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Radius construction and structure in the orb-web of *Zilla diodia* (Araneidae)

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Abstract In orb-webs, the tension of the sticky spiral produces a centripetal force on the radii, resulting in an increase in tension along each radius from the centre of the web to the periphery. *Zilla diodia* (Walckenaer, 1802) atypical of araneids, was found to adapt the structure of its radii to this tension gradient by building radii that are double stranded at the periphery of the web and single stranded near the centre. Furthermore, the proportion of each radius that is doubled was found to be larger in the upper part of the web – where the overall tensions in the radii are known to be higher – than in the lower part of the web, suggesting that the spider adjusts the proportion of each radius that is doubled to the overall tension in the radius.

Key words Adaptation · Biomechanics · Spider web · Tension control · Web construction

Introduction

Orb-webs stand out from other spider webs through their regular structure and highly optimised use of material (Denny 1976; Craig 1987). In the past they have often been taken to represent the climax of the evolution of the spider's web (Kaston 1964; Kullmann 1972) and are also considered as one of nature's most ingenious engineering products (Bach 1975; Lin et al. 1995). Many aspects of the orb-web have been studied and generally found to be well adapted (Eberhard 1986; ap Rhisiart and Vollrath 1994; Sandoval 1994; Schneider and Vollrath 1998; Krink and Vollrath 2000). However, in one aspect, no adaptation has been described so far. Since

each of the sticky spiral loops exerts a centripetal force on the radii, the tension within each radius increases from the centre to the periphery of the web. In the radii of finished webs of *Araneus diadematus* Clerck, 1757, the tensions are 19–48% higher near the periphery than near the centre of the web (Wirth and Barth 1992). Since this difference is the result of the sum of the forces exerted by the sticky spiral loops, we can expect even larger differences in webs with more sticky spiral loops, e.g. in the webs of *Zilla diodia*. Despite this difference in tension along the radii, no differentiation between the inner and the outer part of the radius has been described in detail, even though spiders are known to be able to reinforce threads by increasing the number of strands if necessary. In the web of *Araneus sericatus* (= *Larinioides scolopetarius* (Clerck 1757)) for example, anchor threads which are under very high tension consist of up to four strands, whereas frame threads which are under somewhat lower tensions consist of two strands and the radii consist of a single strand (with each strand consisting of two fibres; Denny 1976).

In a comparative study, Zschokke and Vollrath (1995) found that the track of *Z. diodia* showed a characteristic dip during the construction of the radii (cf. Fig. 1). They suggested that this may indicate "... that the spider had at that point (roughly half-way back to the hub) broken the provisional radius." (p 529) which would indicate that the outer half of the radius in the webs of this species might be doubled. Similar observations have been made by Eberhard (1981) for five different, unrelated species (*Micrathena sexspinosus*, *Neoscona* sp., *Tetragnatha* sp., *Tylorida striata* and *Cyclosa caroli*). Previously, the radii of araneid spiders have generally been described to be always single, since – during radius construction – most araneid orb weavers cut and reel up the provisional radius (also called exit line) as they return to the hub (cf. Fig. 3b; Eberhard 1982; Coddington 1986). Uloborid spiders, on the other hand, leave the provisional radius in place, so that their radii are doubled. This distinction between double and single radii has been used as a character in phylogenetic

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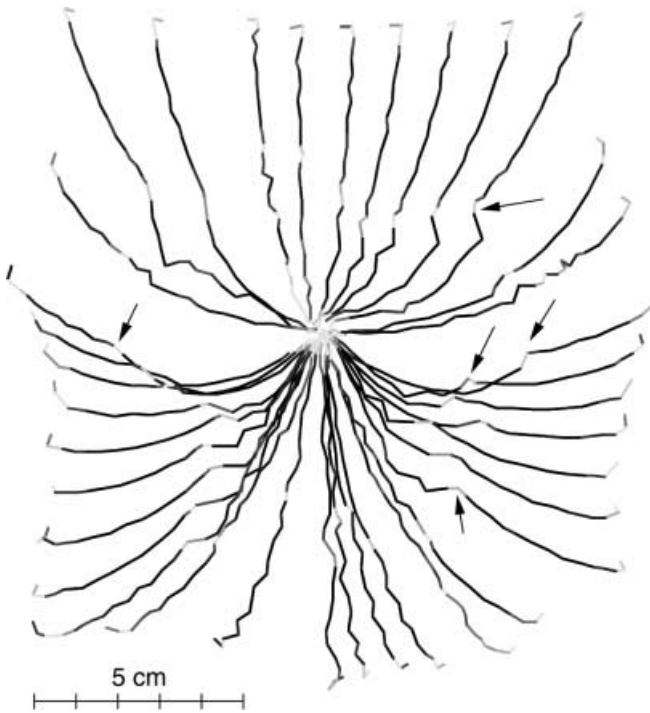


