

The effects of wind on trap structural and material properties of a sit-and-wait predator

Chen-Pan Liao,¹ Kai-Jung Chi,² and I-Min Tso^{3,4}

¹Department of Life Science, Tunghai University, Taichung 407, Taiwan, ²Department of Physics and Institute of Biophysics, National Chung-Hsing University, Taichung 402, Taiwan, ³Center for Tropical Ecology and Biodiversity, Tunghai University, Taichung 407, Taiwan, and ⁴Department of Life Science, National Chung-Hsing University, Taichung 402, Taiwan

Numerous terrestrial invertebrates use secretions produced by themselves to build prey traps. Potentially, the structural as well as material properties of such constructions will reflect adaptations to wind disturbances, but most relevant studies only focus on trap structural characteristics. In this study, we examined how wind disturbances affected the structural and material properties of prey traps constructed by a sit-and-wait Araneae predator. We first compared web structures and major ampullate (MA) silk properties of 2 *Cyclosa* spider species inhabiting seashores and forests to see whether these properties reflected the habitat-specific wind disturbances these spiders experienced. The MA silks of the seashore-dwelling *Cyclosa mulmeinensis* were significantly thicker and contained higher percentage of glycine and lower glutamine. Congruent with such amino acid variation pattern were higher ultimate tension and breaking energy of *C. mulmeinensis* MA silks. However, despite that this species' silks were relatively glycine rich and glutamine poor, they also showed greater extensibility. Compared with webs built by *Cyclosa ginnaga*, those built by *C. mulmeinensis* were composed of fewer drag-reducing silk threads but were stiffer. In a laboratory manipulation, MA silk amino acid composition and diameter did not differ between *C. mulmeinensis* receiving different levels of wind. However, those receiving persistent wind disturbances built smaller webs composed of fewer but stronger MA silks to reduce drag and prevent the web from damage. Orb web spiders inhabiting areas with different levels of wind disturbances exhibit variation and plasticity in structural and material properties of prey traps. Furthermore, the silk property plasticity does not have to involve alterations of amino acid composition. **Key words:** *Cyclosa*, drag, major ampullate silk, web geometry. [*Behav Ecol*]

Many animals build structures to control microclimates, enhance intraspecific communication or increase foraging success, sometimes using their own body secretions to construct traps to enhance hunting of terrestrial or aquatic prey (Hansell 2005; Ruxton and Hansell 2007). Additionally, males of numerous organisms build various forms of constructions to enhance signal transmission (Daws et al. 1996) or to be used as quality indicators (Borgia 1995; Barber et al. 2001; Madden 2003). Wind is one major environmental factor affecting the building and design of animal constructions. Some animals utilize winds to control the microclimate of their burrows (Vogel et al. 1973; Facemire et al. 1990) or colonial mounts (Kleineidam et al. 2001; Turner 2005) and take advantages of aerodynamic forces to achieve certain functional optima (Vogel 1978; Kleineidam et al. 2001; Turner 2001). In other organisms, however, winds may negatively affect organisms by directly exerting physical disturbances (Kim and Monaghan 2005) or by indirectly altering temperature and humidity (Furness and Bryant 1996; Reid et al. 2002). Animals may adjust the direction of nest or burrow openings (Borges et al. 2002; Burton 2006; Quader 2006) or choose appropriate nest insulating material (Facemire et al. 1990; Reid et al. 2002; Summers et al. 2002) to reduce the adverse impacts. How wind affects building and design of prey trap, however, is still not well understood.

The most representative terrestrial trap builders are web spiders (Eberhard 1990; Foelix 1996). Unlike traps constructed by other organisms, spider webs exhibit considerable intraspe-

cific variability in various aspects (Heiling and Herberstein 2000). For example, the structural properties of webs can be adjusted when spiders encounter different prey types (Pasquet et al. 1994; Sandoval 1994; Schneider and Vollrath 1998; Tso et al. 2007) and experience changes in foraging conditions (Higgins and Buskirk 1992; Sherman 1994; Blackledge 1998; Heiling and Herberstein 1999; Herberstein and Heiling 1999; Tso 1999; Herberstein et al. 2000; Venner et al. 2000; Nakata 2008) or under different nutrient or social conditions (Blackledge and Zevenbergen 2007; Salomon 2007; Zevenbergen et al. 2008). Web spiders may adjust the chemical or mechanical properties of silks when encountering various conditions. For example, some orb web and cobweb spiders were reported to adjust amino acid composition, protein crystallization, diameter, or stiffness of major ampullate (MA) silks when they were fed with different quantity or types of prey (Craig et al. 2000; Tso et al. 2005, 2007; Blackledge and Zevenbergen 2007). Vollrath and Köhler (1996) showed that the stress-strain relationship of MA silks was changed when spider body weight was increased by various ways.

Strong wind disturbance can potentially be an important factor influencing various properties of spider webs and silks. Sticky spirals of an orb web play important roles in prey capture through aerodynamic damping. However, the cost of such aerodynamic drag is that during very windy conditions, the webs would potentially be damaged (Lin et al. 1995). Spiders exhibit various behavioral ways to avoid web damages under windy conditions. For example, some orb-weaving spiders oriented their webs to parallel the direction of wind to minimize exposure area (Schoener and Toft 1983; Ramirez et al. 2003). *Araneus* spiders reduce radii number, spiral length, and web area when they experience strong winds (Hieber 1984), and webs changed in this way are also stiffer (Vollrath et al. 1997). These studies suggested that orb-weaving spiders may adjust

Address correspondence to I-M. Tso. E-mail: spider@thu.edu.tw.

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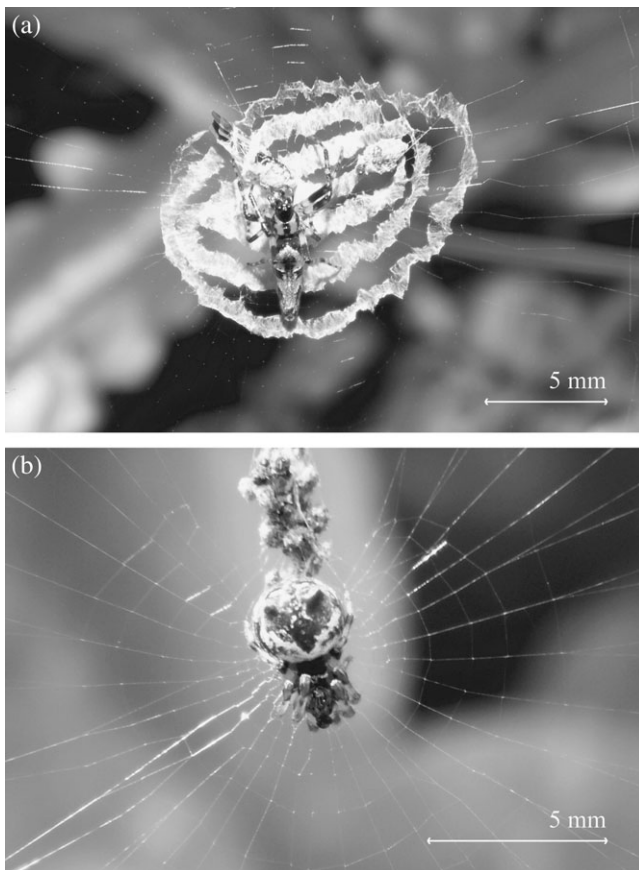


Figure 1
The forest-dwelling *Cyclosa ginnaga* (a) and seashore-dwelling *Cyclosa mulmeinensis* (b). (Both are adult females.)

web orientation or constructions to minimize drag. However, there are no empirical data demonstrating that these web structural changes found in webs lead to a reduced drag. Nor is it clear whether the chemical or mechanical properties of spider silks can be influenced by wind disturbances. In this study, we tested the hypothesis that spiders inhabiting areas of different level of wind speed would differ in silk properties and web designs. We predicted that spiders inhabiting areas of stronger wind disturbance would use stronger silks containing

more crystal-forming amino acids to build smaller, stiffer, and less dense webs to reduce drag. These predictions were tested by comparing the structural designs of orb webs and mechanical/chemical properties of MA silks produced by 2 *Cyclosa* species inhabiting seashores and forests. Furthermore, we predicted that spiders could adjust silk properties and web structures according to wind disturbance levels. These predictions were evaluated by manipulating wind speed in the laboratory and comparing the responses of *Cyclosa mulmeinensis* receiving different treatments.

