
<i>Micrathena duodecimspinosa</i> (Araneidae) below	0.34	0.12	64.1	1, 481	-0.34	< 0.00001
<i>Micrathena duodecimspinosa</i> (Araneidae) above	0.47	0.22	131	1, 456	-0.47	< 0.00001
<i>Metepeira</i> sp. (Araneidae) below	0.23	0.055	31.99	1, 550	+0.23	< 0.00001
<i>Zosis geniculata</i> (Uloboridae) longest	0.17	0.03	12.4	1, 400	-0.17	0.00048
<i>Nephila clavipes</i> (Nephilidae) below	0.14	0.0192	10.8	1, 515	+0.14	0.0016

Table 2. Means (± 1 SD), and web by web analyses of the medians of the standardized spaces between sticky spiral loops in the outer ('O': 0–20% of loops from edge to hub), the middle ('M': 20–80%) and the inner ('I': 80–100%) portions of orbs (means are values for each web; N = number of webs)

Spider	N	Means			Medians for each web*	
		Outer	Middle	Inner	O > M	I > M
					Yes/no	Yes/no*
<i>Anapisona simoni</i>	21	0.96 \pm 0.23	0.99 \pm 0.23	1.47 \pm 0.48	13(1)/8(2)	19(13)/2
<i>Leucauge mariana</i> 45°						
Below hub	24	1.43 \pm 0.50	1.00 \pm 0.19	0.92 \pm 0.26	21(19)/3	3(1)/21(9)
Above hub	24	1.72 \pm 0.55	1.00 \pm 0.26	0.86 \pm 0.25	23(20)/1	4/20(6)
<i>Leucauge mariana</i> 0°						
Longest	7	1.61 \pm 0.60	1.07 \pm 0.25	0.86 \pm 0.21	7(7)/0	1/6(4)
Opposite longest	7	1.77 \pm 0.48	1.02 \pm 0.22	0.83 \pm 0.16	7(7)/0	0/7(4)
<i>Micrathena duodecimspinosa</i>						
Below hub	14	1.34 \pm 0.36	0.96 \pm 0.24	1.12 \pm 0.45	14(13)/0	11(3)/3
Above hub	14	1.50 \pm 0.50	0.99 \pm 0.20	0.87 \pm 0.21	14(12)/0	0/11(4)
<i>Metepeira</i> sp.	25	0.94 \pm 0.24	1.01 \pm 0.20	1.25 \pm 0.35	10(1)/16(6)	23(12)/2

*Numbers in parentheses are the numbers of webs in which the differences in the standardized spaces were significantly different ($P < 0.05$) comparing different sectors of the same web, using two-tailed Mann–Whitney U-tests.

need to lift its abdomen to make attachments. Nor does it explain the clear patterns of standardized spacing in the horizontal orbs of *L. mariana* and *Z. geniculata*.

The attack time hypothesis (Heiling & Herberstein, 1998) fits the trends toward larger standardized distances near the outer edge of the capture zone, and also the above- vs. below-the-hub differences in standardized sticky spiral spacing in the webs of *M. duodecimspinosa*. The webs of these species had larger standardized distances near the edge above the hub; this is the area of the web least quickly accessible for the spider, because spiders of this species nearly always face directly downward at the hub (W. Eberhard unpubl. data) (as is typical of many orb weavers – Masters & Moffat, 1983; Nakata & Zschokke, 2010). Orb weavers in general attack prey below the hub more rapidly than prey above it, and prey in front of them than those behind them (Heiling & Herberstein, 1998; Nakata & Zschokke, 2010; Briceño & Eberhard, 2011).

The attack time hypothesis does not fit easily, however, some other data presented here. The smaller absolute values of sticky spiral spacing above vs. below the hub of *L. mariana* 45° webs was not predicted. More importantly, the attack time hypothesis is contradicted by the inverse relationships between standardized sticky spiral spacing in the modified orbs of *N. clavipes* and *Metepeira* sp.

