

RESEARCH ARTICLE

Wind induces variations in spider web geometry and sticky spiral droplet volume

Chao-Chia Wu¹, Sean J. Blamires², Chung-Lin Wu³ and I-Min Tso^{1,2,*}

¹Department of Life Science, National Chung-Hsing University, Taichung 40227, Taiwan, ²Department of Life Science, Tunghai University, Taichung 40704, Taiwan and ³Center for Measurement Standards, Industrial Technology Research Institute, Hsinchu 30011, Taiwan

*Author for correspondence (spider@thu.edu.tw)

SUMMARY

Trap building by animals is rare because it comes at a substantial cost. Using materials with properties that vary across environments maintains trap functionality. The sticky spiral silks of spider orb webs are used to catch flying prey. Web geometry, accompanied by compensatory changes in silk properties, may change across environments to sustain web functionality. We exposed the spider *Cyclosa mulmeinensis* to wind to test whether wind-induced changes in web geometry are accompanied by changes in aggregate silk droplet morphology, axial thread width or spiral stickiness. We compared: (i) web catching area, (ii) length of total silks, (iii) mesh height, (iv) number of radii, (v) aggregate droplet morphology and (vi) spiral thread stickiness, between webs made by spiders exposed to wind and those made by spiders not exposed to wind. We interpreted co-variation in droplet morphology or spiral stickiness with web capture area, mesh height or spiral length as the silk properties functionally compensating for changes in web geometry to reduce wind drag. Wind-exposed *C. mulmeinensis* built webs with smaller capture areas, shorter capture spiral lengths and more widely spaced capture spirals, resulting in the expenditure of less silk. Individuals that were exposed to wind also deposited larger droplets of sticky silk but the stickiness of the spiral threads remained unchanged. The larger droplets may be a product of a greater investment in water, or low molecular weight compounds facilitating atmospheric water uptake. Either way, droplet dehydration in wind is likely to be minimized.

Key words: environmental stress, spiral silk properties, orb webs, *Cyclosa mulmeinensis*.

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INTRODUCTION

The use of traps to capture prey has evolved independently in arachnids, larval dipterans, trichopterans and neuropterans (Viviani et al., 2002; Hansell, 2005; Scharf et al., 2011). The principal advantage of building a trap is that once the trap is built, prey is captured at minimal expense of foraging time and energy (Lucas, 1985; Willis et al., 2011). The principal costs of trap building are the pre-investment in the raw materials and the time and energy required to build, repair and maintain it (Craig, 2003; Hansell, 2005; Hansell and Ruxton, 2013). Thus, for traps to be profitable they must be composed of readily synthesizable materials that sustain their functionality for prolonged periods (Hansell, 2005). Additionally, as the traps may be exposed to spatially and temporally variable environments (Scharf et al., 2011), it is likely that the physical and chemical properties of the building materials will vary across different environments (Fudge et al., 2003; Hansell, 2005; Liao et al., 2009; Hansell and Ruxton, 2013).

Silk is a material consisting predominantly of protein that is secreted by some organisms. It has been a key innovation facilitating the building of aerial traps among spiders, larval dipterans and trichopterans (Craig, 1997; Craig, 2003). The type of silk used differs between spiders, dipterans and trichopterans but they all serve the function of absorbing the energy of moving prey (Craig, 2003; Hansell, 2005; Willis et al., 2011). The use of sticky silk by spiders is considered a key innovation that facilitated the radiation of >9000 species of web builders (Craig, 2003; Blackledge et al., 2009). Two types of sticky silk are used by orb-web spiders: (1) cribellar sticky

silk, a 'wooly' silk used by the Deinopoidea, who have retained these ancestral capture silks, and (2) the more derived ecribellar sticky silk, which is used by most other orb-web spiders (Blackledge et al., 2009). Ecribellar sticky silk, or spiral silk, is secreted from a single flagelliform spigot and two flanking aggregate spigots, which form a spigot 'triad' (Opell et al., 2011a). The viscous aggregate silk and solid flagelliform fibers are secreted simultaneously so the flagelliform fiber is spun doused with viscous silk (Sahni et al., 2011). As the silk is spun, surface tension forces result in the coalescence of the viscous aggregate silk into droplets along the flagelliform thread so as to superficially resemble beads along a string (Kane et al., 2010; Opell and Hendricks, 2010; Sahni et al., 2011; Sahni et al., 2012).

Aggregate silk is a mixture of dissolved silk proteins, glycoprotein and low molecular weight compounds (LMWCs) (Vollrath and Tillinghast, 1991; Vollrath and Knight, 2001). The stickiness of spiral silk is conferred by the concentration of glycoproteins within the aggregate silk and the extensibility of the flagelliform threads (Bontrone et al., 1992; Sahni et al., 2010; Opell et al., 2011b). The well-hydrated aggregate silk increases flagelliform thread extensibility by supercontracting (plasticization of the thread accompanied by a loss of protein alignment) the spiral thread (Guinea et al., 2010). The highly extensible flagelliform thread dissipates much of the kinetic energy when prey strike the spirals (Opell and Hendricks, 2010; Sahni et al., 2010; Tarakanova and Buehler, 2012), while the glycoproteins in the aggregate silk serve to retain the prey once it has been captured (Sahni et al., 2011; Tarakanova and Buehler, 2012). The LMWCs

facilitate water uptake from the environment to the viscous droplets, thereby keeping the sticky spirals hydrated (Vollrath et al., 1990; Townley et al., 1991; Edmonds and Vollrath, 1992; Sahni et al., 2010); the greater the LMWC concentration, the greater the uptake of water from the atmosphere (Sahni et al., 2011). The LMWCs also influence spiral stickiness by keeping the glycoproteins soft and 'tacky', a property implicit in the retention of prey (Sahni et al., 2011; Opell et al., 2011b).