Fig. 1 Tracks of the movements of *Zilla diodia* during the return to the hub of all secondary radius constructions of the web shown in Figure 4. *Light lines* indicate slow speed, *dark lines* indicate faster speeds, up to 8 cm s^{-1} . Note the dips in the track (*arrows*) roughly half-way back to the hub where the spider also slowed down. Other orb-weavers (e.g. *Araneus diadematus*; cf. Fig. 3) show no such dip and no slowing-down. The larger gaps between two tracks are at the positions of the primary radii not analysed in this study (cf. Fig. 4)

analysis (Scharff and Coddington 1997; Griswold et al. 1998).

There is a fundamental rule in construction engineering (Maxwell's lemma) which states, that if every member of a structure built of one substance is under tension such that the *stress in all members is equal* ..., the structure is built with the minimum volume necessary (Parkes 1965; Denny 1976). Following this rule, spiders should distribute the stress (the force per cross sectional area) along the radii as equally as possible. This is most easily achieved by doubling the outer part of the radius (where the tension is highest) and by increasing the proportion of each radius that is doubled in radii under higher tension.

Earlier studies have shown that tensions vary considerably among the radii of orb-webs (Work 1977; Wirth and Barth 1992; Köhler and Vollrath 1995). Most orb-webs have fewer radii in the upper half of the web compared to the lower half (Mayer 1952; Krieger 1992). Considering the forces acting on the hub of the orb-web, the sum of the forces pulling it in one direction (e.g. upwards) must be exactly equal to the sum of the forces pulling in the opposite direction (e.g. downwards). Since the upward force is divided among fewer radii than the downwards force, it follows that the force per radius is stronger for the radii above the hub (Le Guelte 1969;

Eberhard 1981). Additionally, the weight of the spider sitting on the hub further increases the force acting on the radii above the hub and decreases the force on the radii below (Langer 1969). Empirical studies have shown that the tensions in the radii above the hub are indeed on average higher than the tensions in the radii below the hub (Le Guelte 1969; Wirth and Barth 1992; Köhler and Vollrath 1995).

The present study describes in detail the structure of the radii in the orb-web of *Z. diodia*. In particular, I address the following questions: (1) are the radii in the orb-webs of *Z. diodia* doubled on the periphery and single near the centre of the web?; (2) if this is the case, do the radii leading up from the hub (which are under higher tension) have a larger proportion of their length doubled compared to the radii leading down from the hub?; and (3) which other factors can be identified that possibly influence the proportion of each radius that is doubled?

Material and methods

Animals

Z. diodia is an orb-weaving spider that builds an extremely fine web with many (often more than 50) radii and sticky spiral loops (cf. Fig. 4; Wiehle 1927; Zschokke and Vollrath 1995). The spider always sits in the hub of its web which it builds in forests and hedges (Jones 1983). It occurs in the Mediterranean and in the temperate parts of Europe, whereas its congeneric relatives can only be found in Eastern Asia (Platnick 1989). With an adult body length of 2–4 mm (Roberts 1995), it is one of the smallest orb-weaving spiders in Europe. All spiders used in this study were collected as sub-adults or adults on hedges and forest edges near Basel, Switzerland. In the laboratory, the spiders were temporarily placed in transparent plastic frames (30 cm×30 cm×5 cm) where they built some webs.