MATERIAL AND METHODS

Sample collection

We compared web architectures and MA silk physical and chemical properties of *Cyclosa ginnaga* (Figure 1a) inhabiting forests and *C. mulmeinensis* (Figure 1b) inhabiting seashores. *Cyclosa mulmeinensis* were collected from Orchid Island (designated as seashore site) (22°04'50"N 121°30'05"E), Taitung County, Taiwan, in July 2006 and February 2007. *Cyclosa ginnaga* were collected from a lowland broadleaf forest near Lien-Hua-Chih Research Center in Yu-Chi (designated as forest site) (23°55'01"N 121°53'24"E), Nantou County, Taiwan, in July 2006 and 2007. In both species, only adult females were collected. Taiwan is an East Asian subtropical island that receives strong northern monsoon during winter months and typhoon during summer months. The documented average wind speed of seashore and forest sites between 1971 and 2002 were 9.0 and 1.1 m/s, respectively (Central Weather Bureau, Taiwan). In July 2007, we also measured the wind speed of the seashore and forest collection sites. In both areas, we took recordings 6 times a day (from 9:00 AM to 3:00 PM at an interval of 1 h) for 3 days (each recording value represented the mean of 10 min of continuous measuring). The recorded wind speed in the seashore site (3.67 ± 0.10 m/s) was significantly higher than that recorded in forest site (0.11 ± 0.04 m/s) ($t = 34.556$, degrees of freedom [df] = 22, $P < 0.001$). In 2 collection sites, we measured 3 structural variables of webs constructed by adult females: number of radii, orb radius, and number of spirals (both from 4 cardinal directions). These variables were used to calculate mesh height and catching area of each web following the formula of Herberstein and Tso (2000). Total silk length was calculated by the equation reported in Tso et al. (2007). Because webs constructed by both *Cyclosa* species were symmetric and were similar in shape (Figure 2a, b), the potential bias in estimation caused by differences in web symmetry or shape (Blackledge and Gillespie

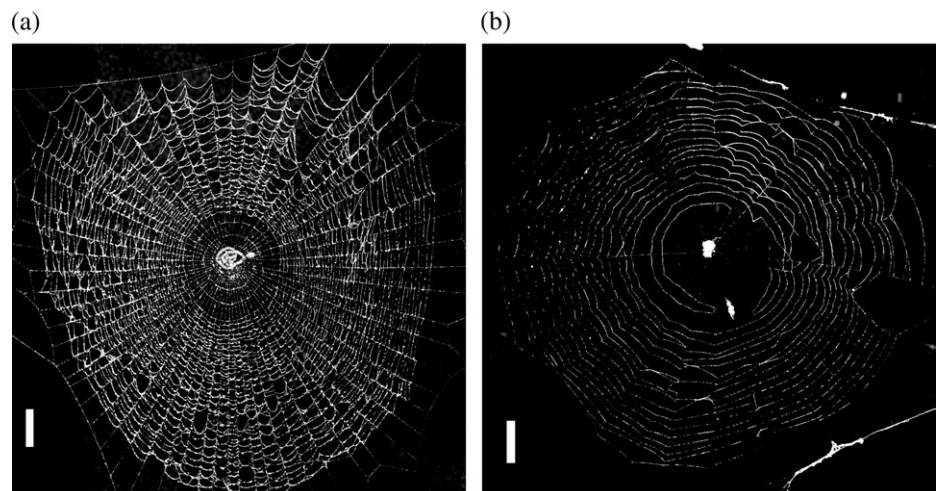


Figure 2
Typical orb webs built by *Cyclosa ginnaga* (a) and *Cyclosa mulmeinensis* (b) (scale = 1 cm).

2002) was unlikely to occur. We compared number of radii, mesh height, catching area, and total silk length of webs built by *C. ginnaga* and *C. mulmeinensis* by multivariate analysis of variance (MANOVA) because these variables were not independent of each other.

After web measurements, circular woody frames (diameter 20 cm) coated with adhesive were used to collect the webs for stiffness and wind drag measurements. All the *C. ginnaga* webs in the study site contained discoid silk decoration in the hub area, so all the web samples used were decorated, whereas for *C. mulmeinensis*, only undecorated webs were collected for subsequent analyses. Special attention was paid to make sure that the original web tension was not affected during the collection process and the hub was positioned in the center of the frame. The spiders were carefully removed from the webs, kept individually in containers, and brought back to the laboratory for MA silk collection. In the laboratory, we first anesthetized the spiders by carbon dioxide and measured their body weight with an electronic balance (PJ3000; Mettler-Toledo, Greifensee, Switzerland). Then each spider was fixed on a Styrofoam plane with its MA silk gently pulled out under a dissecting microscope. Two threads of MA silk (5 cm in length) were carefully mounted on a frame made of cardboard (5 cm in width and 7 cm in length) to measure the mechanical properties. All obtained values were divided by 2 to estimate the properties of a single silk thread. From each individual spider, 3 MA silk samples were collected.

Results of previous studies showed that spider web architectures were also determined by prey size (Sandoval 1994; Schneider and Vollrath 1998; Venner et al. 2000) and spider leg length (Vollrath 1987). To determine whether any observed web differences between 2 *Cyclosa* species were associated with these factors, we conducted 2 field studies in April 2009. The first (14 and 15 April) was conducted in an estuary area in Huwei (23°42'00"N 120°26'00"E), Yunlin County, Taiwan, to survey the prey size distribution of *C. mulmeinensis*. The survey was performed from 9 AM to 4 PM, and the webs in the study site were monitored once each hour. The prey trapped by webs was measured with a caliper (accuracy to the nearest mm) and prey's taxonomic order was recorded. During 2 days of study, around 100 webs were monitored daily. The second field study was conducted in a lowland broadleaf forest in Yu-Chi (Nantou County, Taiwan) to survey the prey size distribution of *C. ginnaga* following the same procedures of the previous survey. During 2 days of study, around 50 webs were surveyed daily. Prey size difference of 2 *Cyclosa* species was compared by a Mann-Whitney *U* test and prey taxonomic composition by a χ^2 test of homogeneity. A total of 29 *C. mulmeinensis* and 24 *C. ginnaga* were brought back to the laboratory for leg length measurements. Spiders were first preserved in 70% alcohol, and immediately before measurement, the 4 legs from right side of the body were removed. The images of legs were taken under a dissecting microscope (Olympus SZX 12, Tokyo, Japan) mounted with a digital camera (Olympus Camedia C5050, Tokyo, Japan). ImageJ software was used to estimate the leg length to the nearest 0.1 mm. Because the lengths of all legs of a spider were not independent of each other, a MANOVA test was used to compare the leg length of 2 *Cyclosa* species.