Spider orb webs are placed into spatially and temporally unpredictable environments, which may induce physical and chemical property changes in the silks (Blamires et al., 2012). Orb-web spiders, accordingly, often build webs with varying geometries across environments (Sandoval, 1994; Vollrath et al., 1997; Liao et al., 2009; Blamires et al., 2011). Orb-web spiders may modulate the performance of their webs by modifying one or a combination of the following parameters: (i) size of the capture area, (ii) mean spacing between sticky spiral threads, or mesh height (although spider webs are not 'meshed', we use this term to represent capture spiral spacing because it is the most commonly used term among comparable studies), or (iii) the number of spirals or radii used (Sandoval, 1994; Vollrath et al., 1997; Tso et al., 2007; Liao et al., 2009; Blamires, 2010). As mesh height influences the size of the prey that can be retained by orb webs (Herberstein and Heiling, 1998; Blackledge and Zevenbergen, 2006), mesh height may change in response to expected changes in the type or size of prey present (Sandoval, 1994; Herberstein and Heiling, 1998; Blamires, 2010; Blamires et al., 2011). Environmentally induced changes in the stickiness of the spirals (Opell et al., 2011a; Sahni et al., 2011) may, however, also be associated with changes in mesh height as a means to maintain the ability to effectively absorb the kinetic energy of intercepted prey (Blackledge and Hayashi, 2006).

Wind is an example of an unpredictable environmental parameter that spiders may face and must be accounted for by an adjustment in web building and/or prey-catching behaviors (Vollrath et al., 1997; Liao et al., 2009; Turner et al., 2011; Cranford et al., 2012). Indeed, orb-web spiders that have been exposed to wind substantially alter the geometry of their webs. Such geometric alterations are characterized by a reduction in the number of radial threads in their webs, smaller web capture areas, greater spacing between spirals and a reduction in the length of the sticky spiral thread (Vollrath et al., 1997; Liao et al., 2009). In the orb-web spider *Cyclosa mulmeinensis*, exposure to wind also induces the deposition of considerably stiffer radial threads, which, combined with a reduction in web capture area and spiral thread length, serves to reduce wind drag on the web and minimize tearing (Liao et al., 2009). The likely cost of such changes in web geometry and silk properties is a reduction in the number of prey that can be effectively caught (Blackledge and Zevenbergen, 2006; Blamires et al., 2011; Tarakanova and Buehler, 2012).

As evaporative water loss across organic membranes substantially increases with the rate of air flow (Mellanby, 1934; Willmer et al., 2000), water is lost from the sticky spiral silks more readily when they are exposed to wind than when they are in still air. It thus seems that an additional cost of placing an orb web into wind is a high risk of silk property variation through dehydration. Accordingly, in order to maintain the efficiency at which the web absorbs and dissipates the kinetic energy of intercepted prey and retains any intercepted prey, orb-web spiders exposed to windy conditions should use silk with some degree of resistance to dehydration. For instance, wind-exposed spiders might reduce dehydration from the spiral threads by secreting aggregate silk with specific properties: silk that forms larger droplets so the proportion of droplet surface area that is exposed to wind is reduced, or silk with droplets of greater LMWC concentration, thus

shifting the droplet-atmospheric water exchange equilibrium (Vollrath et al., 1990; Townley et al., 1991; Edmonds and Vollrath, 1992; Opell et al., 2011a).

Spiders make decisions about the geometry and properties of a web they will build at a particular location based on their previous experiences at the location (Venner et al., 2000; Blamires, 2010). These experiences are likely to be assessed by their prey-capture experiences (Heiling and Herberstein, 1999; Venner et al., 2000; Mestre and Lubin, 2011), or by the quality and quantity of specific stimuli (Blamires et al., 2011). The stimuli received may include a combination of web-borne tactile stimuli detected by the strain-sensitive slit sensilla, or changes in air pressure detected by the pressure-sensitive trichobothriae (Barth, 2002; French et al., 2002). Exposure to strong wind is likely to influence the type and frequency of prey caught and the tactile and airborne stimuli received by spiders. Accordingly, the spider may use a combination of these cues to make decisions about the geometric features of its web when building at a location where it has experienced strong wind.

Here, we tested the role of wind in inducing concurrent web geometric and spiral thread property variations using the dust spider *C. mulmeinensis*, an orb-web spider that regularly builds its webs in strong winds (Liao et al., 2009; Blamires et al., 2010). We measured and compared the geometries of *C. mulmeinensis* webs with and without prior wind exposure and measured and compared the viscous silk droplet morphology and spiral thread stickiness. We interpreted changes in droplet volume, surface area to volume ratio or thread stickiness, congruent with variations in web capture area, mesh height or sticky spiral length, across treatments as *C. mulmeinensis* functionally varying their silk properties to account for changes in web geometry. Conversely, we interpreted a lack of congruency between changes in droplet morphology, thread stickiness and changes in web capture area, mesh height or spiral length as implying that when *C. mulmeinensis* builds webs in locations exposed to wind they compromise between prey-capture efficiency, web dehydration and protection from wind drag.