Data collection

After the spiders had constructed several webs in frames in the laboratory, web constructions on a U-shaped setup were recorded using a computerised image analysis similar to that described in Zschokke (1994) but with an improved temporal analysis capability. This recording method allows tracking of the spiders' movements as well as analysis of the speed of these movements. Additionally, parts of one web construction were videotaped using a SONY Hi8 Camcorder and later copied to Digital Video for better viewing of single frames and detailed analysis of temporal aspects. The complete webs ($n=17$, built by six individuals) of which the construction had been successfully recorded, were photographed and later digitised using a Summagraphics MM II digitising tablet. The angular position of the radii, the angles between the radii, and the proximity of the radii to the nearest anchor point (measured as the angle between the radius and a line between the centre of the web and the nearest anchor point) were measured in the digitised webs. The positions of the transitions along the secondary radii and the order of radius construction were reconstructed from the recording of the spider's tracks during web construction. The building order rank of each radius was divided by the number of radii in that web and then arcsine transformed to obtain a normally distributed variable, termed 'build-order'.

Samples of the radii of some of these webs with the inferred transition from double to single stranded thread were transferred to SEM stubs, sputtered with 20 nm of gold and observed with a

Philips ESEM XL30 at an accelerating voltage of 5 kV. Despite the low voltage, the thread often broke during observation. Primary radii (i.e. those built together with a frame thread) were not analysed in this study because I could not observe any indication of a transition from double- to single-stranded thread during their construction and because their whole construction differs from that of the secondary radii (e.g. Zschokke and Vollrath 1995).

Data analysis

To test the hypothesis that radii at the top of the web have a larger proportion of their length doubled, I examined the relationship between the angular position of the radius and the proportion of each radius that is doubled with a two-way ANCOVA with spider and web(spider) as factors, and the angular position of the radius and the interaction web \times angular position as covariates. Pearson correlations were performed to examine possible relationships between the average proportion of radii doubling in each web with several other web properties, i.e. diameter of web, number of radii, number of sticky spiral loops and vertical asymmetry of web. To test whether the angles between the radii are indeed larger in the upper part of the web, a Pearson correlation was calculated between the angular position of the radii and the average angle to their two neighbouring radii (normalised for each web). To further identify possible factors influencing the proportion of the doubled part of each radius, a multiple regression was performed on the residuals of the ANCOVA with the following factors: build-order, build-order², and angle to anchor point (square-root transformed). Statistical analyses were performed using the program package SAS 6.08 (SAS Institute 1990).

Nomenclature

'Single' or 'single stranded' thread refers to a thread consisting of one strand with two fibres simultaneously produced by the two spinnerets of the spider (Peters 1990). 'Doubled' or 'double stranded' thread refers to a thread consisting of two strands with two fibres each, giving a total of four fibres. Doubled threads are originally produced as single stranded threads, followed by later addition of a second strand with another two fibres. Nomenclature of orb-web elements follows Zschokke (1999). Angular positions of the radii were expressed in degrees. A radius leading vertically up from the hub to the top of the web was assigned an angular position of 0°, a radius going straight down was assigned an angular position of 180°. Left- and right-hand sides of the web were not differentiated.

Results

A detailed analysis of the movement pattern confirmed the dip in the track of *Z. diodia* during construction of the secondary radii. Additionally, it was found that this dip was always linked to a slowing down of the spider's movement (Fig. 1). A frame by frame analysis of a video recording (resolution 25 fps) of horizontal radius constructions revealed that the spider stops for about 0.5 s before dropping down a short distance, resulting in the dip in the track mentioned above.