Measuring MA silk mechanical properties

To measure the mechanical properties of MA silk, the lower end of the silk-mounted cardboard was fixed on a weight placed on an electronic balance and the upper end on a moveable bracket (Figure 3a). We then cut off the cardboard from the middle and lifted up the bracket at a speed of 2 mm/s. The readings of the balance would decrease when the bracket lifted the upper end of the cardboard and, thus, pulled the

silk and weight gradually. Hence, the decreased reading represented the tensile load applied to the silk, and the bracket displacement indicated the silk extension. The load for each 1-mm silk extension was recorded until the silk was broken. From these data, we could obtain the ultimate tension and calculate the breaking energy of the MA silks. The ultimate tension (μN) is the tension when the silk is broken, and the breaking energy (μJ) is determined by taking the integral underneath the load-extension curve. To estimate the standardized mechanical properties of the MA silk, the true strain and true stress were first calculated under the assumption of constant silk volume. The true strain (ε_T %) is the silk extension ratio and was determined by:

$$\varepsilon_T = \ln\left(\frac{l_f}{l_0}\right),$$

where l_f is the length of the silk and l_0 is the original length of the silk. The true stress (σ_T MPa) is the tension per cross-section area and was determined by:

$$\sigma_T = \frac{F}{A} = \frac{F}{A_0} \times \frac{l}{l_0},$$

where F is the instantaneous tension of the silk, A is the instantaneous cross-sectional area of the silk, A_0 is the original cross-section area of the silk estimated by a scanning electron microscope (SEM, Inspect S; FEI, Hillsboro, OR), l is the instantaneous length of the silk, and l_0 is the original length of the silk (Köhler and Vollrath 1995). The toughness was estimated by taking the integral underneath the true stress–true strain curve until the silk was broken. The ultimate tension, breaking energy, extensibility (i.e., the maximum strain), strength (i.e., the maximum stress), and toughness of MA silks produced by *C. ginnaga* and *C. mulmeinensis* were compared by a MANOVA test because these variables were not independent of each other.

Estimating silk amino acid percentages

We collected MA silks and followed the method of Tso et al. (2005) to dissolve the silk (500 μl hexafluoroisopropanol per 1 milligram of MA silk). The amino acid composition of the silk samples was analyzed by reverse-phase high-performance liquid chromatography, which was performed in the Instrument Center, Department of Chemistry, National Tsing-Hua University, Taiwan. The silk solution samples were first dried and then hydrolyzed at 115 °C in 6 N HCl for 24 h. The resulting product was transferred to a Waters PICO.TAG Amino Acid Analysis System to obtain percentages of various amino acids. Recent researches have revealed that dragline silks are composed of the products of at least 2 genes: major ampullate spidroin 1 (*MaSp1*) (Xu and Lewis 1990) and major ampullate spidroin 2 (*MaSp2*) (Hinman and Lewis 1992). The β -sheet crystal structure of *MaSp1* products is regarded as being responsible for the tensile strength of the silk and are composed of poly(A) and poly(GA) motifs (A: alanine, G: glycine) (Gosline et al. 1999; Winkler and Kaplan 2000). *MaSp2* products, on the other hand, exhibit GPGXX and GPGQQ motifs (P: proline, Q: glutamine) (Hayashi et al. 1999). The β -turn spirals of *MaSp2* products are considered to be responsible for the extensibility of the silk and are composed of GPGXX and GPGQQ motifs (P: proline, Q: glutamine, X: any amino acid) (Hayashi et al. 1999). Therefore, the relative composition of major MA silk amino acids may affect the strength and extensibility of the silk. The percentages of 5 major amino acids (alanine, glycine, glutamine, proline, and serine) of MA silks produced by *C. ginnaga* and *C. mulmeinensis* were compared by a MANOVA test because these variables were not independent of each other.

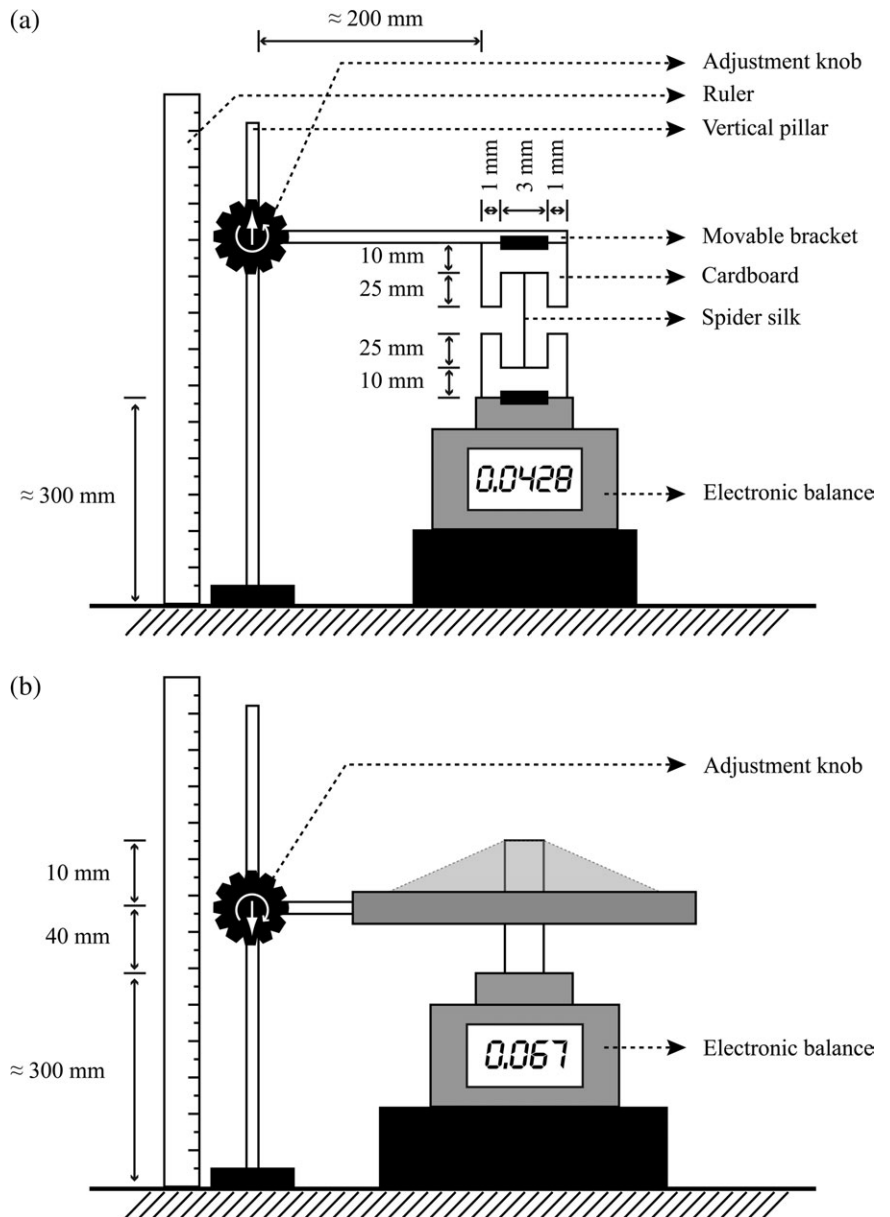


Figure 3
Schematic drawings showing the setups used for measuring MA silk properties (a) and web stiffness (b).

Measuring spider web stiffness

To assess the mechanical properties of the whole web, the woody frames with spider webs mounted were fixed on a movable bracket, and the hub of the spider web was lightly contacted with a 20-mm diameter plastic column placed on an electronic balance (Figure 3b). While the bracket was lowered down at a speed of 2 mm/s, the readings of the balance would increase. The increased reading indicated the load exerted on the web. In this study, the web stiffness was assessed as the tension (in μN) required to cause the web center to have a 10-mm displacement perpendicular to the web plane (i.e., when the bracket was lowered down for 10 mm). The stiffness of webs built by *C. ginnaga* and *C. mulmeinensis* was compared by an analysis of covariance (ANCOVA) using spider biomass and radii number as covariates.