MATERIALS AND METHODS

We collected adult female *C. mulmeinensis* (Thorell 1887) from Huwei, Yunlin County, Taiwan (120°22'31.47"E, 23°38'57.54"N) throughout 2011. Spiders and webs were collected by placing two circular wooden frames (diameter 200 mm) with superglue around their rims on either side of a web and moving them toward each other carefully until they touched. The frames were pressed firmly together in order to stick them to each other. Any web components lying outside the frames were burnt away using a stick of incense. We temporarily removed each spider from the web to measure its mass (± 0.1 mg) using an electronic balance (PJ300; Mettler Toledo, Greifensee, Switzerland). The spiders were returned to their webs and taken back to the laboratory within the frames, and acclimated in the laboratory on their frame-mounted webs under a 12h:12h light:dark cycle for 3 days. We fed them one *Drosophila melanogaster* each day and lightly sprayed the webs with tapwater before destroying the webs.

Experiments

Cyclosa mulmeinensis is a small orb-web spider (adult body length <6 mm), so making repeated measurements on the same individual can be stressful and this may confound the experiments. We thus randomly divided 120 spiders into two groups; a pre-treatment and a treatment group ($N=60$ in each). The individuals in the pre-treatment group were further randomly divided into two subgroups ($N=30$ in each subgroup), designated P1 and P2. These spiders were

given 3 days to build a web on their circular frames, after which web geometry (see ‘Web geometry measurements’) and spiral properties (see ‘Droplet morphology measurements’ and ‘Thread stickiness measurements’) were measured and compared. These web and silk measurements served as the pre-treatment standards for the following experiments.

Spiders in the treatment group were divided into a wind-exposed subgroup (W subgroup) and an unexposed subgroup (N subgroup) ($N=30$ in each subgroup). We subjected individuals in the W subgroup to wind of constant speed (1.1 m s^{-1}) over 7 days while on their webs, while individuals on webs in the N subgroup were placed in the same laboratory as the W subgroup for the same days but not exposed to wind. The wind was generated by $120 \times 120 \text{ mm}$ electric fans (Cooler Master; AREC Peripherals, Taipei, Taiwan) placed 400 mm from the spider’s dorsum. Relative humidity and temperature data loggers (Hobo U23, Pro v2, Onset, Bourne, MA, USA) were set up in the laboratory beside six representative webs from each treatment to make sure that relative humidity (W: $62.81 \pm 1.06\%$, N: $62.57 \pm 0.94\%$, ANOVA: $F=0.03$, $\text{d.f.}=1,12$, $P=0.86$) and temperature (W $18.81 \pm 0.10^\circ\text{C}$, N $18.75 \pm 0.11^\circ\text{C}$, ANOVA: $F=0.16$, $\text{d.f.}=1,12$, $P=0.69$) did not differ significantly between the locations where spiders in the W and N subgroups were placed. After 7 days, the experiment was terminated and we destroyed the webs of all individuals. Spiders built new webs on their frames within 24 h, upon which we immediately measured and compared between subgroups the following parameters from samples of spiral threads: (i) web geometric parameters: catching area, total (sticky and non-sticky) silk length, total spiral thread length, mesh height and the number of radii, (ii) droplet morphology and (iii) spiral stickiness (see below).

Web geometry measurements

We counted the number of radii and sticky spirals in each web along four cardinal directions (up, down, left and right). We then measured the hub and total radius of the upper and lower portions of each web. These variables were used to calculate: (1) catching area, (2) total silk length, (3) total spiral length and (4) mesh height, using the formulae (Herberstein and Tso, 2000):

$$\left[\frac{\pi(r_{\text{au}})^2}{2} - \frac{\pi(r_{\text{u,hub}})^2}{2} \right] + \left[\frac{\pi(r_{\text{al}})^2}{2} - \frac{\pi(r_{\text{l,hub}})^2}{2} \right], \quad (1)$$

where r_{au} and r_{al} are parameters representing the upper and lower web radius with the hub excluded, respectively, calculated by:

$$r_{\text{au}} = \frac{r_{\text{u}} + (d_{\text{hub}}/2)}{2}, \quad (2)$$

and

$$r_{\text{al}} = \frac{r_{\text{l}} + (d_{\text{hub}}/2)}{2}, \quad (3)$$

where r_{u} is the radius of the upper portion of the web, r_{l} is the radius of lower portion of the web, d_{hub} is the diameter of the web, $r_{\text{u,hub}}$ is the radius of the upper portion of the hub and $r_{\text{l,hub}}$ is the radius of the lower portion of the hub.

