An Observational Study of Ballooning in Large Spiders

: Nanoscale Multi-Fibres Enable Large Spiders' Soaring Flight

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Abstract. The physical mechanism of aerial dispersal of spiders, 'ballooning behavior', is still unclear because of the lack of evidential observation and experiments. Therefore, as a first step to clarify the phenomenon, we observed the ballooning behavior of relatively large spiders (heavier than 5 mg) in nature. Additional wind tunnel tests to identify ballooning silks were implemented in the laboratory. From our observation it seems obvious that spiders actively sense the condition of the wind with their front leg (leg I), which means that spiders decide selectively their takeoff moment to increase the probability of the successful aerial dispersal. In the wind tunnel tests, as yet unknown physical properties of ballooning fibres (length, thickness and the number of fibres) were first identified. Large spiders, 16-20 mg *Xysticus* species, spun 50 to 60 nanoscale fibres, with a diameter of 121 to 323 nm. The length of these threads was 3.22 ± 1.31 m (N = 22). These physical properties of ballooning fibres can explain the ballooning of large spiders in a light breeze of 1.5-3.3 ms^{-1}. Additionally, in line with previous research on turbulence in atmospheric boundary layers, it is hypothesized that spiders use the ascending air current, the "ejection" regime, which is induced by hairpin vortices in the atmospheric boundary layer turbulence, for their aerial dispersal. This regime is highly correlated with lower wind speeds. Therefore, this hypothesis coincides with the fact that spiders usually balloon when the wind speed is lower than 3 ms^{-1}.

Keywords: spider ballooning, nanoscale fibre, dispersal, turbulence, hairpin vortex, coherent structure

1. Introduction

The earliest detailed observation of a ballooning spider was documented in 1715 by a thirteen year old boy, Jonathan Edwards, who later became a revivalist preacher and philosopher (Crosby et al. 1936, McCook 2006). He sketched the takeoff phase of a ballooner in rafting position. In 1827 Blackwall provided a first scientific description of tip-toe behavior as the initial process of spider ballooning (Blackwall 1827). Rafting and tip-toe poses are the most representative pre-ballooning behaviors of spiders (Bell at al. 2005). Many studies, which aimed to find meteorological determinants of ballooning spiders, have focused on the ballooning behavior of spiderlings (young spiders) just a few days after eclosion from their eggs (Coyle 1983, Morse 1992, Lee et al. 2015). To elucidate the physical mechanisms of ballooning, the information from the ballooning of young spiders is limited due to their small sizes of 0.5-2 mm. The observation of larger spiders with body sizes of up to 10 mm and weights of 5-100 mg could provide a good basis for the physical characterization of ballooning. The ballooning behavior of adult spiders was observed by a couple of researchers (Eberhard 1987, Wickler and Seibt 1987, Schneider et al. 2001). Eberhard observed the initiation of airborne lines as “spanning” or “ballooning” lines in at least 46 genera in 16 *araneomorphic* families (Eberhard 1987). Wicker and Seibt observed the ballooning of an adult of *Stegodyphus mimosarum* (Wicker and Seibt 1986). However the observed physical properties of ballooning silks and spider size (60-80 cm long and 3-4 silk threads, 85 to 150 mg body weight) seemed to be unrealistic for ballooning, because the required vertical speed of wind was 9.2 to 21.6 ms^{-1} according to Henschel’s calculation (Henschel 1995, Suter 1991). Later, Schneider observed the ballooning of an adult of *Stegodyphus dumicola*, which spun at least tens to hundreds of threads forming a triangular sheet (1 m length and width) (Schneider et al. 2001). In spite of these observations, some questions of spiders’ ballooning have not yet been answered, e.g.: (i) How many and how long are the silk fibres needed for ballooning, especially in the case of large spiders with weights over 5 mg? (ii) Which silk fibres and glands are used for ballooning? (iii) How do ballooning silks shape during the flight?

To answer these questions, the ballooning behavior of adult or sub-adult crab spiders (*Xysticus* spec., *Thomisidae*) was investigated. The whole process from takeoff to landing was observed and monitored in nature. Additional experiments were performed in the laboratory in a wind tunnel, for a precise observation and documentation of ballooning silks and the details of ballooning behavior. Finally, physical properties of ballooning silks were identified together with previously undescribed behaviors during ballooning: (i) an active sensing motion of the wind, (ii) an anchoring behavior during tip-toe takeoff, (iii) a tiding up motion of an anchor line (drag line or safety line), (iv) an outward stretching pose during a flight.

2. Materials and Methods

2.1 Field observations

Crab spiders *(Xysticus cristatus*, *Xysticus audax*, etc.) were collected in the Lilienthal park and along the Teltow canal in the Berlin area, Germany, and observed during each autumn, especially October, from 2014 to 2016.