Measuring web wind drags

After the stiffness was measured, the drag of each web specimen subjected to wind was measured. The experimental setup

was composed of 3 components: specimen mount, force measurement using an electronic balance, and a self-made wind generator hanged in between. The specimen mount was made of a circular frame attached to a wooden frame suspending from the electronic balance. The wind generator used 4 electric fans (FD128025HB; Yen Sun Technology Corp., Kaohsiung, Taiwan) at its top and beneath with a flow straightener composed of a large number of 6-cm plastic straws arranged side by side. The velocity of the wind coming out from the flow straightener was about 1.47 m/s when the fans were turned on. After the web ring was mounted onto the specimen mount, the fans were turned on and the force subjecting to the web and the whole setup was recorded. A second reading was obtained when the web ring was removed from the specimen mount and placed on top of the balance, whereas the rest of the setup remained unchanged. Because the web specimen was no longer subjected to the drag in the latter case, the difference of these 2 readings could be used as an estimate of the web's drag (in mN). An ANCOVA test was used to compare

Table 1**Mean (\pm SE) percentages of major amino acids of MA silks produced by *Cyclosa ginnaga* and *Cyclosa mulmeinensis* and results of MANOVA tests**

	Alanine	Glycine	Glutamine	Proline	Serine	Other
<i>C. ginnaga</i> (<i>N</i> = 18)	18.13 \pm 0.24	39.49 \pm 0.2	11.36 \pm 0.06	9.98 \pm 0.11	7.37 \pm 0.07	13.67 \pm 0.5
<i>C. mulmeinensis</i> (<i>N</i> = 16)	18.4 \pm 0.34	41.92 \pm 0.98	8.49 \pm 0.27	9.68 \pm 0.31	7.92 \pm 0.20	13.59 \pm 0.91
<i>F</i>	0.475	6.536	121.461	0.937	7.330	0.007
<i>P</i>	0.496	0.016	<0.001	0.340	0.011	0.935

the drags of webs built by *C. ginnaga* and *C. mulmeinensis* using total silk length as the covariate.

Design of manipulative study

In this part of the study, we tested whether spiders inhabiting areas with a high level of wind disturbances exhibited plasticity in web architectures and silk properties. Stable populations of *C. mulmeinensis* were found on shrubs near the seashore or open estuary area all year round (Tso IM, personal observations). In such habitats, there is no effective shelter for wind disturbance, and spiders' webs are quite exposed. Because *C. mulmeinensis* do not actively seek out appropriate microhabitats to reduce wind disturbances, they may exhibit special adaptations in webs and silks to cope with such environmental factor. We manipulated wind velocity in the laboratory and quantified the responses of *C. mulmeinensis* to various treatments. *Cyclosa mulmeinensis* were collected from an estuary area in Huwei (Yunlin County, Taiwan) in the summer of 2007. The spiders and webs were collected as described above, but the spiders were allowed to stay on their own webs. The spider webs were brought back to the laboratory and were fed 3 fruit flies every other day. The light–dark cycle was kept at 12:12 h, and the temperature was kept at 25 °C. After 3 days of acclimation, the spiders were randomly designated into pretreatment or treatment groups. Owing to *Cyclosa* spiders' small size and handling difficulties, we were uncertain whether forcefully drawing MA silks from *C. mulmeinensis* to evaluate their pretreatment condition would cause harmful effects to the subjects. Under such considerations, we used half of the spiders to perform a pretreatment comparison to test for homogeneity of initial silk and web properties. *Cyclosa mulmeinensis* assigned to the pretreatment group were further divided into 2 groups, control-disturbance (CD) and control-no disturbance (CN) groups, and various web and silk properties were compared. Only when various properties were not significantly different between CD and CN groups, could we confidently assume that *C. mulmeinensis* randomly assigned to different manipulations had similar initial conditions. The other half of the spiders assigned to a treatment group was also divided into 2 groups. Spiders assigned to the wind-disturbed (ED) group were treated by wind disturbance

24 h a day for 7 days. Those assigned to the no-wind disturbance (EN) group did not receive any wind disturbance. The wind disturbance received by each ED spider was generated by a 12 \times 12 cm electric fan (WFD1212H; Delta Electronics, Inc., Taipei, Taiwan). A fan was placed 40 cm away from each web-mounted wooden ring with spider dorsum facing the fan. The average wind speed was 1.138 m/s, which was comparable to that experienced by spiders in their natural habitats (Central Weather Bureau, Taiwan). After 7 days of wind disturbance manipulations, silk property and web structural/mechanical data of spiders in the EN and ED groups were collected and analyzed following the aforementioned methods.

RESULTS

Interspecific comparison: MA silk properties

MA silk amino acid percentage data were available from 18 forest-dwelling *C. ginnaga* and 16 seashore-dwelling *C. mulmeinensis*. There was a significant difference in major MA silk amino acid percentages (MANOVA test, $\Lambda = 0.132$, $F_{5,28} = 36.90$, $P < 0.001$). The MA silks of *C. mulmeinensis* contained significantly higher percentages of glycine, serine, and lower percentage of glutamine (Table 1). The percentages of the other major MA silk amino acids did not differ significantly between these 2 spider species (Table 1).

MA silk samples from 37 *C. ginnaga* and 28 *C. mulmeinensis* showed significant differences in various mechanical properties (MANOVA test, $\Lambda = 0.261$, $F_{6,58} = 27.397$, $P < 0.001$) (Table 2). The MA silks of *C. mulmeinensis* were significantly thicker than those of *C. ginnaga*. Moreover, the extensibility, ultimate tension, and breaking energy of MA silks of *C. mulmeinensis* were significantly larger than those of *C. ginnaga*. The superior properties of *C. mulmeinensis* silks seemed to be due to their larger diameter because the standardized MA silk mechanical properties such as strength and toughness did not differ significantly between these 2 species (Table 2).

Interspecific comparison: web properties

A total of 54 *C. ginnaga* and 21 *C. mulmeinensis* webs were measured for body weight and web architecture comparisons.

Table 2**Mean (\pm SE) mechanical properties of MA silks produced by *Cyclosa ginnaga* and *Cyclosa mulmeinensis* and results of MANOVA tests**

	Diameter (μ m)	Extensibility (%)	Strength (MPa)	Toughness (MPa)	Ultimate tension (μ N)	Breaking energy (μ J)
<i>C. ginnaga</i> (<i>N</i> = 37)	0.59 \pm 0.04	9.67 \pm 1.05	1360 \pm 229	86.59 \pm 21.8	324 \pm 57	1.10 \pm 0.27
<i>C. mulmeinensis</i> (<i>N</i> = 28)	1.57 \pm 0.08	14.45 \pm 1.17	984 \pm 96	70.55 \pm 8.84	1469 \pm 143	6.48 \pm 0.95
<i>F</i>	134.444	9.159	1.853	0.084	85.601	53.295
<i>P</i>	<0.001	0.004	0.178	0.733	<0.001	<0.001

Table 3

Mean (\pm SE) web structural properties, stiffness and drag of *Cyclosa ginnaga* and *Cyclosa mulmeinensis*, and results of MANOVA (architectures) and ANCOVA (stiffness and drag) tests

	Web structural properties				Stiffness ^b (μ N)	Drag ^c (mN)
	Radii number ^a	Mesh height ^a (mm)	Catching area ^a (cm ²)	Total silk length ^a (cm)		
<i>C. ginnaga</i>	72.63 \pm 1.41	1.49 \pm 0.05	114.43 \pm 5.33	416 \pm 122	983 \pm 49	5.33 \pm 0.17
<i>C. mulmeinensis</i>	51.52 \pm 2.13	1.75 \pm 0.09	50.25 \pm 8.14	122 \pm 150	1020 \pm 102	3.27 \pm 0.16
<i>F</i>	65.09	7.677	41.7	183	9.289	0.185
<i>P</i>	<0.001	0.007	<0.001	<0.001	0.003	0.67

^a *N* of *C. ginnaga* and *C. mulmeinensis* are 54 and 21, respectively.

^b *N* of *C. ginnaga* and *C. mulmeinensis* are 44 and 21, respectively.

^c *N* of *C. ginnaga* and *C. mulmeinensis* are 17 and 16, respectively.