Total silk length was estimated from the formula (Tso et al., 2007):

$$\text{Total silk length} = \pi (\bar{r}_{\text{web}} + \bar{r}_{\text{hub}}) \bar{N}_{\text{spiral}} + (\bar{r}_{\text{web}} + \bar{r}_{\text{hub}}) \bar{N}_{\text{radii}}, \quad (4)$$

where \bar{r}_{web} is the average radius of the web, \bar{r}_{hub} is the average radius of the hub, \bar{N}_{spiral} is the average number of sticky spirals and \bar{N}_{radii}

is the average number of radii. Because the total silk length was the sum of radii and sticky spiral length in a web, we used the following formula for the length of the sticky spiral to calculate the total spiral length:

$$\text{Total spiral length} = \pi (\bar{r}_{\text{web}} + \bar{r}_{\text{hub}}) \bar{N}_{\text{spiral}}. \quad (5)$$

The mesh height was calculated by the formula (Tso et al., 2007):

$$\text{Mesh height} = \frac{(r_{\text{u}} + r_{\text{l}}) - (r_{\text{u,hub}} + r_{\text{l,hub}})}{S_{\text{u}} + S_{\text{l}} - 2}, \quad (6)$$

where S_{u} is the number of sticky spirals in the upper half of the web and S_{l} is the number of sticky spirals in the lower half of the web.

Droplet morphology measurements

We collected three spirals from each web between two $25 \times 35 \text{ mm}$ plastic frames with double-sided adhesive tape around their 5 mm wide border. The frames were placed in front of and behind a selected set of spirals and moved together until they touched, securing the spirals within. The spirals mounted within the frames were freed from the surrounding web using a hot soldering iron. The frames always contained at least five rows of spirals so the ensuing measurements were replicated five times per sample. Spirals were collected from the lower portion of the web on all occasions.

The spiral-containing frames were gently placed onto parallel matchsticks placed 20 mm apart on a microscope slide so that the threads and their droplets had no contact with any surface that could distort their shape. We viewed and photographed the spirals under $100\times$ and $1000\times$ magnification using a polarized light microscope (Olympus BX-50, Tokyo, Japan) connected to a digital camera (UC-Series, Nikon, Tokyo, Japan). From the photographs, we calculated the number of gluey silk droplets per 0.5 mm length of flagelliform thread ($V_{\text{D}}/0.5 \text{ mm}$) and the diameter of the flagelliform spiral thread (d_{spiral}), and measured the length and width of nine randomly selected droplets using VIS Plus (Liion Opto-Electronics Technology, Taichung, Taiwan) imaging software. From these last measurements, we determined the mean droplet volume (V_{D}) using the formulae (Opell and Hendricks, 2007):

$$V_{\text{D}} = \frac{2\pi(w)^2 L}{15}, \quad (7)$$

where w is the width of the droplet and L is the length of the droplet. We then calculated the average spacing between droplets (S_{D}) and $V_{\text{D}}/0.5 \text{ mm}$ as detailed elsewhere (Opell and Hendricks, 2007). As it is an indicator of water loss potential from sticky silk, we calculated the surface area to volume ratio of the droplets by first calculating droplet surface area using the formula:

$$\text{Droplet surface area} = \frac{4\pi w L}{3}. \quad (8)$$

The droplet surface area to volume ratio was then calculated as the droplet surface area divided by droplet volume. All measurements were made as soon as possible after collection and the treatments were sampled in random order so that the time taken after web building to view the droplets had minimal effect on the measurements made.

Thread stickiness measurements

We used $11 \times 11 \text{ mm}$ U-shaped cardboard frames (Agnarsson and Blackledge, 2009) to collect three spiral threads from the lower portion of each web. We lightly touched the tips of the U-frame to a length of spiral thread. Threads within the U-frames were freed

from the rest of the web using a hot iron and their attachment sites on the frame border were reinforced using a drop of Elmer's glue. We placed the top (i.e. so the open end of the U faced downward) of the frame within the uppermost grips of a Nano Bionix tensile tester (MTS Systems Corporation, Oakridge, TN, USA) and a 6×2 mm stainless steel stage was mounted securely onto a pin using super glue and placed in the lowermost grips. We then lowered the card at 0.01 mm s⁻¹ until the thread touched the stage. The specimen was held in position for 60 s, allowing the thread to adhere to the stage, before the thread was pulled up at 1 mm s⁻¹ until the thread detached from the stage. The force (μN) required to pull the thread off the stage was measured and indicated the stickiness of the thread (Opell, 1989). We repeated this procedure 10 times, using a different part of the stage each time, for each of the three threads from each web to obtain an average per thread. The stage was cleaned with alcohol before testing each thread. As for droplet morphology, all measurements were made as soon as possible after collection and the treatments were sampled in random order. All measurements of droplet morphology and thread stickiness were made at room temperature (~20°C) and relative humidity (~60%).

Analyses

We assessed whether the web and spiral properties differed between the P1 and P2 subgroups using ANOVA. We assessed whether spider mass and spiral features differed between the pre-treatment subgroups, and the W and N treatment subgroups using ANOVA. We used multivariate ANOVA (MANOVA) to determine whether web geometric parameters, thread stickiness and/or droplet morphology differed between the P1 and P2 pre-treatment subgroups and between the W and N treatment subgroups. When a MANOVA showed a significant difference, we performed individual ANOVA on each of the variables to ascertain the significantly differing variable across the treatments. We performed Kolmogorov–Smirnov tests to assess the normality of the data prior to all analyses. log₁₀ transformations were done on data that failed the test ($P < 0.05$), which normalized the data ($P > 0.05$) on all occasions. Variations in thread droplet morphology, spacing or stickiness with web capture area, mesh height or spiral length across treatments were used to interpret whether, and to what extent, silk properties compensated for changes in web geometry.

