Orb web architecture of *Wixia abdominalis* O. Pickard-Cambridge, 1882 (Araneae: Araneidae): intra-orb variation of web components

Gabriel Máximo Xavier[1], **Rafael Rios Moura**[1] and **Marcelo de Oliveira Gonzaga**[2]:   [1]Pós-graduação em Ecologia e Conservação de Recursos Naturais, Universidade Federal de Uberlândia, Uberlândia, MG, Brazil; E-mail: gabriel.m.x@hotmail.com; [2]Instituto de Biologia, Universidade Federal de Uberlândia, Uberlândia, MG, Brazil.

Abstract.   The distribution of sticky spirals and radii within orb webs is usually not uniform. Distinct patterns of silk investment in inner and outer portions of the orb may influence the web's capacity to stop and retain specific prey types. Several incidental and functional hypotheses have been proposed previously to explain the variation in web patterns. Herein, we describe the webs built by spiders of the monospecific genus *Wixia* O. Pickard-Cambridge, 1882 (Araneidae) and evaluate web-building hypotheses, considering the presence of a free-sector, vertical symmetry, sticky spiral distribution and radii spacing. Because all information available on the ecology of *Wixia* is restricted to the species that were subsequently transferred to other araneid genera, there is no information about the webs of the last species remaining in this genus, *Wixia abdominalis* O. Pickard-Cambridge, 1882. We observed that this spider builds complete orbs, but some individuals add a free-sector, remaining resting on a twig above the orb and holding a signaling thread. On the upper part of the orb the spiral distribution follows the pattern of increasing densities from the edge to the hub. However, on the lower part of orbs, this pattern is seen only in complete webs; in contrast, in webs with a free-sector the pattern of spiral distribution observed in lower part of webs is homogeneous from the edge to the hub. We discuss possible implications of the web structure of *W. abdominalis* for prey capture and how the incidental and functional hypotheses may explain the patterns of spiral spacing observed in this species.

Keywords: Free-sectors, sticky spiral spacing, prey capture, web-building hypotheses

Webs spun by araneoid ecribellate orbicularians are composed of distinct types of silk, each one with particular mechanical properties and functions (Blackledge et al. 2011). The non-adhesive radii, for example, are responsible for stopping prey by absorbing its kinetic energy upon impact with the web (Sensenig et al. 2012). Sticky spirals, on the other hand, retain prey in the web long enough to the spider to move to the interception site and subdue the prey (Blackledge & Zevenbergen 2006). In addition, spiders may regulate vertical displacement of the hub from the web's geometric center to increase the probability of prey capture (Nakata & Zschokke 2010; Zschokke & Nakata 2010; Blackledge et al. 2011). Therefore, measurements of the spacing of sticky spirals and radii, and vertical asymmetry of the web provide important information regarding the spider's foraging behavior.

Despite their apparent geometrical uniformity, there is significant inter- and intraspecific variation in orb web design (e.g., presence and types of shelters; free sectors; patterns of symmetry; presence, shape, and composition of stabilimenta) (Manicom et al. 2008; Blackledge et al. 2011; Gonzaga & Vasconcellos-Neto 2012; Eberhard 2014). For example, sticky spiral distribution is usually not uniform from the edge to the hub within orb webs (Herberstein & Heiling 1999; Zschokke 2002; Eberhard 2014). Moreover, the distribution of sticky spirals typically varies between the upper and lower parts of the web, as does distribution of radii (Zschokke & Nakata 2015). These features are, in some way, linked with web dimensions. For example, the more extensive the web part (upper or lower) is, the greater the spacing between the spirals and the more parallel the radii will be (Zschokke & Nakata 2015). However, the upper part typically has a lower density of sticky spirals, and the radii are less parallel than are those in the lower part. This difference can persist even in symmetric webs (Zschokke & Nakata 2015).