RADIUS DENSITY

The radius density hypothesis can explain the same trends explained by the attack time hypothesis (above); in addition, it explains the contradictions to the attack time hypothesis seen in *L. mariana* 0° and 45° webs. The radius density hypothesis leaves apparently unexplained, however, the reverse trend in the orbs of *Metepeira* sp. (Fig. 4D). There are, nevertheless, some potentially mitigating conditions in this species: the radii in the lower portions of the orb are both split and pulled out of line in the lower portion of the web in ways that partially fill the larger holes between radii (arrows in Fig. 1). This bending reduces the especially large distances between certain radii. In addition, the orbs of *Metepeira* sp. are accompanied by a relatively dense tangle of lines on at least one side of the orb. The tangle almost certainly reduces the velocity of many of the prey that strike the web from that side (e.g. the 'ricochet effect' – Uetz, 1989), and may thus increase the likelihood that some originally high-energy prey will be stopped, even near the outer edge of the catching zone; this partially reduces the contradiction of the radius density hypothesis.

Also unexplained are the above-the-hub versus below-the-hub differences in patterns in the vertical orbs of *M. duodecimspinosa* (Fig. 4B, C). Perhaps the tendency of some prey to slide or 'tumble' downward makes tighter sticky spiral spacing more important in the lower portion of the upper capture zone. Or

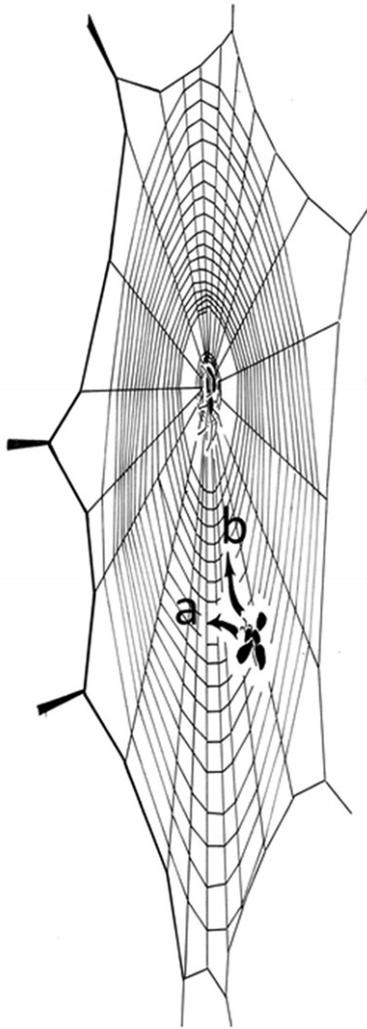


Figure 6. The impact of a flying insect which approaches the plane of an orb at a more acute angle is more likely to involve multiple radii, and thus more likely to result in the insect being stopped. When the insect's path is more nearly perpendicular to the radius or radii that it hits (a), it may be more likely to be stopped than when its path is more nearly parallel to them (b), because the force imposed on the radius to absorb the momentum of an acute angle impact in b is less equally distributed on the two sides of its impact, and thus more likely to over-stress the radius.

perhaps some prey are more difficult to retain in areas of the web with especially high densities of radii, because they offer the struggling prey more non-sticky lines against which to push (e.g. Eberhard, 2013). These are only speculative alternatives.

As noted by Zschokke (2002), one test of the radial organization hypotheses is to compare sticky spiral spacing patterns in orbs in which the radii are more nearly parallel to each other and in which radius

density is thus more nearly uniform from edge to hub. The webs of *Nephila clavipes*, with their many nearly parallel radii, have such a design (Fig. 2) (for a discussion of the unusual stress relationships on radii and temporary spiral lines in *Nephila* webs, see Hesselberg & Vollrath, 2012). The prediction of these hypotheses is that *N. clavipes* orbs will show less marked trends to have larger sticky spiral spacing near the outer edge. This prediction was confirmed: the edge-to-hub relationship with sticky spiral spacing was relatively weak, and showed the opposite slope (Fig. 4I, Table 1). Zschokke (2002) also stated that sticky spiral loops nearer the hub of *N. clavipes* were not more closely spaced, but gave no quantitative data, referring only to a single, previously published photograph (Peters, 1953) that had no accompanying measurements or comments regarding sticky spiral spacing.