Observations of single radii by SEM revealed a transition from double stranded (in the outer part of the web) to single stranded at the position where the spider had slowed down and then dropped down during construction (Fig. 2). Such transitions were only found at these positions. Based on this information, I conclude that *Z. diodia* – unlike most other araneid spiders –

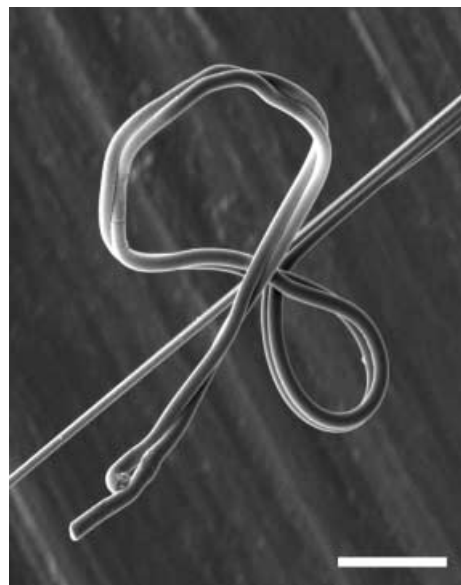


Fig. 2 Scanning electron micrograph of a transition of a radius from double-stranded (*top right*) to single-stranded (*bottom left*). Each strand consists of the two fibres produced simultaneously by the two spinnerets of the spider. One of the fibres of the continuous strand is only barely visible since it is largely hidden behind the other fibre. Scale bar = 5 μ m

incorporates a part of the provisional radius into the definitive radius, thus producing a definitive radius which is doubled on the outer part and single on the inner part (Fig. 3). No additional fusing threads were found between the two strands, neither at the points of transition, nor further out. The exact way the strands are fastened to each other remained unclear. In the taut strands, the diameter of the fibres was observed to be smaller than in the loose strand. This is probably a direct result of the tension in the taut strand, since the diameters of the fibres in the discontinuous strand change in the region where they detach from the continuous strand.

The position of the transition varied greatly among the radii of each web and also between webs (Figs. 4, 5). The results of an ANCOVA confirmed the hypothesis that the radii in the upper part of the web have a larger proportion of their length doubled (Table 1, Angle). Furthermore, there were significant differences in the average amount of doubling between spiders (Spider), but not among the webs built by the same individual [Web (Spider)]. The relationship between the proportion

Table 1 Summary of the ANCOVA testing the influence of the angular position of the radius (Angle) on the proportion of the radius that is doubled. $r^2 = 0.532$

Source	<i>df</i>	SS	MS	<i>F</i>	<i>P</i>
Angle	1	10805.4	10805.4	134.21	<0.0001
Spider	5	8007.5	1601.5	19.89	<0.0001
Web (Spider)	11	670.0	60.9	0.76	0.6837
Web \times Angle	16	895.2	55.9	0.69	0.8003
Residual	554	44603.8	80.5		

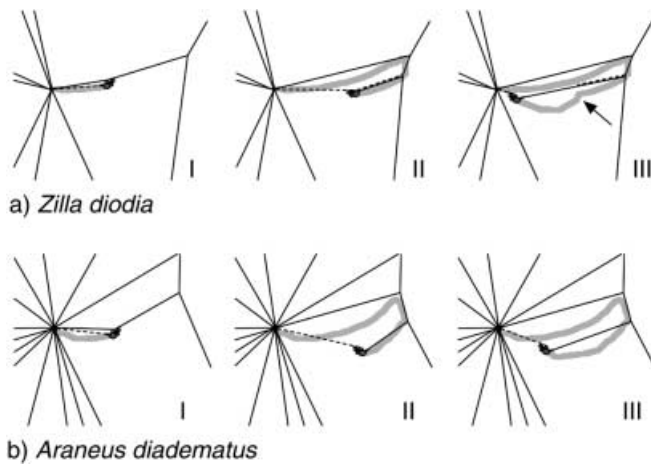


Fig. 3a, b Comparison of radius construction between *Zilla diodia* and *Araneus diadematus*. Both species walk out along an existing radius, trailing the provisional radius (dashed line) behind (I). When they reach the frame, they walk down along the frame and attach the provisional radius. After attaching the provisional radius, *A. diadematus* immediately cuts the provisional radius and reels it up as it returns to the hub producing the definitive radius (bII, bIII), whereas *Z. diodia* walks back along the provisional radius – simultaneously merging it with the definitive radius – until roughly half way back to the hub (aII) where it breaks the provisional radius and returns to the hub (aIII). When the spider breaks the provisional radius, it drops down a little bit, producing a dip in the recorded track (arrow). Black lines show threads, grey lines represent the track of the spider

of each radius that is doubled and its angular position did not differ between webs (Web \times Angle).