RESULTS

Web geometric parameters did not differ significantly between P1 and P2 pre-treatment subgroups (MANOVA: $\lambda = 0.92$, $F = 0.95$, d.f.=5,55, $P = 0.45$; Table 1), so we were confident that web geometric parameters were homogeneous among pre-treated spiders. Web geometry differed significantly between W and N subgroups (MANOVA: $\lambda = 0.79$, $F = 5.07$, d.f.=5,96, $P < 0.001$). We therefore used ANOVA to examine the individual variables and found that capture area ($F = 4.35$, d.f.=1,100, $P < 0.001$), total silk length ($F = 10.31$, d.f.=1,100, $P = 0.004$) and total spiral length ($F = 12.55$, d.f.=1,100, $P = 0.001$) of the webs of spiders in the W subgroup were

significantly smaller than those of spiders in the N subgroup (Fig. 1A–C). Moreover, the mesh height in the webs of spiders in the W subgroup was significantly greater ($F = 11.40$, d.f.=1,100, $P = 0.001$) than that of the webs of spiders in the N subgroup (Fig. 1D).

No features of the sticky spirals differed between the P1 and P2 pre-treatment subgroups (MANOVA: $\lambda = 0.82$, $F = 1.07$, d.f.=7,35, $P = 0.40$; Table 2), so we were confident that droplet morphology and spiral stickiness were homogeneous among pre-treated spiders. Among the treatment subgroups, we found that the V_D ($F = 5.43$, d.f.=1,100, $P = 0.02$), $V_D/0.5$ mm ($F = 11.79$, d.f.=1,100, $P < 0.001$) and droplet surface area (SA_D ; $F = 5.21$, d.f.=1,100, $P = 0.02$) in the W subgroup were significantly greater than those of the N subgroup (Fig. 2C–E) and the droplet surface area to volume ratio (SA_D/V_D) in the W subgroup was significantly smaller ($F = 3.94$, d.f.=1,100, $P = 0.05$) than that of the N subgroup (Fig. 2F). Droplet number (N_D), S_D and d_{spiral} , however, did not differ significantly ($P > 0.05$) between the subgroups (Fig. 2A,B,G). Despite these morphological changes to the droplets, the stickiness of the capture spirals did not differ significantly between any of the pre-treatment ($F = 1.22$, d.f.=1,35, $P = 0.31$; Fig. 3A) or treatment ($F = 1.64$, d.f.=1,36, $P = 0.21$; Fig. 3B) subgroups.

DISCUSSION

We found that recent exposure to wind induces the orb-web spider *C. mulmeinensis* to build webs with smaller capture areas, shorter spiral thread length and larger mesh heights, and using less silk than they would in the absence of wind exposure. These changes in web geometry are consistent with findings for these and other orb-web spiders when exposed to wind (Vollrath et al., 1997; Liao et al., 2009), which are predicted to constitute a response to reduce wind-induced damage to webs (Liao et al., 2009; Cranford et al., 2012). *Cyclosa mulmeinensis* increases radial thread stiffness upon exposure to wind (see Liao et al., 2009), and this may enable the radii to take more of the burden of prey impact absorption away from the spiral threads (Lin et al., 1995; Cranford et al., 2012; Sensenig et al., 2012), thus partially offsetting the effects on prey-capture performance induced by the shorter spiral thread.

We found that the spiral threads of spiders exposed to wind had a similar number of, albeit larger, aggregate (viscous) droplets compared with those of spiders that had not been exposed to wind. However, the larger droplets did not correspond to the spiral threads being any stickier. The lack of change in thread stickiness despite an increase in droplet size, a reduction in spiral length and an increase in mesh height across treatments is inconsistent with our *a priori* prediction of aggregate silk properties functionally compensating for any necessary changes in web geometry. A likely consequence of the larger glue droplets was a reduction in droplet surface area to volume ratio, which may serve to reduce evaporative water loss from the droplets. There are two possible mechanistic explanations for the larger droplets in wind-exposed spiders. One is that there is a trade-off between the investment in glycoprotein and LMWCs

Table 1. Mean (±s.e.m.) web geometric parameters of *Cyclosa mulmeinensis* webs from the P1 and P2 pre-treatment subgroups

Treatment	Catching area (cm ²)	Total silk length (cm)	Total spiral length (cm)	Mesh height (mm)	Number of radii
P1	84.96±4.22	617.00±28.26	419.40±20.59	1.55±0.06	36.61±0.85
P2	79.97±4.57	597.10±32.89	413.36±24.42	1.48±0.06	35.10±0.94
$F_{1,59}$	0.65	0.76	0.04	0.21	1.44
P	0.42	0.39	0.85	0.65	0.24

Results of ANOVA tests comparing the subgroups for each parameter are shown.