INNER PORTION OF CAPTURE ZONE AND FREE ZONE

None of the previous hypotheses regarding sticky spiral spacing explains the increase in sticky spiral spacing near the inner edge of the capture zone in *M. duodecimspinosa* and *A. simoni* webs, nor do they explain the usual existence of an area near the hub that is free of sticky lines (the 'free zone') (Figs 1, 3).

NEW HYPOTHESES FOR PATTERNED VARIATION IN STICKY SPIRAL SPACING

STICKY SPIRAL ENTANGLEMENT HYPOTHESIS

A new idea, also based on the larger distances between adjacent radii farther from the hub, concerns the danger that adjacent loops of sticky spiral will be displaced (e.g. by the wind) and will adhere to any other lines that they touch, in effect 'wasting' sticky silk by creating holes in the array of sticky lines. The larger the distance between adjacent radii, the longer the segment of sticky line that hangs free, and thus the wider the arc in which this line can swing. The larger distances between loops of sticky spiral near the edge could function to reduce their chances of entanglement by keeping these longer segments of sticky spiral farther apart.

PREY TUMBLING HYPOTHESIS

Prey that have been stopped and are struggling in a vertical orb sometimes work partially free and fall downward into portions of the web below the impact site; such 'tumbling' (Eberhard, 1989; Nakata & Zschokke, 2010) is likely to be more frequent in more nearly vertical orbs. Smaller spacing at the lower edges of capture zones (e.g. the innermost spaces

above the hub, the outermost spaces below the hub) could increase returns when prey tend to escape by tumbling.

DANGER FROM PREY

Large, powerful or heavily armed prey that are struggling in a web after being stopped may represent potential dangers for spiders. There are apparently no systematic studies of the importance of this type of danger, but such a prey that strikes the web very close to the spider could be dangerous in the short period of time before the spider can move away.

Danger of this sort might explain the otherwise puzzling existence of the free zone immediately surrounding the hub (especially in horizontal orbs, in which another possible function of the free zone – to allow the spider to shuttle defensively from one side of the hub to the other as in *Argiope* – is not feasible). The wider spacing between the innermost loops of sticky spiral in *M. duodecimspinosa* and *A. simoni* might also function to reduce the danger of this sort for the spider while resting at the hub. A second type of danger – to the orb rather than to the spider – could also favour wider distances between loops or absence of sticky spiral very near the hub. Even if the spider successfully attacked a prey here, extracting it from the web could entail damage to multiple radii, thus inflicting substantial damage on the orb.

TESTING THE NEW HYPOTHESES

The sticky spiral entanglement hypothesis does not explain the smaller standard sticky spiral spacing near the edge of *Metepeira* sp. webs. The webs of this species are built at relatively exposed sites, often near the edge of plant cover in second growth, so it is not reasonable to save this hypothesis by supposing that *Metepeira* sp. orbs do not need to tolerate windy conditions.

The tumbling prey hypothesis cannot explain the clear edge-to-hub patterns of differences in sticky spiral spacing in horizontal orbs such as those of *L. mariana* 0° webs and *Z. geniculata*. It could, however, explain two other patterns that no other hypothesis explains: the inverse pattern of larger spaces nearer the hub on radii below the hub in *Metepeira* sp. and *N. clavipes*; and the relatively small distances above the hub but not below it in *M. duodecimspinosa* and *Z. x-notata* webs (LeGuelte, 1966).

I know of no comparative data that would allow evaluation of the dangerous prey hypothesis.