Several incidental and functional hypotheses have been proposed to explain intra-orb variation in sticky spiral and radii distribution (see Eberhard 2014), as well as differences in investment between the upper and lower parts of the web. Incidental hypotheses are explanations associated with physical or physiological constraints during web building (Eberhard 2014). The first incidental hypothesis, hereafter "Peters' segment rule," states that the gradual decrease in sticky spiral spacing from the edge to the hub is a consequence of the geometric spacing between adjacent radii, which decreases in the same direction. Therefore, spiders would adjust sticky spiral spacing based on the distance between adjacent radii (Peters 1954). According to Peters' segment rule, it is expected that sticky spiral spacing always increases from the hub to the edge, and this increase should be greatest where adjacent radii are less parallel. The second incidental hypothesis is referred to as the "energetic constraint hypothesis" (Herberstein & Heiling 1999). Because spiders usually have to lift their abdomens to make attachments above the hub, the greater spiral spacing in the upper part of the web is a result of the larger energetic cost imposed during the web building in that part. As the spider fixes the spirals higher up, the greater is the energy expenditure, because the turns are larger than web part bellow the hub. According to this hypothesis, therefore, a larger increase from the hub to the edge in sticky spiral spacing and greater distances between spirals in the upper part compared to the lower part of the web is expected. Additionally, asymmetric webs with smaller upper parts are expected to be common, because building the upper part is energetically more expensive.

Functional hypotheses consider that edge-to-hub differences in sticky spiral spacing improve the foraging efficiency (Eberhard 2014). The first functional hypothesis, hereafter the "attack-time hypothesis," is based on the assumption that

spiders would invest more silk in web areas where they are more likely to capture prey successfully (Heiling & Herberstein 1998). Therefore, larger investment in sticky threads near the hub is expected because these locations can be reached faster by spiders. A higher investment in the lower part of the web is also expected because orb-weavers usually rest facing downward and run faster in this direction (Heiling & Herberstein 1998). This hypothesis is supported by the vertical asymmetry of several orb webs, which typically have a longer bottom part (below the hub) than top part (Heiling & Herberstein 1998; Herberstein & Heiling 1999; Zschokke 2002; Hesselberg 2010; Nakata 2012). The "radii-density hypothesis," on the other hand, suggests that spiders invest more silk in sticky spirals in segments with a greater capacity to stop prey. Therefore, the high investment in sticky spirals follows the density of radii (Zschokke 2002). Thus, a higher investment in sticky spirals near the hub and in the web part where radii are more parallel is expected. Finally, there are two additional hypotheses, the "sticky spiral entanglement" (Eberhard 2014) and the "prey tumbling" hypotheses (de Crespigny et al. 2001). The first is concerned with the idea that larger distances between sticky spirals near the edge may assure a lower chance of contact between adjacent loops because of the disturbance caused by the wind. The latter hypothesis states that smaller spaces between loops at the innermost area above the hub and outermost area below the hub of some spider species' webs could increase capture success when prey tend to escape by tumbling in vertical orb webs.

Tests of these hypotheses are restricted to a few common model species (Eberhard 2014). Therefore, the extension of evaluation to other orb web weavers must provide information on each hypothesis. In this study, we describe the orb web of *Wixia abdominalis* O. Pickard-Cambridge, 1882, and discuss the implications of web architecture in the scope of the functionality of its components. Stowe (1978) first described the unusual "asterisk" web of a *Wixia* species. According to him, the webs of *W. ectypa* (Walckenaer, 1841) presented a simple hub and typically only eight radii. Adhesive spirals were absent and spiders preyed exclusively on pedestrian arthropods. This adaptation to prey-specific capture is often mentioned in the literature on orb webs (Blackledge et al. 2011) and is attributed in general to *Wixia*. However, with the exception of *W. abdominalis*, all 49 species previously included in *Wixia* have been transferred to other genera, mostly to *Ocrepeira* Marx, 1883, and also to *Acacesia* Simon, 1895, *Alpaida* O. Pickard-Cambridge, 1889, *Wagneriana* F.O. Pickard-Cambridge, 1904, or considered as *nomen dubium* (*Wixia proxima* Mello-Leitão, 1940) (World Spider Catalog 2015). Data available in the literature on *W. abdominalis* are restricted to its morphology (Pickard-Cambridge 1882; Levi 1993) and to a few records of distribution in Guyana, Brazil (Pirenópolis, State of Goiás) and Bolivia (Levi 1993). Herein, we present the first record of the web pattern of the sole species remaining in the genus *Wixia*, showing that there is no impressive modification from the conventional orb web structure, such as those described in asterisk webs.