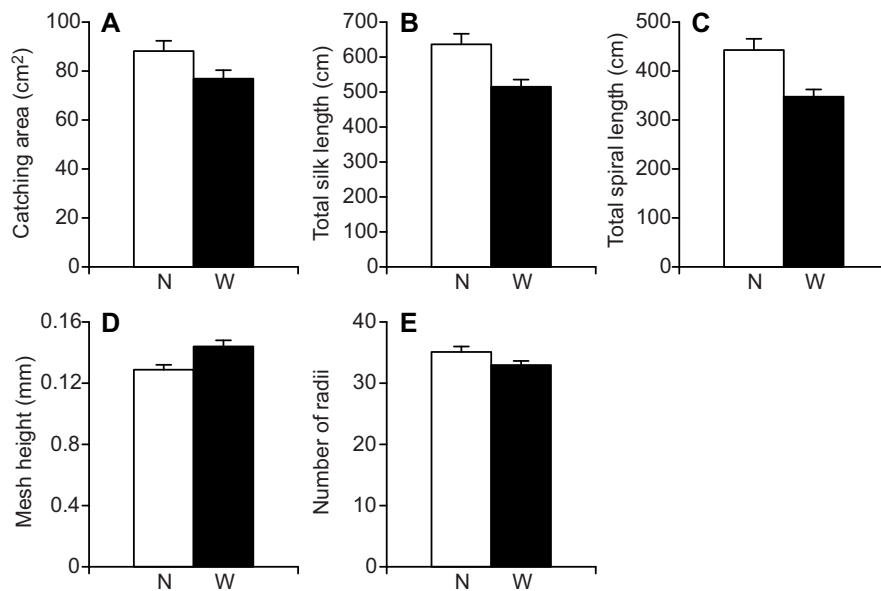


Fig. 1. Comparison of web geometric features between treatment subgroups W (spiders exposed to wind) and N (spiders not exposed to wind): (A) web catching area, (B) total length of silk used per web, (C) total length of spiral thread, (D) mesh height and (E) number of radii. Error bars represent s.e.m.

with wind exposure favoring LMWCs, perhaps for greater desiccation resistance. The other possibility is that the larger droplets of wind-exposed spiders have the same amount of glycoprotein as the control group, but greater amounts of the LMWCs. The consequence of this would be that at a given humidity the wind-exposed droplets would be more fully hydrated and more prone to losing adhesion due to the over lubrication phenomena documented elsewhere (Sahni et al., 2011). Thus, it seems that enhanced droplet hydration or water retention as a result of the larger surface area to volume ratio would be at odds with optimal glycoprotein hydration and adhesive optimization.

Empirical studies (Herberstein and Heiling, 1998; Blackledge and Zevenbergen, 2006; Blamires et al., 2011; Sensenig et al., 2012) and computer simulations (Lin et al., 1995; Cranford et al., 2012; Tarakanova and Buehler, 2012) demonstrate that many aspects of web geometry are important predictors of prey-capture performance in orb webs. Indeed, the combined influence of geometry and silk properties on prey-capture performance of spider webs (Lin et al., 1995; Sensenig et al., 2012; Cranford et al., 2012) explains why spiders that switch diets vary both the geometry of their webs and the properties of their silks (Tso et al., 2005; Tso et al., 2007; Blamires et al., 2011; Blamires and Tso, 2013). These variations include changes to mesh height, number of radials and spiral length, which affect the number, size, shape, mass and kinetic energy of the prey that can be effectively caught (Blackledge and Zevenbergen, 2006; Sensenig et al., 2010; Sensenig et al., 2012; Blamires et al., 2011; Cranford et al., 2012). The geometric differences that we found between webs built by spiders that had been exposed to wind compared with those that had not been exposed to wind are likely to correspond with variation in prey-capture performance of the

respective webs (Cranford et al., 2012). We predict that the geometry of the webs built by spiders that had been exposed to wind means that the webs are likely to ultimately accommodate fewer prey than webs built by the spiders that had not been exposed to wind (Herberstein and Heiling, 1998; Blackledge and Zevenbergen, 2006; Blamires et al., 2011).

The radii and spiral threads are the web components that bear much of the burden of absorbing the kinetic energy of prey on impact (Cranford et al., 2012; Sensenig et al., 2012; Tarakanova and Buehler, 2012). Accordingly, they need to be incorporated into webs under specific tensions (Craig, 2003; Sensenig et al., 2012). Too much tension will mean that prey, depending on its size and flight velocity, will either fly through the web or bounce off the web, a phenomenon known as the ‘trampoline effect’ (Craig, 2003; Blackledge and Hayashi, 2006; Kelly et al., 2011; Sensenig et al., 2012). Moreover, localized tearing becomes increasingly likely in strong wind if webs are under excessive tension. Accordingly, radii tension might be loosened or fewer radial threads used when webs are exposed to wind (Lin et al., 1995; Aoyanagi and Okumura, 2010; Cranford et al., 2012). We found that *C. mulmeinensis* used fewer radii, although we did not directly measure radii tension herein. The longer the spiral, the more likely a web is to experience sagging under wind drag (Lin et al., 1995; Sensenig et al., 2010). This explains why *C. mulmeinensis* uses shorter spiral threads with wider spaces between spiral turns when they build their webs during exposure to wind (Liao et al., 2009).