The Lilienthal park was selected for the observation of pre-ballooning behavior, because the ballooning phenomenon of adult and sub-adult crab spiders is frequently observed in this region. On September 24-28, 2015, sunny and partly cloudy days, about fourteen crab spiders (8 females, 2 males and 4 not identified; adult or sub-adults) were collected at the Lilienthal park. These spiders were released in the same place on a self-built artificial mushroom-like platform (5.5 cm diameter, 1.2 m high, gypsum material). This platform was intended to stimulate 'tip-toe' pre-ballooning behavior. Because of its convex surface (half sphere), spiders can easily recognize that the top of the convex surface is the highest position that may promote 'tip-toe' behavior. The white color of this platform allowed the visual clarity of the spider's behavior. During the observation, the ballooning behaviors were recorded by digital camera. Additionally, titanium tetrachloride was used for the flow visualization of the wind. The local wind speed and temperature were not available, but the values from the Dahlem weather station (4.5 km distance from the observation site) were used.

Gliding and landing of crab spiders was observed along the Teltow canal, due to ecological and topographical benefits for the observation of ballooners. (i) Crab spiders frequently glide along the canal during the autumn season. (ii) The angle of the sun rays in the morning time was appropriate for the detection of the ballooning silks during their flight. (iii) The dense trees on the opposite side of the canal provide a dark background, which facilitates the observation of floating silks. The shape of the ballooning silks was sketched and documented. Two landing phenomena on the water surface were observed. These spiders were collected and later identified in the laboratory.

2.2 Observations using a wind tunnel

Twelve crab spiders (9 females and 3 males, adult or sub-adult), collected in the Lilienthal park, were used for the wind tunnel experiment. Pre-ballooning behavior of these spiders was induced in front of an open jet wind tunnel in which the diameter of the nozzle exit is 0.6 m. There were no obstacles next to the wind tunnel, leaving about 9 m of free space from the nozzle, to allow ballooning fibres to float horizontally without any adhesion to other objects. The wind speed and temperature were measured with a PL-135 HAN hot-wire anemometer. The wind speed was fixed at 0.9 ms^{-1}. The room temperature was 20-25°C. The ballooning behavior was stimulated with a hair dryer that produces warm air and the fluctuation of wind. Spun ballooning fibres were collected on a microscope slide, on which two narrow strips of a double sided bonding tape were attached. One strip is sampled

from the portion near the spinnerets. The other is sampled on another slide at the end of ballooning threads far from the spinnerets. A total of 2 successful samples were prepared from several trials. If it was failed to capture all ballooning fibres on a single microscope slide or even a little mess on the slide, the sample was excluded. Simultaneously, those silk fibres were captured on a square wire frame and carefully wound around it in order to measure the length of ballooning threads. The length of silks can be calculated by multiplying the total number of half revolutions by the width of the square wire frame, 20 cm (Fig 1). The successfully sampled ballooning fibres were later observed with a field emission scanning electron microscope.