I found no correlation between the average amount of doubling and other web properties, i.e. diameter of web, number of radii, number of sticky spiral loops and vertical asymmetry of web ($n=17$, $P>0.36$ in all cases).

The correlation between the angular position of a radius and the average angle to its neighbouring radii was very strong ($\rho=-0.658$, $n=588$, $P<0.0001$), indicating that the angles between the radii were indeed larger in the upper part of the web. Tested separately for each web, all correlations were negative and all but one significant ($n=17$).

The multiple regression performed to identify additional factors that may influence the proportion of each radius that is doubled explained about 17% of the remaining variation (Table 2). The strongest factors were those related with build-order. The positive correlation with build-order indicates an increase in the proportion

Table 2 Summary table of the multiple regression on the residuals of the ANCOVA shown in Table 1. $r^2=0.175$

	Coefficient	SE	<i>t</i>	<i>P</i>
Intercept	-27.970	2.763	-10.12	<0.0001
Build-order	52.150	5.589	9.33	<0.0001
Build-order ²	-27.503	3.026	-9.09	<0.0001
Angle to anchor point	1.538	0.243	6.33	<0.0001

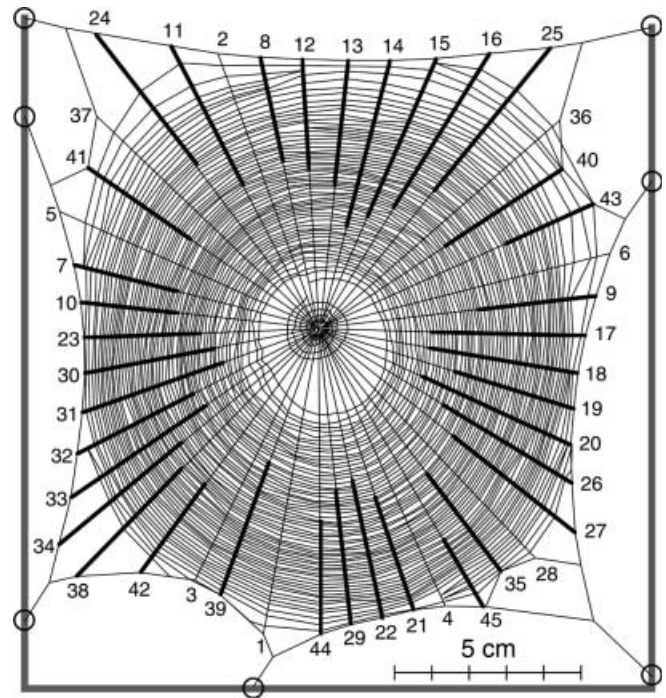


Fig. 4 Example of a web of *Z. diodia*. Bold lines along the radii indicate length of doubled thread. Radii without any bold part are primary radii not analysed in this study. Numbers indicate order of radius construction, circles denote anchor points

of doubling during radius construction, whereas the negative correlation with build-order² indicates a convex relationship. We can therefore conclude that the first radii built and to a lesser degree those built at the end of radius construction had a smaller proportion doubled than those built in between. The analysis further suggested that radii built close to an anchor point had a relatively small proportion of their length doubled.

Discussion

The results of my study showed that *Z. diodia* not only optimises the radius structure by doubling the radii at the periphery of the web where the tension within a radius is higher, it also adjusts the proportion of each radius that is doubled in such a way that the radii towards the top of the web – which are known to be under the highest tension – have a larger proportion of their length doubled compared to those towards the bottom of the web. There is furthermore some evidence that the proportion of doubled thread in each radius is lower in the first and the last radii built, compared to those built in between and that this proportion is also influenced by the proximity of the radii to the nearest anchor point.