Although the body weight of *C. ginnaga* ($\bar{x} \pm$ standard error [SE] = 12.98 \pm 0.67 mg) was slightly smaller than that of *C. mulmeinensis* ($\bar{x} \pm$ SE = 15.29 \pm 1.93 mg), the difference did not reach statistical significance (*t*-test, $t_{25.86} = 1.130$, $P = 0.164$). There were significant differences in various web properties (MANOVA test, $\Lambda = 0.240$, $F_{4,70} = 55.558$, $P < 0.001$). In general, the webs of *C. ginnaga* were larger in area and denser (i.e., greater radii number, smaller mesh height, and longer total silk) than those built by *C. mulmeinensis* (Table 3). When considering the effects of radii number and spider body weight, web stiffness of *C. mulmeinensis* was significantly higher than that of *C. ginnaga* (Table 3). The effect of radii number on web stiffness was statistically significant (ANCOVA test, $F_{1,61} = 9.541$, $P = 0.003$), but spider body weight was not (ANCOVA test, $F_{1,61} = 2.366$, $P = 0.129$). In both species, there was a significant positive relationship between web stiffness and radii number (linear regressions, $r^2 = 0.094$, $F_{1,43} = 4.447$, $P = 0.041$ for *C. ginnaga* and $r^2 = 0.203$, $F_{1,19} = 4.818$, $P = 0.041$ for *C. mulmeinensis*) (Figure 4). The web stiffness/radii number correlation patterns of 2 species showed that for webs with identical stiffness, those built by *C. mulmeinensis* contained fewer radii than those built by *C. ginnaga*. Drag data were available from 17 *C. ginnaga* and 16 *C. mulmeinensis* webs. *Cyclosa mulmeinensis* webs experienced significantly smaller drag than the larger *C. ginnaga* webs under the same wind speed (*t*-test, $t_{31} = 12.621$, $P < 0.001$). When we performed the ANCOVA test, the species difference was no longer significant (Table 3), but total silk length turned out to be a significant determinant of drag ($F_{1,30} = 8.921$, $P = 0.006$).

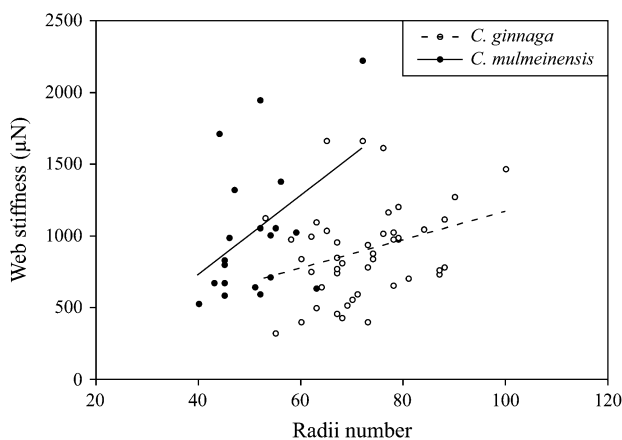


Figure 4
Relationship between stiffness and number of radii silks of webs built by *Cyclosa ginnaga* and *Cyclosa mulmeinensis* with linear regression lines plotted.

Interspecific comparisons: prey size and spider leg length

From 2 days of field survey, a total of 220 prey trapped on *C. mulmeinensis* webs were recorded. Among them, the most dominant insect taxa was Hemiptera (60%), followed by Diptera (23%) and Hymenoptera (15%). From another 2 days of field survey, a total of 130 prey trapped on *C. ginnaga* webs were recorded. These prey were composed of Diptera (47%), Hemiptera (38%), and Hymenoptera (10%). A χ^2 test of homogeneity showed that prey composition of 2 *Cyclosa* species differed significantly ($\chi^2 = 32.4$, $df = 5$, $P < 0.001$). The prey size distribution of both species deviated significantly from normality (Kolmogorov–Smirnov tests, $P < 0.001$ for both species), so a Mann–Whitney *U* test was used. The size of prey trapped by webs built by *C. mulmeinensis* ($\bar{X} \pm$ SE = 2.55 \pm 0.07 mm) was significantly larger than that of *C. ginnaga* ($\bar{X} \pm$ SE = 1.67 \pm 0.09 mm) (Mann–Whitney $U = 7301$, $P < 0.001$). Although 2 *Cyclosa* species did not differ significantly in body weight, the lengths of all legs of *C. ginnaga* were significantly longer than those of *C. mulmeinensis* (Table 4).

Wind effect on *C. mulmeinensis*: MA silk properties

MA silk amino acid percentage data were available from 19 CN, 19 CD, 16 EN, and 14 ED spiders, respectively. The amino acid percentages of MA silks produced by spiders in the CN and CD groups did not differ significantly (MANOVA test, $\Lambda = 0.908$, $F_{5,32} = 0.652$, $P = 0.622$, Table 5). This result indicated that after 3 days of acclimation in the laboratory, the MA silk amino acid percentages were similar among *C. mulmeinensis* individuals. There was no significant difference in MA silk amino acid percentages between silks produced by spiders in the EN and ED groups (MANOVA test, $\Lambda = 0.712$, $F_{5,24} = 1.940$, $P = 0.125$, Table 5). Such result suggested that *C. mulmeinensis* did not alter MA silk amino acid compositions when encountering short-term fluctuations of wind levels.

Table 4

Mean (\pm SE) leg lengths (mm) of *Cyclosa ginnaga* and *Cyclosa mulmeinensis* and results of MANOVA tests

	Leg 1	Leg 2	Leg 3	Leg 4
<i>C. ginnaga</i> (<i>N</i> = 24)	6.09 \pm 0.21	5.60 \pm 0.20	3.79 \pm 0.15	5.63 \pm 0.22
<i>C. mulmeinensis</i> (<i>N</i> = 29)	4.69 \pm 0.05	4.17 \pm 0.06	2.80 \pm 0.03	4.26 \pm 0.05
<i>F</i>	48.337	55.118	49.677	34.893
<i>P</i>	<0.001	<0.001	<0.001	<0.001

Table 5
Mean (\pm SE) percentages of major amino acids in MA silks produced by *Cyclosa mulmeinensis* receiving different wind disturbance treatments

	MA silk major amino acids					
	Alanine	Glycine	Glutamine	Proline	Serine	Others
CN ($N = 19$)	15.11 \pm 0.69	32.16 \pm 1.62	8.97 \pm 0.26	9.61 \pm 0.27	7.47 \pm 0.21	26.69 \pm 2.53
CD ($N = 19$)	16.60 \pm 0.69	34.84 \pm 1.13	9.44 \pm 0.34	10.41 \pm 0.38	7.34 \pm 0.18	21.77 \pm 2.10
F	1.246	1.825	1.232	3.009	0.204	2.239
P	0.272	0.185	0.274	0.091	0.654	0.143
EN ($N = 16$)	18.28 \pm 0.58	39.16 \pm 1.44	9.50 \pm 0.30	10.55 \pm 0.23	7.57 \pm 0.21	14.93 \pm 2.39
ED ($N = 14$)	18.46 \pm 0.18	39.19 \pm 0.62	9.83 \pm 0.21	11.20 \pm 0.23	8.30 \pm 0.27	13.03 \pm 0.93
F	0.080	0.001	0.748	3.984	4.609	0.490
P	0.780	0.985	0.394	0.056	0.041	0.490

CN and CD, pretreatment groups; EN, treatment control group; ED, treatment experimental group.

MA silk mechanical property data were available from 16 CN, 10 CD, 13 EN, and 13 ED spiders, respectively. MA silk produced by spiders in the CN and CD groups did not differ significantly in all properties measured ($\Lambda = 0.885$, $F_{6,19} = 0.412$, $P = 0.862$, Table 6). This result indicated that after 3 days of acclimation, various MA silk properties were similar among *C. mulmeinensis* individuals. Wind disturbance caused significant changes in various MA silk mechanical properties (MANOVA test, $\Lambda = 0.332$, $F_{6,19} = 6.369$, $P < 0.001$). Although MA silk diameter did not differ significantly between EN and ED groups (Table 6), when encountering wind disturbances, *C. mulmeinensis* considerably enhanced the mechanical properties of MA silks. The extensibility, strength, toughness, ultimate tension, and breaking energy of MA silks produced by ED spiders were all significantly higher than those of silks produced by EN spiders (Table 6).