METHODS

Webs of *W. abdominalis* were located in a *Eucalyptus* plantation in Fazenda Nova Monte Carmelo (18°45′11″S,

47°51′28″W), Estrela do Sul, MG, Brazil. Areas covered by *Eucalyptus* were interspersed by fragments of Cerrado vegetation, but our surveys were restricted to regions within the monoculture. All webs were located at night during monthly expeditions and photographed after being lightly coated with cornstarch (see Eberhard 1976). Expeditions were conducted from August to December 2014 and surveys were restricted to the period from 19:00 to 0:00. All web measurements were performed from the photographs using the software ImageJ (National Institutes of Health, USA).

Web asymmetry (departure of shape of the web from a circle) and hub asymmetry (displacement of the hub from the web's geometric center) indices were evaluated according to Blackledge and Gillespie (2002). For the first index, positive values indicated vertically elongated webs. For the second index, positive values indicated upwardly eccentric webs. In both indices, values close to zero indicated symmetric webs.

Procedures to evaluate spacing of sticky spirals and radii were established following Eberhard (2014). We calculated the distance ratio between adjacent radii for each part of the webs, upper and lower. This ratio was obtained by dividing the distance between two adjacent radii at the outer edge by that of adjacent radii at the inner edge of the capture zone. We selected three pairs of adjacent radii for each part of the web (three pairs nearest to 0° and three pairs nearest to 180°), and used these to measure distance ratios. Then, we averaged the values for each part of the web. Ratios close to one indicate parallel radii. The distance ratios between adjacent radii in the upper and lower part of the webs were compared using a paired *t*-test.

We measured the distances between all the spiral loops on the most vertical radius for each part of the webs, upper and lower. These distances were standardized by dividing each measurement by the median value of distances on that radius. The standardized measure of distance between spiral loops was plotted against the relative distance to the hub, defined as the fraction of the number of spaces between loops attached to that radius. The value of one was closest to the hub. We conducted a linear regression analysis of standardized spaces between loops of sticky spirals and the relative distance from edge-to-hub. In this regression, we excluded 20% of these standardized spaces in the inner and outer portions of the capture zone and used the 60% in the middle portions. We used this approach, because these innermost and outermost portions have spaces between spiral loops especially smaller or greater in many species, generating non-linear data (Eberhard 2014). We compared the spaces of these portions with the middle portion, using Friedman paired tests and Nemenyi *post-hoc* tests (see Pereira et al. 2015) by means of the 'PMCMR' R package (Pohlert 2014). We performed data analysis in R software, version 3.3.2 (R Development Core Team 2016).

Previously, we observed that some individuals constructed webs with a free-sector. These spiders remain out of the hub, holding a signal line connected to the hub from a position on a branch of *Eucalyptus* (Fig. 1D). The presence of free-sectors may imply behavioral changes during prey capture and may impose constraints on other web components. Hence, we evaluated webs with and without free-sectors separately. We performed analyses of covariance (ANCOVA) in order to
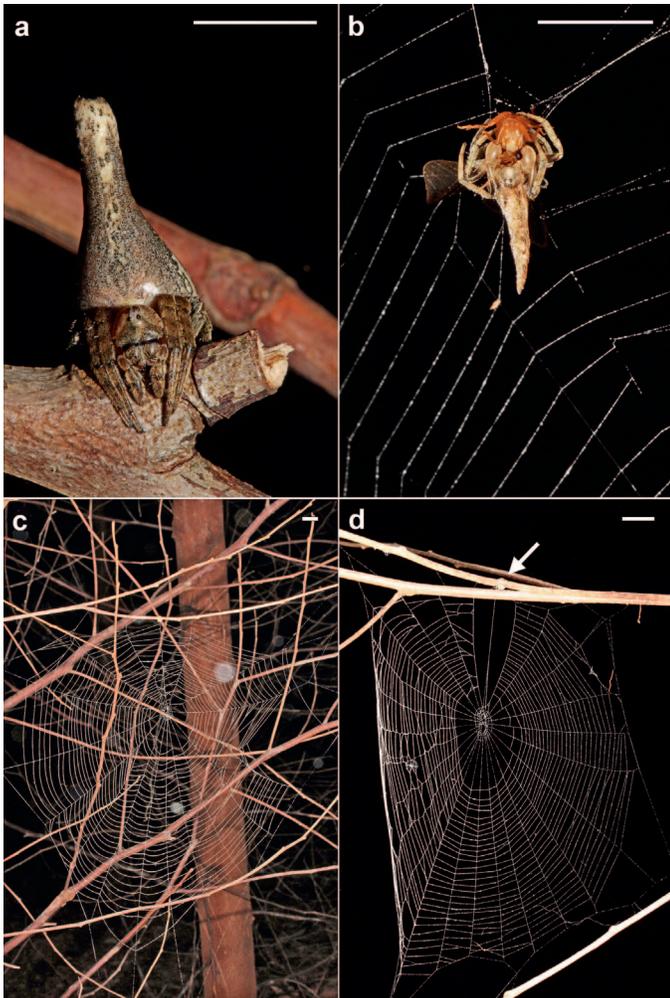
Figure 1.—*Wixia abdominalis*. (A) Resting position on an *Eucalyptus* branch. (B) Subadult male capturing a termite. (C) Web without free sector. (D) Web with a free-sector. The arrow indicates the spider position. Scales: A, B: 5mm; C, D: 1cm.