Compared to radii that are entirely single stranded, the partially doubled radii in the web of *Z. diodia* have the advantage that their outer part is reinforced without the necessity to produce thicker threads. Compared to radii that are doubled throughout, the partially

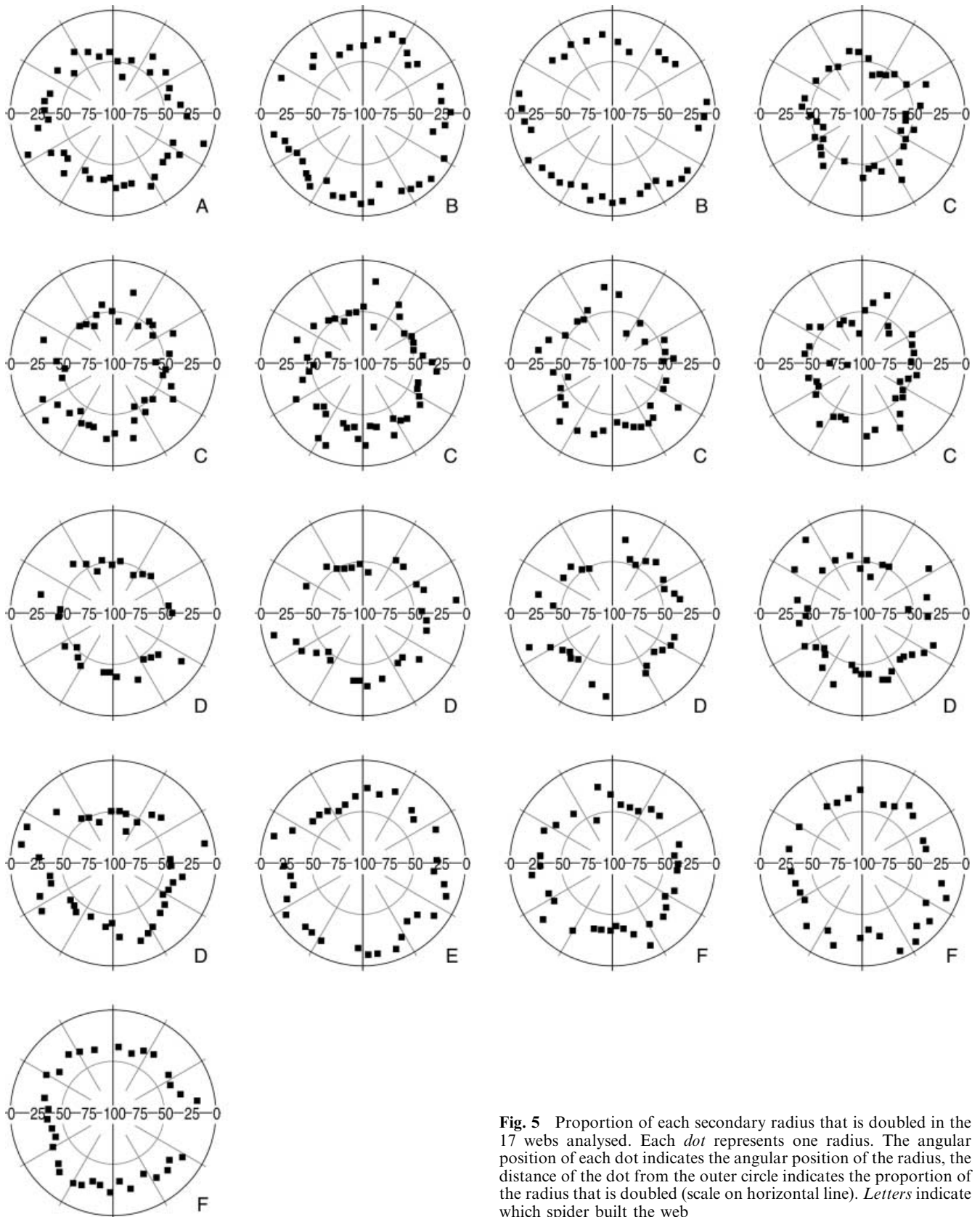


Fig. 5 Proportion of each secondary radius that is doubled in the 17 webs analysed. Each *dot* represents one radius. The angular position of each dot indicates the angular position of the radius, the distance of the dot from the outer circle indicates the proportion of the radius that is doubled (scale on horizontal line). *Letters* indicate which spider built the web

doubled radii have the advantage that it is probably easier for the spider to adjust their tensions and that the radii are less stiff, an important property for the absorption of the kinetic energy of prey (Denny 1976; Lin et al. 1995). These advantages seem to outweigh the disadvantages of a more complicated behaviour and of the resulting increase in construction time of about 1 s per radius, equivalent to about 5% of the radius construction time or about 1% of the total web construction time.