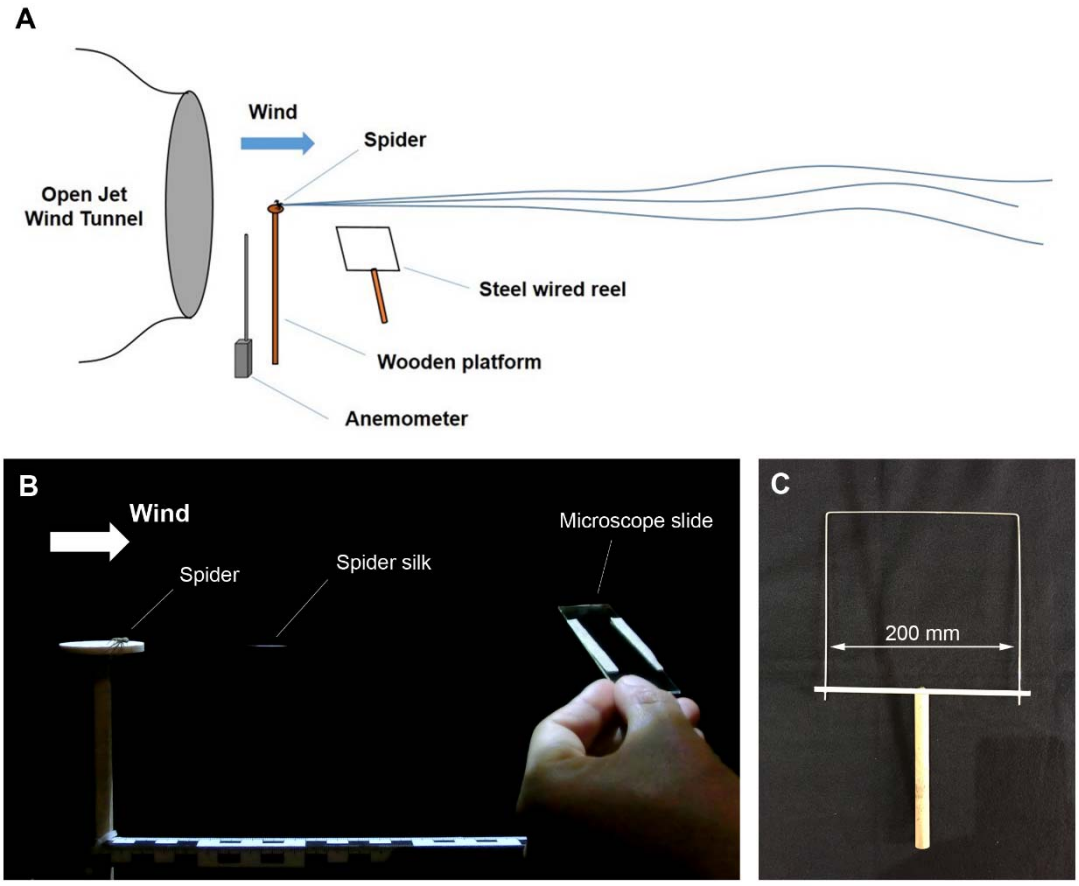

Fig 1. (A) A schematic view of wind tunnel tests (B) Sampling of ballooning fibres in front of an open jet wind tunnel. (C) Reel with a steel wire to measure the length of ballooning silks.

2.3 Field emission scanning electron microscopy (FESEM)

The sampled ballooning fibres were coated with gold using a sputter coater (SCD 030, Balzers Union) and observed with a field emission scanning electron microscope (DSM 982 Gemini, ZEISS, with 5-10 kV accelerating voltage). The number of ballooning fibres was carefully counted and the thickness of fibres was measured. The spinnerets of a female *Xysticus cristatus*, were also observed with the FESEM. For sample preparation, the female spider was fixed in 2.5% glutaraldehyde and dehydrated in ascending concentrations of acetone from 30 to l00% (10 min at each concentration). After dehydration the sample was dried with a critical point dryer (CPD 030, BAL-TEC). The prepared sample was coated with gold using a sputter coater (SCD 030, Balzers Union) and observed

with the FESEM (SU8030, Hitachi, with 20 kV accelerating voltage).

2.4 Animal care

Each adult and sub-adult crab spiders (*Xysticus* genus) was raised separately in a plastic box (length × width × height: 13 × 13 × 7 cm), which has ventilation holes. Once a week the spiders were fed with a mealworm, *Tenebrio molitor,* and moisture was provided by a water spray.

2.5 Ethics

The species used in the experiments (*Xysticus* genus) are not endangered or protected species. No specific permissions were required. All applicable international, national and institutional guidelines for the care and use of animals were followed.

3. Results

3.1 Field observations

3.1.1 Takeoff

On the artificial platform at the experimental site, crab spiders, not only female but also male, showed pre-ballooning behaviors, 'tip-toe' and 'rafting'. It is well known that young instars and adult female spiders balloon for their biological dispersal (Schneider et al. 2001). However in the *Thomisidae* family, male adults also balloon, too (Fig S1, Dean and Sterling 1985). During the days of investigation, the temperature was 16-19°C and the mean wind speed was 6-7 ms^{-1} (gust 14-17 ms^{-1}) as reported by the nearest weather station in Dahlem.

At warm temperatures and under a mild wind speed of about 3 ms^{-1} the spiders mostly showed 'tip-toe' behavior. This pre-ballooning behavior led to another interesting finding. The crab spider evaluated the wind condition, not just passively through the sensory hairs on its legs, but rather actively, by raising one of its front-legs (leg I) or sometimes both, and waited in this position for 5-8 sec. This sensing behavior was often repeated a couple of times before the 'tip-toe' pose. After each sensing step, the crab spider rotated its body in wind direction (Fig 2).

If the spider decided that the wind was adequate to balloon, it raised its abdomen (already known as a 'tip-toe' behavior) and spun its ballooning silks. It would spin a group of silk fibres spontaneously without any help of the legs. This process was called 'spontaneous spinning' (Eberhard 1987). There was a motion of a rear leg (leg IV) (Fig S2), resembling the behavior earlier described by Eberhard as wiping the spinnerets or 'wrap spinning' (Eberhard 1987). However, in our case, from careful video investigation, it was obvious that the spiders did use their leg IV not to initiate ballooning lines, but to hold their safety line, that connected their spinnerets to the substrate. It seemed that this leg IV motion tidied the unfamiliarly positioned safety line, which might have obstructed the spinning of ballooning silks.