assess if: (1) the linear regressions differ between webs with and without free-sector, (2) the linear regressions differ between upper and lower part of all webs. To use parametric tests, we assessed the assumptions of normality and homoscedasticity by means of graphical analysis of residual distribution.

RESULTS

Individuals of *W. abdominalis* are active nocturnally, ingesting their webs at dawn. During the day, the spiders remained motionless in a cryptic position on the branches of *Eucalyptus* trees (Fig. 1A). In this position, they resembled a piece of broken wood.

We recorded webs of 28 juvenile individuals (all at antepenultimate or penultimate instars, weighing 0.024 ± 0.007g, mean $\pm$ se, min. 0.0059g and max. 0.1819g) and two adult females (weighing 0.047 and 0.074g). All webs appear to be more or less vertically oriented (Fig. 1B–D). Some webs spun by juveniles included a free-sector ($n = 16$). The angle of

signal lines in the free sectors deviated slightly from vertical orientation ($16.69° \pm 4.02$, mean $\pm$ se) . In these webs, spiders remained on a branch located immediately above the orb at night, holding a thread connected to the web hub. In webs without a free-sector ($n = 14$), spiders waited for prey interception at the hub, facing downward. However, the frequency of these behaviors was not quantified herein. Webs with and without free-sectors were analyzed separately, because there was no information on how or whether this variation in orb design would influence other web parameters.

Juvenile individuals built slightly vertically asymmetric webs (web asymmetry index = 0.119 ± 0.03) and webs with hubs were displaced upward (hub asymmetry index = 0.325 ± 0.03). The two webs built by adults were more vertically asymmetric (web asymmetry index = 0.328 and 0.273), and their hubs were displaced upward (hub asymmetry index = 0.494 and 0.129).

From the analysis of the webs of immature and adults pooled, the average distance ratio between adjacent radii was 7.15 ± 0.404 in the upper part and 5.96 ± 0.45 in the lower part of the webs ($n = 29$). The upper part had greater ratios than the lower part of the webs (paired *t*-test: $t = 2.818$, $P = 0.009$). Therefore, in the upper part, the radii were less parallel and the difference in radii density between inner and outer portions was more pronounced than in the lower part of the webs. Webs with and without free-sectors were not different in distance ratios between adjacent radii in the upper (*t*-test: $t = -1.569$, $P = 0.128$) or lower part of the webs (*t*-test: $t = -1.753$, $P = 0.091$).

The tendency of increasing sticky spiral spacing from the hub to the edge of the capture zone was confirmed (Tables 1, 2, Fig. 2). However, when only webs with free-sectors were analyzed, a uniform pattern of sticky spiral spacing in the lower part was detected (Table 2, Fig. 2). In the upper part of the webs, the increase of sticky spiral from the hub to the edge was more accentuated in webs with free-sectors than webs without free-sectors (ANCOVA: $F_{1,835} = 6.882$, $P < 0.01$). In the lower part of webs, the increase of sticky spiral spacing from the hub to the edge was more accentuated in webs without than webs with free-sectors (ANCOVA: $F_{1,360} = 7.108$, $P < 0.01$). In general, the increase in sticky spiral spacing from the hub to the edge was more accentuated in the upper part than in lower part of the webs (ANCOVA: $F_{1,119} = 30.601$, $P < 0.001$), but the 20% outermost distances between sticky spirals in the upper and lower web parts were similar ($t = 0.410$, df = 26, $P = 0.685$).