My results on the proportion of each radius that is doubled confirm the hypothesis that radii at the top, which have larger angles between them and are therefore on average under higher tension, have a larger proportion of their length doubled than radii at the bottom of the web. This suggests that *Z. diodia* adjusts the proportion of each radius that is doubled to the overall tension in that radius.

The results of the multiple regression suggest that the first radii built and to a lesser degree those built at the end of radius construction have a smaller proportion of their length doubled than those built in between. If we assume that the proportion of each radius that is doubled reflects the tension in the radius, radii built early and late are under weaker tension than those built in between. When the early radii are built, only few other radii are already in place. If the spider would put any one of these radii under high tension, it would risk deforming the construction. During the construction of the last radii, the spider needs to balance finely the forces at the hub. Earlier results suggest that the spider does not plan the construction of the last radii, it rather circles the hub and inserts a radius wherever there is a large gap between two existing radii (Peters 1937; Reed 1969; Zschokke 1995). It is therefore not reasonable to put the last radii under high tension, since an additional radius under high tension which is not counterbalanced by another radius on the opposite side of the web might endanger the balance of tensions at the hub. This in turn suggests that the spider not only measures the size of the gap between the existing radii but may also need to measure their tensions in order to adjust properly the tension in the new radius.

The results of the multiple regression also suggest that radii close to anchor points have a smaller proportion of their length doubled than those further away from the anchor points. This is somewhat counter-intuitive: when the web is deformed under load, radii near the anchor points could be expected to be under higher tension than those between the anchor points, because the frame thread is less flexible near the anchor points. We would therefore expect the radii near the anchor points to have a larger proportion of their length doubled. On the other hand, radii near the anchor points should be less stiff than those between the anchor points, because they need to expand more upon prey impact, and should therefore have a smaller proportion of their length doubled. My results suggest that the latter reason is more important than the first one.

The question of single, doubled or partially doubled radii should not be discussed in isolation from other aspects of orb web structure and construction. Doubled radii (as built by uloborid spiders; Eberhard 1982) are stiffer than single radii. This probably goes in line with the uloborid sticky spiral which is also stiffer compared to the araneid sticky spiral (Köhler and Vollrath 1995), since the stiffness of the two components should be matched (Eberhard 1981). In terms of radii doubling, *Z. diodia* seems to be intermediate between other araneid spiders and uloborid spiders. For other web parameters, however, this is not the case. Uloborid spiders are known to build webs with a low number (<20) of sticky spiral loops, whereas the webs of most araneid spiders have 20–40 loops (e.g. Wiehle 1927; Tyshchenko 1986), and webs built by *Z. diodia* often feature more than 50 sticky spiral loops; the webs used in this study had on average 52.8 (SD=7.3) sticky spiral loops.

During the construction of a single or partially doubled radius, the spider reels up the remains of the provisional radius and deposits them at the centre of the hub, where they can be seen as quite conspicuous balls of silk (e.g. Witt et al. 1968). At the end of orb-web construction, araneid orb-weavers will then remove the inner part of the hub together with the remains of the provisional radii, whereas uloborid spiders and nephiline spiders (which build radii in yet another way; Hormiga et al. 1995; Zschokke and Vollrath 1995; Bleher 2000) do not remove the inner part of the hub. Eberhard (1981) listed several possible reasons, related to the tensions in the radii, why spiders remove the inner part of the hub. I suggest that the removal of the conspicuous silk balls produced during the construction of single or partially doubled radii may also be a reason for the removal of the inner part of the hub.

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