Wind effect on *C. mulmeinensis*: web properties

Web structural property data were available from 15 CD, 13 CN, 20 ED, and 13 EN spiders, respectively. In pretreatment comparisons, there was no significant difference in various web structural properties measured (MANOVA test, $\Lambda = 0.729$, $F_{4,23} = 2.142$, $P = 0.108$, Table 7). Web stiffness was not significantly different between webs built by CN and CD spiders (Table 7), and neither spider body weight (ANCOVA test, $F_{1,24} = 0.333$, $P = 0.570$) nor radii number (ANCOVA test, $F_{1,24} = 0.617$, $P = 0.440$) had significant effects. In addition, results of both an ANCOVA (Table 7) and a t -test ($t_{23,59} = 0.949$, $P = 0.372$) showed that drag was also similar between webs built by CN and CD spiders (although total silk length

turned out to be a significant determinant of this variable, $F_{1,25} = 7.187$, $P = 0.013$). These results indicated that before spiders received different wind disturbance treatments, various aspects of their webs were similar. Wind disturbance had a significant effect on various web properties (MANOVA test, $\Lambda = 0.372$, $F_{4,28} = 11.806$, $P < 0.001$). Compared with webs built by EN spiders, those built by ED spiders contained significantly fewer radii (31% fewer), larger mesh height (51% larger), shorter silk (49% shorter), and were significantly smaller (36% smaller) (Table 7). However, the reduction of material used in constructing webs was not associated with lower web stiffness. Although webs built by ED spiders contained much fewer radii, their stiffness was similar to that of EN spiders (Table 7). Spider body weight had little effect (ANCOVA test, $F_{1,29} = 0.978$, $P = 0.331$), but radii number had a significant effect on web stiffness (ANCOVA test, $F_{1,29} = 6.702$, $P = 0.015$). The drag of webs built by ED spiders was significantly smaller than that of EN spider webs (t -test, $t_{19,87} = 3.440$, $P = 0.003$). When we performed the ANCOVA test, the treatment effect was no longer significant (Table 7), but total silk length turned out to be a significant determinant ($F_{1,30} = 4.761$, $P = 0.037$). Such results indicated that the smaller, less dense but equally strong webs built by spiders disturbed by artificial wind exhibited a reduced drag and therefore might be less likely to be damaged by strong wind.

DISCUSSION

Results of this study show that orb spiders inhabiting environments with different levels of wind disturbances exhibit adaptations in web and MA silk properties. The architectures of

Table 6
Mean (\pm SE) mechanical properties of MA silks produced by *Cyclosa mulmeinensis* receiving different treatments and results of MANOVA tests

	Mechanical properties					
	Diameter (μ m)	Extensibility (%)	Strength (MPa)	Toughness (MPa)	Ultimate tension (μ N)	Breaking energy (μ J)
CN ($N = 16$)	0.99 \pm 0.08	16.65 \pm 1.23	1509 \pm 313	110.43 \pm 16.12	852 \pm 116	4.11 \pm 0.62
CD ($N = 10$)	1.13 \pm 0.13	18.32 \pm 1.32	1017 \pm 160	93.55 \pm 14.46	821 \pm 213	4.62 \pm 1.19
F	1.000	0.795	1.389	0.519	0.019	0.175
P	0.327	0.382	0.250	0.478	0.891	0.679
EN ($N = 13$)	1.27 \pm 0.09	16.38 \pm 0.88	742 \pm 89	62.12 \pm 7.83	719 \pm 55.18	3.49 \pm 0.31
ED ($N = 13$)	1.10 \pm 0.08	19.21 \pm 0.89	1472 \pm 211	138.70 \pm 19.50	1012 \pm 59.18	5.99 \pm 0.51
F	2.132	5.116	10.200	13.287	13.071	17.615
P	0.157	0.033	0.004	0.001	0.001	<0.001

CN and CD, pretreatment groups; EN, treatment control group; ED, treatment experimental group.

Table 7

Mean (\pm SE) web structural properties of *Cyclosa mulmeinensis* receiving different treatments and results of MANOVA (architectures) and ANCOVA (stiffness and drag) tests

	Web structural properties					
	Radii number	Mesh height (mm)	Catching area (cm ²)	Total silk length (cm)	Stiffness (μ N)	Drag (mN)
CN ($N = 13$)	43.36 \pm 3.58	1.34 \pm 0.11	30.58 \pm 3.72	92.04 \pm 7.50	802 \pm 92	2.64 \pm 0.08
CD ($N = 15$)	41.73 \pm 2.72	1.33 \pm 0.07	35.34 \pm 2.61	104.42 \pm 7.20	912 \pm 94	2.55 \pm 0.06
<i>F</i>	0.153	0.006	1.145	1.418	0.631	2.585
<i>P</i>	0.699	0.938	0.294	0.244	0.435	0.120
EN ($N = 13$)	43.08 \pm 4.03	1.26 \pm 0.05	32.69 \pm 3.41	98.71 \pm 9.10	933 \pm 90	2.53 \pm 0.10
ED ($N = 20$)	29.60 \pm 1.60	1.90 \pm 0.16	20.9 \pm 1.75	50.72 \pm 3.70	853 \pm 68	2.15 \pm 0.06
<i>F</i>	12.69	9.882	11.441	31.058	0.864	1.493
<i>P</i>	0.001	0.004	0.002	< 0.001	0.360	0.231

CN and CD, pretreatment groups; EN, treatment control group; ED, treatment experimental group.

webs built by *C. mulmeinensis* and *C. ginnaga* differed significantly in various aspects. *Cyclosa mulmeinensis* webs have fewer radii silks, larger mesh height, smaller catching area, and shorter silks than those of *C. ginnaga*, indicating that the orb webs of the former contain less material to build into a less dense structure to reduce drag. We found that the variation of *C. mulmeinensis* webs' catching area and total silk length was considerably larger than that of *C. ginnaga*. Such a pattern might result from the fact that *C. mulmeinensis* inhabited areas with heterogeneous wind disturbances and, therefore, had huge intraspecific variation in web architectures. *Cyclosa ginnaga*, on the other hand, inhabited forest interior with relatively constant and calm conditions and, consequently, had lower variation in web structural values. Even the webs built by the seashore-dwelling *C. mulmeinensis* contained much fewer radii silks, and their stiffness was higher than that of the webs built by the forest-dwelling *C. ginnaga*. Such a phenomenon could be explained by the different mechanical properties of MA silks produced by these 2 species. The ultimate tension and breaking energy of MA silks produced by *C. mulmeinensis* were higher than those of *C. ginnaga*, potentially due to larger silk diameter. Although *C. ginnaga* webs contained discoid silk decorations and *C. mulmeinensis* webs were undecorated, because decorations silks were loosely applied on the radii silks (Foelix 1996), they should have had little effect on web stiffness. Therefore, it is the web and silk characteristics that help this seashore-dwelling species cope with environments with a high level of wind disturbances.

Other factors responsible for different web and silk properties of 2 *Cyclosa* species might be silk decorations and body weight. Both *C. ginnaga* and *C. mulmeinensis* incorporate prey pellets on webs, but only the former will build silk discoid decorations. Discoid silk decorations might further increase wind drag of the webs and might potentially increase the risk of web damages. This may explain why the seashore-dwelling *C. mulmeinensis* never decorate their webs with silk decorations. On the other hand, although results of previous studies showed that spider body weight also played important roles in web and silk properties (Reed et al. 1982), in our analyses, such variable had little effect on various variables, perhaps, because body weight varied little among the spiders of both *Cyclosa* species that we used.

The longer legs of *C. ginnaga* should have been associated with larger mesh height (Vollrath 1987), and yet it was the shorter legged *C. mulmeinensis* that produced webs with the larger mesh height. This suggests that leg length is not the sole determinant of web mesh height. Spiders exhibit flexibility in adjusting this structural property according to the ecological conditions they encounter. From the field surveys, we also found that the size of prey intercepted by *C. mulmeinensis*

webs was significantly larger than that of *C. ginnaga* webs. This may be because web structural properties were influenced by strong wind disturbances in 2 ways. *Cyclosa mulmeinensis* individuals building stiffer webs with lower wind drag might have been favored by selection. In addition, because larger insects cope better with wind, the larger mesh height and higher stiffness of *C. mulmeinensis* webs might enable greater success with larger prey. The availability of large prey might be one of the reasons why *C. mulmeinensis* inhabit areas of high wind disturbance even though in such habitats there is higher risk of web damages.