DISCUSSION

Wixia abdominalis webs were vertically elongated with upwardly displaced hubs. The radii were always less parallel in the upper part and there was increasing sticky spiral spacing from the hub to the edge of the capture zone. The increase was larger in the upper part. However, webs presenting a free-sector exhibited uniform spiral spacing. Despite that, we observed a similar enlargement in the 20% outermost spacing in both parts of the webs. These results did not fit well in any single hypothesis proposed to explain differential investment in distinct web segments. Based on our results, more than one hypothesis could be used to explain web architecture of *W. abdominalis*.

Table 1.—Analyses of differences in the sticky spiral standardized spaces between the portions of orbs: the outer (0–20% of spirals from the edge to the hub), the middle (20–80%) and the inner (80–100%). We assessed the difference between the means of standardized spaces of each web portion using Friedman paired tests. The letters indicate differences between orb portions in the Nemenyi *post-hoc* tests with $P < 0.05$, and n corresponds to the number of webs.

Web	n	Means ± SD			Friedman test	
		Outer	Middle	Inner	χ^2	P
Upper						
With free-sector	16	1.55 ± 0.70 a	1.05 ± 0.45 b	0.85 ± 0.37 b	22.87	< 0.05
Without free-sector	11	1.30 ± 0.66	1.03 ± 0.32	1.02 ± 0.55	3.81	0.14
All	27	1.45 ± 0.70 a	1.04 ± 0.40 b	0.92 ± 0.46 b	24.22	< 0.01
Lower						
With free-sector	16	1.28 ± 0.70 a	1.01± 0.38 b	1.15 ± 0.49 ab	7.87	< 0.05
Without free-sector	11	1.43 ± 0.71 a	1.03 ± 0.35 b	1.03 ± 0.45 b	13.16	< 0.01
All	27	1.34 ± 0.71 a	1.01 ± 0.37 b	1.11 ± 0.47 ab	18.28	< 0.01

According to Peters' segment rule, we would expect sticky spiral spacing to increase from the hub to the edge. In addition, this increase would be greater for segments adjacent to less parallel radii (at the upper part). However, we observed that the 20% innermost spirals of webs were not less spaced than the 60% spirals of the middle part. Another pattern that contradicts Peters' segment rule is the uniform pattern of sticky spiral spacing in the lower part of the web of *W. abdominalis*. Similarly, spiral spacing of other species, including *Nephila clavipes* (Linnaeus, 1767), *Metepeira* sp. F.O. Pickard-Cambridge, 1903, (Eberhard 2014), *Argiope keyserlingi* Karsch, 1878, (de Crespigny et al. 2001), and some *Cyclosa* species Menge, 1866, (Zschokke & Nakata 2015), cannot be explained by this incidental hypothesis.

The "energetic constraint" incidental hypothesis, on the other hand, was partially corroborated by the greater increase in sticky spiral spacing from the hub to the edge in the upper part. However, at the higher distances at the outer segment of the upper part this would be expected. Instead, the webs of *W. abdominalis* showed similar distances between sticky spirals at outer edges of upper and lower web parts. Despite this contradiction, the asymmetric webs observed in *W. abdominalis* and in other species (Herberstein & Heiling 1999) suggest some degree of energetic constraint during web building. Indeed, it was found that spiders spent more energy building the upper part of vertical orb webs than the lower part (Coslovsky & Zschokke 2009). However, it is difficult to accept that variation in sticky spirals could be determined solely by energetic constraints during web building, especially when accounting for the functional value of the uneven distribution of silk (Masters & Moffat 1983).