We found, in addition to variations in web geometry, that webs built by *C. mulmeinensis* that had been exposed to wind have larger aggregate silk droplets. Nevertheless, the larger droplets did not affect the stickiness of the spiral thread. The extensibility of the

Table 2. Mean (\pm s.e.m.) features of the sticky spirals from webs built by *C. mulmeinensis* in the P1 and P2 pre-treatment subgroups

Treatment	N_D per 0.5 mm	S_D (μm)	V_D (μm^3)	V_D per 0.5 mm (μm^3)	SA_D (μm^2)	$SA_D:V_D$	d_{spiral} (μm)
P1	18.43 \pm 0.8	19.06 \pm 1.1	386.67 \pm 39.2	6326.39 \pm 448.4	363.49 \pm 24.7	1.23 \pm 0.04	1.20 \pm 0.01
P2	17.62 \pm 0.8	20.11 \pm 1.4	434.44 \pm 42.6	6837.94 \pm 431.3	394.90 \pm 25.7	1.17 \pm 0.04	1.21 \pm 0.02
$F_{1,59}$	0.44	0.35	0.68	0.67	0.77	1.05	0.19
P	0.51	0.55	0.41	0.41	0.38	0.31	0.66

Results of ANOVA tests comparing the subgroups for each parameter are shown.

N_D , droplet number; S_D , droplet spacing; V_D , droplet volume; SA_D , droplet surface area; $SA_D:V_D$, droplet surface area to volume ratio; d_{spiral} , spiral thread diameter.

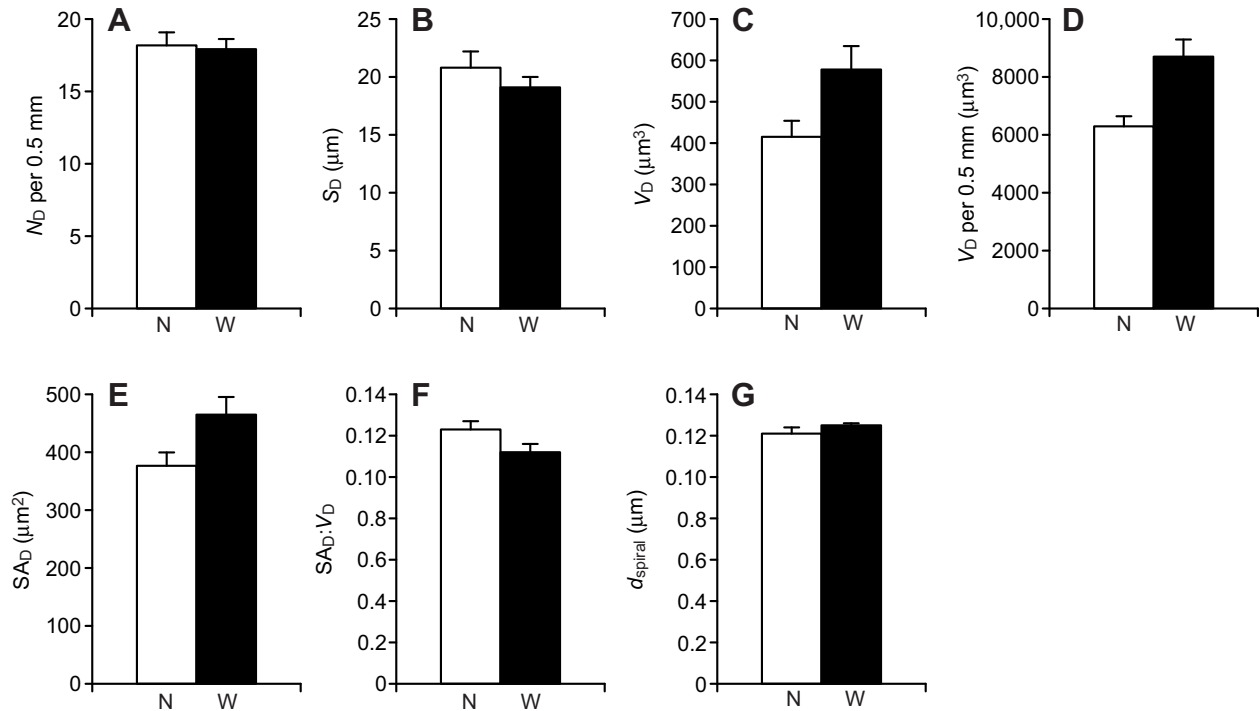


Fig. 2. Comparison of the droplet morphometric features between treatment subgroups W and N: (A) droplet number (N_D) per 0.5 mm of thread, (B) droplet spacing (S_D), (C) droplet volume (V_D), (D) droplet volume per 0.5 mm of thread, (E) droplet surface area (SA_D), (F) droplet surface area to volume ratio ($SA_D:V_D$) and (G) flagelliform spiral thread diameter (d_{spiral}). Error bars represent s.e.m.

flagelliform thread principally influences the stickiness of the spiral threads (Opell and Hendricks, 2010; Sahni et al., 2010; Tarakanova and Buehler, 2012). It seems that the larger droplets had no effect on flagelliform thread extensibility *via* supercontraction of the flagelliform thread; if they had, we would have found significant differences in thread stickiness between treatment subgroups. The production of larger droplets could have been a result of the secretion of aggregate silk with greater water content forming larger droplets. This would suggest that there were reductions in the glycoprotein and LMWC concentrations. We consider this scenario unlikely as the droplets in the W and N treatment group would have had different surface tensions, which would have been identifiable by a difference in the flatness of droplets of the W and N groups under magnification (Opell and Schwend, 2007), which we never observed. In addition, windy conditions are typically drying conditions (Willmer et al.,

2000), so it seems counterintuitive that under these conditions a relatively small spider would expend more water on silk, particularly when the threads produced under these conditions are no stickier and no more likely to capture enough prey to recover their water investment. A more plausible explanation, but one requiring confirmation, is that the aggregate silks of the spiders exposed to wind had greater concentrations of LMWCs, so took in more water from the atmosphere post-deposition (Townley et al., 1991; Opell et al., 2011a).