Results of this study demonstrate for the first time that orb-weaving spiders can adjust their silk properties when encountering different degree of wind disturbance, and such phenotypic changes do not have to involve silk amino acid composition alterations. Persistent wind induces *C. mulmeinensis* to produce MA silks of higher strength, extensibility, toughness, ultimate tension, and breaking energy as found in ED spiders. Such mechanical property enhancements can help spiders reduce potential web damage caused by winds. We found that strength, toughness, ultimate tension, and breaking energy of silks produced by EN spiders were lower than those of CD and CN spiders. Such results suggest that when *C. mulmeinensis* experienced consistent calm conditions for some period of time, they produced silks of lower mechanical property. Although the silk performance of EN spiders reflect *C. mulmeinensis*'s response to 10 days of relatively calm conditions (3 acclimation + 7 control treatment days), those of CN and CD spiders might partially reflect the wind disturbance they had experienced in the original habitat before the 3-day acclimation period. Surprisingly, we did not find that wind disturbance affects the major amino acid percentages in MA silks. Such a phenomenon suggests that when spiders encounter persistent wind disturbance, they do not significantly alter the expression pattern of *MaSp1* and *MaSp2* genes. Even so, the ultimate tension and breaking energy of MA silk produced by *C. mulmeinensis* in the ED group were significantly higher than those produced by EN spiders. The better performance of MA silks of *C. mulmeinensis* was not achieved by increasing silk diameter, like the case when comparing to *C. ginnaga* but by enhancing silk strength and toughness.

The incongruence of MA silk amino acid and mechanical property data indicates that wind disturbance does not affect silk at the gene expression stage but, perhaps, at the protein assembling stage. Previous studies show that the mechanical properties of MA silk are not only determined by relative amounts of *MaSp1* and *MaSp2* proteins but also by how they are assembled (Sponner et al. 2005b). During the spinning process, orb spiders seem to be able to adjust the relative amount of *MaSp1* and *MaSp2* gene products and their

arrangement pattern in the silk (Sponner et al. 2005a). MaSp1 molecules that were arranged more homogeneously seemed to facilitate the formation of crystalline area in MA silk and, thus, enhance silk mechanical property (Sponner et al. 2005b). On the other hand, owing to the biochemical nature of the MaSp2 molecule, this protein is proposed to interfere with MaSp1 molecule alignment and, thus, may affect crystalline formation (Sponner et al. 2005b). Theoretically, it is much faster to adjust MA silk mechanical properties by physiologically rearranging MaSp1 and MaSp2 molecules than by genetically altering the expression patterns of these 2 genes. Therefore, it is possible that orb spiders achieve silk property plasticity by physiologically adjusting the arrangement patterns of 2 silk proteins to quickly respond to environmental disturbances. The use of spidroin-specific antibodies may help determine whether MA silks produced by spiders receiving different levels of wind disturbance exhibit different MaSp1 and MaSp2 protein arrangement patterns.

Results of our manipulations showed that *C. mulmeinensis* could adjust web architectures when encountering persistent wind disturbance to reduce drag. Webs built by *C. mulmeinensis* in ED group were smaller, contained fewer radii and larger mesh height, and such result is congruent with those of previous studies (Hieber 1984; Vollrath et al. 1997). Even though ED spider webs contained much fewer radii, their stiffness was similar to that of EN spiders. Such result indicates that when orb spiders encounter persistent wind disturbance, they build smaller webs with fewer but stronger silk threads. Here we show for the first time that the aforementioned web structural changes could effectively reduce drag. The smaller drag of webs built by ED spiders seemed to be achieved by web structural changes. Theoretically, the drag force, D , is determined by

$$D = \frac{1}{2} C_d \rho S v^2,$$

where C_d is the drag coefficient, ρ is the density of the air, S is the surface area, and v is the wind velocity (Vogel 2003). Because in our manipulations, all variables except reference area were kept constant, a larger surface area would cause greater drag. The surface area of an orb is theoretically determined by total length as well as diameter of silks. Although we did not measure diameter of web silks and, thus, could not accurately estimate reference area, we used total silk length as an alternative estimator and suggest that the reduction in silk length post-wind disturbances to be the major reason of drag changes. Results of Tso et al. (2007) showed that there was a diameter correlation between forcefully drawn silks and web silks of the same spider individual. Because the diameter of MA silks forcefully drawn from ED and EN spiders was similar, it was very likely that web silk diameter of these 2 groups was also similar. Even though web silk diameter of different treatment groups might vary, the difference of total silk length between 2 treatment groups differed so much and such variation should greatly outweigh the potential difference of silk diameter. Therefore, the alteration in web silk quantities should be the major contributor of drag changes.

Results of this study demonstrate that a trap builder adjusts both trap structural design and material properties when encountering persistent wind disturbance. To cope with strong winds, orb spiders inhabiting seashore area build smaller and less dense webs with thicker and stronger silk threads. Moreover, these spiders exhibit plasticity in these trap characteristics. We suggest that such plasticity can help these trap builders balance the opposing needs of wind resistance and hunting performance. Previous studies showed that catching

area and mesh height significantly influence an orb's prey catching performance. Webs with larger area and smaller mesh tend to intercept more prey (see review in Heiling and Herberstein 2000). Therefore, a potential drawback of a more wind-resistant but smaller web is a reduced prey-catching performance. We suggest that *C. mulmeinensis*'s plasticity in web and silk properties reflect an adaptation to environments with fluctuating wind disturbance to trade-off wind resistance and hunting performance. Such plasticity allows spiders to build webs with smaller drag during windy days to preserve silk protein and to build larger webs with better prey-catching ability during calm days.

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REFERENCES

- Barber I, Nairn D, Huntingford FA. 2001. Nests of ornaments: revealing construction by male sticklebacks. *Behav Ecol*. 12:390–396.
- Blackledge TA. 1998. Stabilimentum variation and foraging success in *Argiope aurantia* and *Argiope trifasciata* (Araneae: araneidae). *J Zool*. 246:21–27.
- Blackledge TA, Gillespie RG. 2002. Estimation of capture areas of spider orb webs in relation to asymmetry. *J Arachnol*. 30:70–77.
- Blackledge TA, Zevenbergen JM. 2007. Condition-dependent spider web architecture in the western black widow, *Latrodectus hesperus*. *Anim Behav*. 73:855–864.
- Borges SD, Desai M, Shanbhag AB. 2002. Selection of nest platforms and the differential use of nest building fibres by the Baya weaver, *Ploceus philippinus* Linnaeus 1766. *Trop Zool*. 15:17–25.
- Borgia G. 1995. Complex male display and female choice in the spotted bowerbird: specialized functions for the different bower decorations. *Anim Behav*. 49:1291–1301.
- Burton NHK. 2006. Nest orientation and hatching success in the tree pipit *Anthus trivialis*. *J Avian Biol*. 37:312–317.
- Craig CL, Rieckel C, Herberstein ME, Weber RS, Kaplan D, Pierce NE. 2000. Evidence for diet effects on the composition of silk proteins produced by spiders. *Mol Biol Evol*. 17:1904–1913.
- Daws AG, Bennet-Clark HC, Flether NH. 1996. The mechanisms of tuning of the mole cricket singing burrow. *Bioacoustics*. 7:81–117.
- Eberhard WG. 1990. Function and phylogeny of spider webs. *Annu Rev Ecol Syst*. 21:341–372.
- Facemire CF, Facemire ME, Facemire MC. 1990. Wind as a factor in the orientation of entrances of cactus wren nests. *Condor*. 77:365–368.
- Foelix R. 1996. *Biology of spiders*. New York: Oxford University Press.
- Furness RW, Bryant DM. 1996. Effect of wind on field metabolic rates of breeding northern fulmars. *Ecology*. 77:1181–1188.
- Gosline JM, Guerette PA, Ortlepp CS, Savage KN. 1999. The mechanical design of spider silks: from fibroin sequence to mechanical function. *J Exp Biol*. 202:3295–3303.
- Hansell M. 2005. *Animal architectures*. Oxford: Oxford University Press.
- Hayashi CY, Shipley NH, Lewis RV. 1999. Hypotheses that correlate the sequence, structure, and mechanical properties of spider silk proteins. *Int J Biol Macromol*. 24:271–275.
- Heiling AM, Herberstein ME. 1999. The role of experience in web-building spiders (Araneidae). *Anim Cogn*. 2:171–177.
- Heiling AM, Herberstein ME. 2000. Interpretations of orb-web variability: a review of past and current ideas. *Ekológia*. 19:97–106.
- Herberstein ME, Gaskett AC, Glencross D, Hart S, Jaensch S, Elgar MA. 2000. Does the presence of potential prey affect web design in *Argiope keyserlingi* (Araneae, Araneidae)? *J Arachnol*. 28:346–350.