The greater investment in sticky spirals near the hub and in the lower part of the web is in accordance with the "attack-time hypothesis" (Heiling & Herberstein 1998). *Araneus diadematus* Clerck, 1757, for example, presents a similar web pattern, with spirals evenly spaced below the hub and it can indeed run faster downward (ap Rhisiart & Vollrath 1994). However, *W. abdominalis* has a special condition regarding spider movements during prey capture events. Individuals with a free-sector in their webs remain on the branch located above the orb, holding a signal line, whereas individuals with complete orbs wait at the hub. In the first case, after the detection of movements of an entangled prey, the spider moves first from the resting position at the twig to the hub and then goes to the location of the prey on the web. Therefore, the spider moves for a longer distance to reach the prey. We observed that webs with free-sectors presented a pattern of spacing in the lower part that was more homogeneous than the pattern of the webs without free-sectors. This architecture is not congruous with the scope of "attack-time hypothesis", because spiders are investing in retention further away from themselves. It may be a compensatory mechanism for spiders that rest out of web. Thus, it occurs just in lower part because it is the web part where spiders reach faster. This "compensation hypothesis" provides a theoretic understanding of the function of the uniform distribution of spirals at the lower part of webs with free-sectors; however, behavioral observations during prey capture events are still needed.

Table 2.—Linear regression analyses of standardized sticky spiral spacing and the relative distance from the edge to the hub in the middle portion of the capture zone (between 0.2 and 0.8).

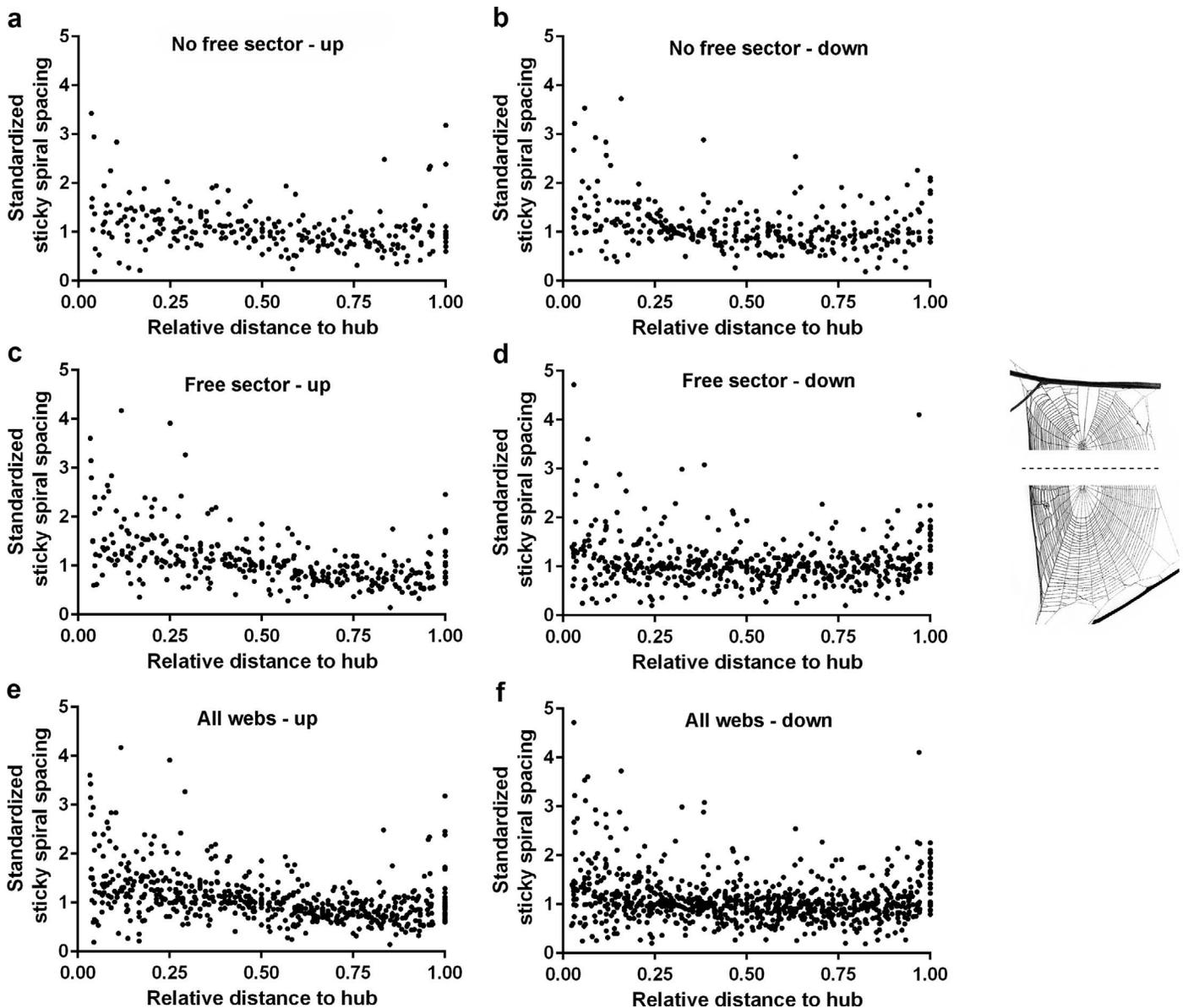| Web part	R^2	F	DF	Equation	P
Upper					
With free sector	0.216	54.921	1, 199	y = -1.223x + 1.668	<0.001
Without free sector	0.167	29.383	1, 147	y = -0.755x + 1.406	<0.001
All	0.192	82.915	1, 348	y = -0.02x + 1.554	<0.001
Lower					
With free sector	0.010	2.864	1, 298	y = -0.217x + 1.114	0.092
Without free sector	0.065	14.554	1, 211	y = -0.478x + 1.25	<0.001
All	0.025	13.149	1, 511	y = -0.33x + 1.174	<0.001