Despite the production of larger aggregate silk droplets and the maintenance of consistent spiral stickiness across treatments, functional augmentation of spiral threads in *C. mulmeinensis* webs was to be expected because of the probable dehydrating influence of persistent strong winds on the silk. Spiral silks may lose their stickiness over time as a result of water loss to the environment (Edmonds and Vollrath, 1992; Opell et al., 2011a). The production of larger aggregate silk droplets by *C. mulmeinensis*, regardless of whether they were deposited with a greater water content or gained water from the atmosphere, probably serves to reduce the droplet surface area to volume ratio and curtail evaporative water loss to some extent. Furthermore, if higher concentrations of LMWCs were added to the viscous silks of wind-exposed spiders, it would potentially facilitate silk rehydration when the wind subsides (Edmonds and Vollrath, 1992; Sahni et al., 2010).

Although variation in the geometry of *C. mulmeinensis* webs has the benefit of reducing wind drag and web damage when in strong wind (Liao et al., 2009), we interpreted the lack of congruent changes in droplet morphology, thread stickiness and web geometry as negatively affecting the prey-capture performance of webs of spiders exposed to wind. Furthermore, in strong wind, prey fly in multiple directions and at a multitude of speeds, and debris may regularly strike and be deposited onto webs, so the responsiveness of orb-web spiders to prey capture is severely hampered (Turner et

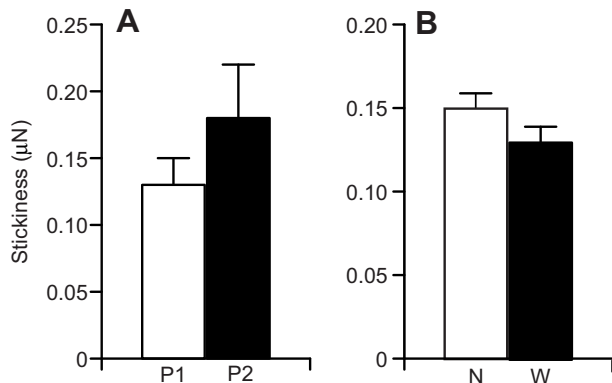


Fig. 3. Mean (\pm s.e.m.) stickiness values for spirals in webs of the (A) P1 and P2 pre-treatment groups and (B) W and N treatment groups. Error bars represent s.e.m.

al., 2011). Despite these austere consequences, *C. mulmeinensis* consistently builds webs in windy locations (Liao et al., 2009; Blamires et al., 2010). We thus expect that they use means other than varying their silk properties to offset the constraints placed on prey-capture performance.

In certain circumstances, aggregating webs may enhance the prey-capture efficiency of spider webs compared with webs in isolation. This is because prey bounce off successive webs before eventually being captured by a centrally placed web. This phenomenon has been called the ‘ricochet effect’ (Uetz, 1989) and competition for the central position has been called ‘shadow competition’ (Rao, 2009). Shadow competition may provide a runaway selective mechanism for the size of spider web aggregations (Uetz, 1989; Rao, 2009; Blamires et al., 2010; Mestre and Lubin, 2011). It might, accordingly, be desirable for *C. mulmeinensis* to aggregate their webs when strong winds are considered likely. Indeed, aggregations of *C. mulmeinensis* webs are often found at locations where the wind is consistently strong, e.g. when webs are placed along the foreshore (Blamires et al., 2010). Aggregation of webs by *C. mulmeinensis* thus could be a means to take advantage of ‘ricochet effects’ under these circumstances.

To summarize, variations in orb-web geometry and spiral silk properties provide a means to maintain web function in variable environments. We found that *C. mulmeinensis* exposed to wind built webs with smaller capture areas and spiral thread lengths but wider mesh heights, and used less silk than those that had not been exposed to wind. However, we found no change in the stickiness of spiral threads, despite significant differences in the size of the aggregate silk droplets. The larger droplets seem to be a consequence of either a greater water investment in aggregate silk or a greater investment in LMWCs facilitating greater water uptake into the droplets from the atmosphere. In either event, dehydration of the silks when in wind is at least partially mitigated. There is likely to be a compromise between prey-capture efficiency and a reduction of wind drag and dehydration in the webs of wind-exposed spiders. It seems plausible that *C. mulmeinensis* aggregate their webs to take advantage of ricochet effects, thereby enhancing their prey-capture efficiency when building webs at windy locations.

AUTHOR CONTRIBUTIONS

C.-C.W. and I-M.T. conceived and designed the study. C.-C.W. and C.-L.W. performed the experiments. C.-C.W., S.J.B., C.-L.W. and I-M.T. discussed, analyzed and interpreted the results. C.-C.W., S.J.B. and I-M.T. wrote the paper.

COMPETING INTERESTS

No competing interests declared.

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