In summary, no single hypothesis is able to explain all of the patterns observed. Three of the six hypotheses are logical consequences of larger distances

between radii farther from the hub that result from radial organization. None of the hypotheses is mutually exclusive of other hypotheses: thus, more than one type of selection could act on the sticky spiral spacing in the same orb, and the relative degrees of importance of different factors could differ in different species. Some hypotheses can be confidently eliminated, however, in particular cases (e.g. the tumbling and energy cost hypotheses in horizontal orbs; the attack time hypothesis in *Metepeira* sp. and *N. clavipes* webs). Probably more than one factor has been important in the widespread evolution of patterned variation in sticky spiral spacing in orb webs documented here. Intra-web differences in the distances between radii have probably been involved.

CONSEQUENCES OF PATTERNED VARIATION FOR UNDERSTANDING FUNCTIONAL DESIGN

Whichever combination of hypotheses best explains the patterns of within-orb variation in sticky spiral spacing, the patterned variations in the spaces between both radii and sticky spiral lines that occur in a wide variety of taxonomic groups confirm the need for a substantial change in interpretation. An orb needs to be seen as a combination of designs that have different prey capture properties in different portions of the web, rather than as a single unit trap. Because of this variation, an orb design is not optimal throughout for any given type of prey. Although it is reasonable to consider an orb as a unitary device for some functions, such as supporting the spider and transmitting vibrations (Japyassú & Ades, 1998), it is best to consider its design for prey capture as an array of different traps that have different properties. Perhaps due to conservation by orb weavers of the ancient trait of building lines radiating from a central point where the spider waits, different portions of the same orb web have very different densities of strong, non-sticky support lines. And, perhaps due largely to these differences (the radius density and entanglement hypotheses), the spider usually adjusts the densities of sticky lines substantially in different parts of an orb. While studies of whole orbs have improved knowledge of the functional significance of different orb web designs, more complete understanding will require analyses that integrate the stopping and retention properties of different portions of the same orb. In one sense, this abandonment of a unitary vision of an orb represents one more skirmish in the long battle of biologists to resist making overly simplified typological analyses of natural phenomena (Mayr, 1982).