Figure 2.—Edge-to-hub patterns of relative standardized sticky spiral spacing in orb webs of *Wixia abdominalis*. 'Relative distance to the hub' was calculated following Eberhard (2014) and is defined as the ratio between the 'number of sticky loops between the site in the orb and the outer edge of the capture zone' and 'total number of sticky spiral loops from the outer edge to the hub'. The value 1 is the closest to the hub.

The "radii-density hypothesis" was also corroborated by our data, because there was a higher increase in sticky spiral spacing from the hub to the edge in the upper part of the webs, where radii were less parallel. However, according to this hypothesis, we would expect heterogeneity in the pattern of spiral distribution in the lower part of the webs with free-sectors. Similarly, the spiral spacing of other species is also not in complete accordance with this hypothesis, for example, *Nephila clavipes* and *Metepeira* sp., have a higher density of spirals at the edge of their orbs and adopt other strategies to increase the absorption of their prey's kinetic energy, such as the maintenance of auxiliary spirals and division of radii, increasing radii density toward the middle and outer edges of the web (Eberhard 2014). However, these auxiliary structures to absorb kinetic energy are absent in webs of *W. abdominalis*.

Therefore, the uniform pattern of spiral distribution in the lower part of the webs with a free-sector may be a result of an interaction between absorbing kinetic energy (Zschokke 2002) and compensating for the longer distance to the interception site (Heiling & Herberstein 1998).

The "sticky spiral entanglement" hypothesis is contradicted by the observation that spiral spacing was not significantly greater at the edge above the hub than at the edge below the hub. Some spiders may use alternative strategies to reduce web damage from the wind, softening the constraints imposed on its web architecture, such as the reduction of sagging of threads making them stiffer under windy conditions (Vollrath et al. 1997) and changing orb web orientation according to wind direction (Hieber 1984). The "prey tumbling" hypothesis also was not supported by our data, because there was an

enlargement in spiral spacing on the outer edge of the lower part of the webs. However, prey tumbling is highly variable depending on web adhesiveness and prey identity (Zschokke et al. 2006).

In the present study, we recorded the web structure of *W. abdominalis* and observed that it differed dramatically from the patterns previously attributed to the genus *Wixia*. The architecture of the *W. abdominalis* web allowed us to discuss several hypotheses based on differential investment in distinct parts of the web as it applied to the observed characteristics. The web architecture of *Wixia abdominalis* was better explained by the "energetic constraint" incidental hypothesis (Herberstein & Heiling 1999), and "attack time" and "radii density" functional hypotheses (Heiling & Herberstein 1998; Zschokke 2002). Our results are in accordance with the findings of Eberhard (2014) and Zschokke and Nakata (2015) in that different parts of the orb web present different properties and functions. The analysis of interspecific variation in orb web designs and the association of these designs with aspects of the natural history of each species are important to understand the conditions determining each pattern. In addition, our study showed there was relevant intraspecific variation in certain web traits (such as inclusion of a free-sector) that might also influence web design.

ACKNOWLEDGMENTS

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