- Herberstein ME, Heiling AM. 1999. Asymmetry in spider orb webs: a result of physical constraints? *Anim Behav.* 58:1241–1246.
- Herberstein ME, Tso IM. 2000. Evaluation of formulae to estimate the capture area and mesh height of orb webs (Araneioidea, Araneae). *J Arachnol.* 28:180–184.
- Hieber CS. 1984. Orb-web orientation and modification by the spiders *Araneus diadematus* and *Araneus gemmoides* (Araneae: Araneidae) in response to wind and light. *Z Tierpsychol.* 65:250–260.
- Higgins LE, Buskirk RE. 1992. A trap-building predator exhibits different tactics for different aspects of foraging behaviour. *Anim Behav.* 44:485–499.
- Hinman MB, Lewis RV. 1992. Isolation of a clone encoding a second dragline silk fibroin. *Nephila clavipes* dragline silk is a two-protein fiber. *J Biol Chem.* 267:19320–19324.
- Kim S-Y, Monaghan P. 2005. Interacting effects of nest shelter and breeder quality on behavior and breeding performance of herring gulls. *Anim Behav.* 69:301–306.
- Kleineidam C, Ernst R, Rocas F. 2001. Wind-induced ventilation of the giant nests of the leaf-cutting ant *Atta vollenweideri*. *Naturwissenschaften.* 88:301–305.
- Köhler T, Vollrath F. 1995. Thread biomechanics in the two orb-weaving spiders *Araneus diadematus* (Araneae, Araneidae) and *Uloborus walckenaerius* (Araneae, Uloboridae). *J Exp Zool.* 271:1–17.
- Lin LH, Edmonds DT, Vollrath F. 1995. Structural engineering of an orb-spider's web. *Nature.* 373:146–148.
- Madden JR. 2003. Bower decorations are good predictors of mating success in the spotted bowerbird. *Behav Ecol Sociobiol.* 53:269–277.
- Nakata K. 2008. Spiders use airborne cues to respond to flying insect predators by building orb-web with fewer silk thread and larger silk decorations. *Ethology.* 114:686–692.
- Pasquet A, Ridwan A, Leborgne R. 1994. Presence of potential prey affects web-building in an orb-weaving spider *Zygiella x-notata*. *Anim Behav.* 47:477–480.
- Quader S. 2006. Sequential settlement by nesting male and female Baya weaverbirds *Ploceus philippinus*: the role of monsoon winds. *J Avian Biol.* 37:396–404.
- Ramirez M, Wall E, Medina M. 2003. Web orientation of the banded garden spider *Argiope trifasciata* (Araneae, Araneidae) in a California coastal population. *J Arachnol.* 31:405–411.
- Reed CF, Witt PN, Scarboro MB. 1982. Maturation and D-amphetamine induced changes in web building. *Psychobiology.* 15:61–70.
- Reid JM, Cresswell W, Holt S, Mellanby RJ, Whitfield DP, Ruxton GD. 2002. Nest scrap design and clutch heat loss in Pectoral Sandpipers (*Calidris melanotos*). *Funct Ecol.* 16:305–312.
- Ruxton GD, Hansell MH. 2007. Why are pitfall traps so rare in the natural world? *Evol Ecol.* doi: 10.1007/s10682-007-9218-0.
- Salomon M. 2007. Western black widow spiders express state-dependent web-building strategies tailored to the presence of neighbors. *Anim Behav.* 73:865–875.
- Sandoval CP. 1994. Plasticity in web design in the spider *Parawixia bistriata*: a response to variable prey type. *Funct Ecol.* 8:701–707.
- Schneider JM, Vollrath F. 1998. The effect of prey type on the geometry of the capture web of *Araneus diadematus*. *Naturwissenschaften.* 85:391–394.
- Schoener TW, Toft CA. 1983. Dispersion of a small-island population of the spider *Metepira datona* (Araneae: Araneidae) in relation to web-site availability. *Behav Ecol Sociobiol.* 12:121–128.
- Sherman PM. 1994. The orb-web: an energetic and behavioural estimator of a spider's dynamic foraging and reproductive strategies. *Anim Behav.* 48:19–34.
- Spöner A, Schlott B, Vollrath F, Unger E, Grosse F, Weisshart K. 2005a. Characterization of the protein components of *Nephila clavipes* dragline silk. *Biochemistry.* 44:4727–4736.
- Spöner A, Unger E, Grosse F, Weisshart K. 2005b. Differential polymerization of the two main protein components of dragline silk during fibre spinning. *Nat Mat.* 4:772–775.
- Summers RW, Humpreys E, Newell M, Donald C. 2002. Nest-site selection by crossbills *Loxia* spp. in ancient native pinewoods at Abernathy Forest, Strathspey, Highland. *Bird Stud.* 49:258–262.
- Tso IM. 1999. Behavioral response of *Argiope trifasciata* to recent foraging gain: a manipulative study. *Am Midl Nat.* 141:238–246.
- Tso IM, Chiang SY, Blackledge TA. 2007. Does the giant wood spider *Nephila pilipes* respond to prey variation by altering web or silk properties? *Ethology.* 113:324–333.
- Tso IM, Wu HC, Hwang IR. 2005. Giant wood spider *Nephila pilipes* alters silk protein in response to prey variation. *J Exp Biol.* 208:1053–1061.
- Turner JS. 2001. On the mound of *Macrotermes michaelseni* as an organ of respiratory gas exchange. *Physiol Biochem Zool.* 74:798–822.
- Turner JS. 2005. Extended physiology of an insect-built structure. *Am Entomol.* 51:36–38.
- Venner S, Pasquet A, Leborgne R. 2000. Web-building behaviour in the orb-weaving spider *Zygiella x-notata*: influence of experience. *Anim Behav.* 59:603–611.
- Vogel S. 1978. Organisms that capture currents. *Sci Am.* 239:108–117.
- Vogel S. 2003. *Comparative biomechanics: life's physical world.* Princeton (NJ): Princeton University Press.
- Vogel S, Ellington CP, Kilgore DL. 1973. Wind-induced ventilation of the burrow of the prairie-dog, *Cynomys ludovicianus*. *J Comp Physiol.* 85:1–14.
- Vollrath F. 1987. Altered geometry of webs in spiders with regenerated legs. *Nature.* 328:247–248.
- Vollrath F, Downes M, Krackow S. 1997. Design variability in web geometry of an orb-weaving spider. *Physiol Behav.* 62:735–743.
- Vollrath F, Köhler T. 1996. Mechanics of silk produced by loaded spiders. *Proc R Soc Lond B Biol Sci.* 263:387–391.
- Winkler S, Kaplan DL. 2000. Molecular biology of spider silk. *Rev Mol Biotechnol.* 74:85–93.
- Xu M, Lewis R. 1990. Structure of a protein superfiber—spider dragline silk. *Proc Natl Acad Sci USA.* 87:7120–7124.
- Zevenbergen JM, Schneider NK, Blackledge TA. 2008. Fine dining or fortress? Functional shifts in spider web architecture by the western black widow *Latrodectus hesperus*. *Anim Behav.* 76:823–829.