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REFERENCES

- Blackledge TA. 2011.** Prey capture in orb weaving spiders: are we using the best metric? *Journal of Arachnology* **39**: 205–210.
- Blackledge TA, Agnarsson I, Kuntner M. 2011.** The form and function of spider orb webs: evolution from silk to ecosystems. *Advances in Insect Physiology* **41**: 175–262.
- Blackledge TA, Scharff N, Coddington JA. 2009.** Reconstructing web evolution and spider diversification in the molecular era. *Proceedings of the National Academy of Sciences of the United States of America* **106**: 5229–5234.
- Briceño RD, Eberhard WG. 2011.** The hub as a launching platform: rapid movements of the spider *Leucauge mariana* (Araneae: Tetragnathidae) as it turns to attack prey. *Journal of Arachnology* **39**: 102–112.
- Carico J. 1986.** Web removal patterns in orb-weaving spiders. In: Shear WA, ed. *Spiders, webs behavior and evolution*. Palo Alto, CA: Stanford University Press, 306–318.
- Chacón P, Eberhard WG. 1980.** Factors affecting numbers and kinds of prey caught in artificial spider webs, with consideration of how orb webs trap prey. *Bulletin of the British Arachnological Society* **5**: 29–38.
- Coddington JA. 1986a.** The genera of the spider family Theridiosomatidae. *Smithsonian Contributions to Zoology* **422**: 1–96.
- Coddington JA. 1986b.** The monophyletic origin of the orb web. In: Shear WA, ed. *Spiders, webs behavior and evolution*. Palo Alto, CA: Stanford University Press, 319–363.
- Coyle FA. 1986.** The role of silk in prey capture by nonaraneomorph spiders. In: Shear WA, ed. *Spiders, webs behavior and evolution*. Palo Alto, CA: Stanford University Press, 269–305.
- Craig C. 1987.** The ecological and evolutionary interdependence between web architecture and web silks spun by orb-web weaving spiders. *Biological Journal of the Linnean Society* **30**: 135–162.
- Craig C. 2003.** *Spiderwebs and silk*. New York: Oxford University Press.
- Cranford SW, Tarakanova A, Pugno NM, Buehler MJ. 2012.** Nonlinear material behaviour of spider silk yields robust webs. *Nature* **482**: 72–76.
- Denny M. 1976.** The physical properties of spider's silk and their role in the design of orb-webs. *Journal of Experimental Biology* **65**: 483–506.
- Eberhard WG. 1982.** Behavioral characters for the higher classification of orb-weaving spiders. *Evolution* **36**: 1067–1095.
- Eberhard WG. 1986.** Effects of orb-web geometry on prey interception and retention. In: Shear WA, ed. *Spiders webs, behaviour and evolution*. Palo Alto, CA: Stanford University Press, 70–100.
- Eberhard WG. 1987.** The effects of gravity on temporary spiral construction by *Leucauge mariana* (Araneae, Araneidae). *Journal of Ethology* **5**: 29–36.
- Eberhard WG. 1989.** Effects of orb web orientation and spider size on prey retention. *Bulletin of the British Arachnological Society* **8**: 45–48.
- Eberhard WG. 1990.** Function and phylogeny of spider webs. *Annual Review of Entomology* **21**: 341–372.
- Eberhard WG. 2007.** Miniaturized orb-weaving spiders: behavioural precision is not limited by small size. *Proceedings of the Royal Society B: Biological Sciences* **274**: 2203–2209.
- Eberhard WG. 2013.** The rare large prey hypothesis: a critical discussion. *Journal of Arachnology* **41**: 76–80.
- Heiling AM, Herberstein ME. 1998.** The web of *Nuctenea sclopetaria* (Araneae, Araneidae): relationship between body size and web design. *Journal of Arachnology* **26**: 91–96.
- Heiling M, Herberstein ME. 1999.** Asymmetry in spider orb-webs: a result of experience? *Animal Cognition* **2**: 171–177.
- Herberstein ME, Heiling AM. 1999.** Asymmetry in spider orb webs: a result of physical constraints? *Animal Behavior* **58**: 1241–1246.
- Herberstein ME, Tso I-M. 2011.** Spider webs: evolution, diversity and plasticity. In: Herberstein ME, ed. *Spider behaviour, flexibility and versatility*. New York: Cambridge University Press, 57–98.
- Hesselberg T. 2010.** Ontogenetic changes in web design in two orb-weaving spiders. *Ethology* **116**: 535–545.
- Hesselberg T, Vollrath F. 2012.** The mechanical properties of the non-sticky spiral in *Nephila* orb webs (Araneae, Nephilidae). *Journal of Experimental Biology* **215**: 3362–3369.
- Higgins L. 1992.** Developmental changes in barrier web structure under different levels of predation risk in *Nephila clavipes* (Araneae: Tetragnathidae). *Journal of Insect Behavior* **5**: 1635–1655.
- Hingston RWG. 1920.** *A naturalist in Himalaya*. Boston, MA: Small, Maynard and Co.
- Hingston RWG. 1922.** The snare of the giant wood spider (*Nephila maculata*). *Journal of the Bombay Natural History Society* **28**: 642–655.
- Japyassú H, Ades C. 1998.** From complete orb to semi-orb webs: developmental transitions in the web of *Nephilengys cruentata* (Araneae: Tetragnathidae). *Behaviour* **135**: 931–956.
- Kaston BJ. 1948.** Spiders of Connecticut. *Connecticut State Geology and Natural History Survey, Bulletin* **70**: 1–874.
- Kuntner M, Coddington JA, Hormiga G. 2008.** Phylogeny of extant nephilid orb-weaving spiders (Araneae, Nephilidae):

- testing morphological and ethological homologies. *Cladistics* **24**: 147–217.
- LeGuelte L. 1966.** Structure de la toile de *Zygiella x-notata* Cl. (Araignées, Argiopidae) et facteurs qui régissent le comportement de l'araignée pendant la construction de la toile. Thèse Pub. Univ. Nancy, 1–77.
- Lin LH, Edmonds DT, Vollrath F. 1995.** Structural engineering of an orb-spider's web. *Nature (London)* **373**: 146–148.
- Lubin YD. 1986.** Web building and prey capture in the Uloboridae. In: Shear WA, ed. *Spiders, webs behavior and evolution*. Palo Alto, CA: Stanford University Press, 132–171.
- Masters WM, Moffat AJM. 1983.** A functional explanation of top-bottom asymmetry in vertical orb webs. *Animal Behavior* **31**: 1043–1046.
- Mayr E. 1982.** *The growth of biological thought: diversity, evolution and inheritance*. Cambridge, MA: Harvard University Press.
- Nakata K, Zschokke S. 2010.** Upside-down spiders build upside-down orb webs: web asymmetry, spider orientation and running speed in *Cyclosa*. *Proceedings of the Royal Society, Series B* **277**: 3019–3025.
- Peters HM. 1939.** Probleme des Kreuzspinnennetzes. *Zeitschrift Morphologie und Oekologie Tiere* **36**: 179–266.
- Peters HM. 1953.** Beiträge zur vergleichenden Ethologie und Ökologie tropischer Webespinnen. *Zeitschrift für Morphologie und Ökologie Tiere* **42**: 278–306.
- Peters HM. 1954.** Estudios adicionales sobre la estructura de la red concéntrica de las arañas. *Comunicaciones del Instituto Tropical de Investigacion y Ciencia* **3**: 1–18.
- ap Rhisiart A, Vollrath F. 1994.** Design features of the orb web of the spider, *Araneus diadematus*. *Behavioral Ecology* **5**: 280–287.
- Savory TH. 1952.** *The spider's web*. London: Frederick Warne.
- Sensenig A, Agnarsson I, Blackledge TA. 2010.** Behavioural and biomaterial coevolution in spider orb webs. *Journal of Evolutionary Biology* **23**: 1839–1856.
- Sensenig A, Lorentz KA, Kelly SP, Blackledge TA. 2012.** Spider orb webs rely on radial threads to absorb prey kinetic energy. *Journal of the Royal Society Interface* **9**: 1880–1891.
- Shear WA. 1986.** The evolution of web-building behavior in spiders: a third generation of hypotheses. In: Shear WA, ed. *Spiders, webs behavior and evolution*. Palo Alto, CA: Stanford University Press, 364–400.
- Shinkai E. 1982.** Web structure of *Nephila clavata* (1). *Atypus* **80**: 1–10 (in Japanese).
- Uetz G. 1989.** The 'ricochet effect' and prey capture in colonial spiders. *Oecologia* **81**: 154–159.
- Venner S, Casas J. 2005.** Spider webs designed for rare but life-saving catches. *Proceedings of the Royal Society, Series B* **272**: 1587–1592.
- Vollrath F, Mohren W. 1985.** Spiral geometry in the garden spider's orb web. *Die Naturwissenschaften* **72**: 666–667.
- Vollrath F, Selden P. 2007.** The role of behavior in the evolution of spiders, silks and webs. *Annual Review of Ecology and Systematics* **38**: 819–846.
- Wiehle H. 1931.** Neue Beiträge zur Kenntnis des Fanggewebes der Spinnen aus den Familien Argiopidae, Uloboridae, und Theridiidae. *Zeitschrift für Morphologie und Ökologie Tiere* **22**: 348–400.
- Witt PN. 1965.** Do we live in the best of all worlds? Spider webs suggest an answer. *Perspectives in Biology and Medicine* **8**: 475–487.
- Witt PN, Reed C, Peakall DB. 1968.** *A spider's web: problems in regulatory biology*. New York: Springer.
- Zschokke S. 2002.** Form and function of the orb-web. In: Toft S, Scharff N, eds. *European arachnology 2000*. Aarhus: Aarhus University Press, 99–106.
- Zschokke S. 2011.** Spiral and web asymmetry in the orb webs of *Araneus diadematus* (Araneae, Araneidae). *Journal of Arachnology* **39**: 358–362.
- Zschokke S, Vollrath F. 1995.** Web construction patterns in a range of orb-weaving spiders (Araneae). *European Journal of Entomology* **92**: 523–541.