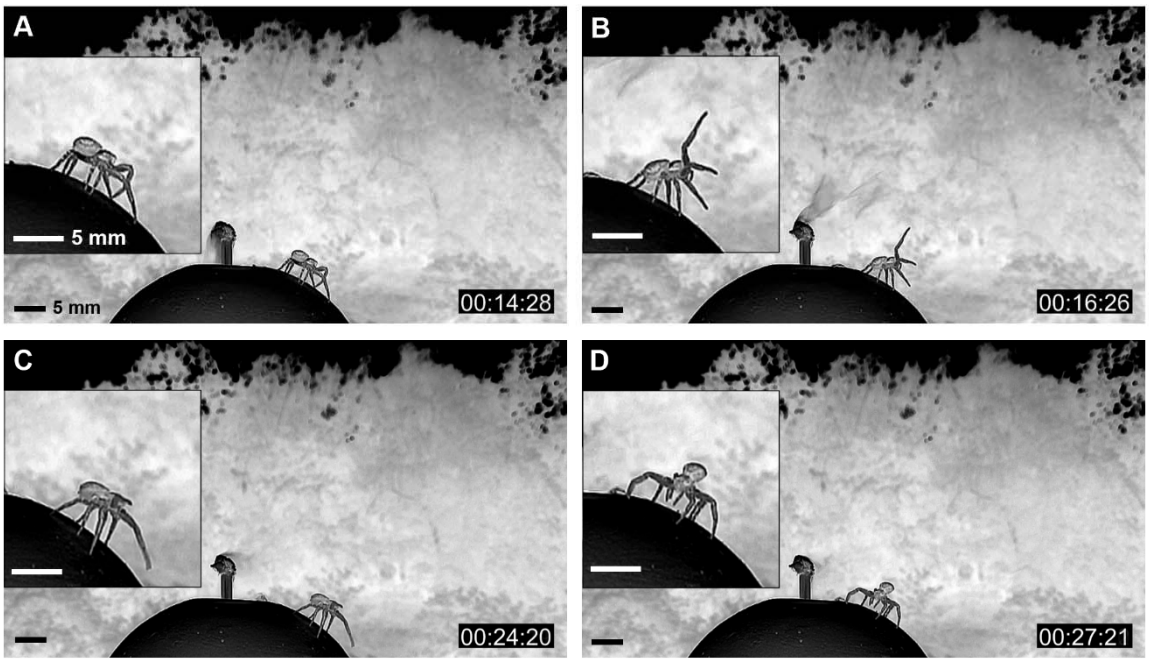

Fig 2. Sequence of active sensing motion with front leg (leg I) (Negative images). (A) The spider first senses the condition of the wind current only through sensory hairs on her legs. (B) Then, if the condition seemed appropriate, the spider sensed more actively by raising its leg I and keeping this pose for 8 sec. (C) If the spider decided to balloon, it altered its posture. (D) The Spider rotated its body in wind direction and postured 'tip-toe'.

With the naked eye, the crab spider first spun a single or a few number of fibres, and then many fibres. The spun ballooning fibres were approx. 2-4 m long and formed a triangular sheet, which fluttered among the turbulent flows of wind. The vertex angle of this triangular sheet was about 5-35 degrees (Fig 3). If the wind condition was not appropriate, the spider cut the silk fibres and spun them again, a phenomenon which had already been observed by Blackwall in 1826 (Blackwall 1827). If the ballooning silks generated enough drag, the spider released the substrate and became airborne. Many ballooned crab spiders soared diagonally upwards along the wind flows. This paths had 5-20 degrees inclination above the horizon. Some spiders traveled quasi-horizontally. Some spiders soared along a steep path (about 45 degree). During this steep takeoff the spider took off with relatively slow speed. The anchored drag line (safety line) between the platform and the spider's spinneret could be seen. This anchored line endured without breaking, until it became 3-5 meters long. At some time, it was broken mechanically. These anchored drag lines are possibly normal drag lines (major ampullate silks), which a spider spins constantly while its crawling and attaching its silk fibres to the ground surface for safety purpose, because it was found from the wind tunnel experiment that the anchored drag line consists of two fibres (Osaki 1999). These drag lines have a 1-2 μm thickness.

Three new facts about ballooning were uncovered. First, the crab spider does not evaluate the wind condition passively, but actively, by raising one of its front-legs (leg I). Second, this adult ballooner anchors its drag lines on the platform not only during its 'rafting' takeoff, but also during "tip-toe" takeoff. Third, the crab spider postures

all its legs outwards and stretched, when airborne, not only at the takeoff moment, but also during the gliding phase (Fig S3). This pose seems to generate a maximum drag during flight.

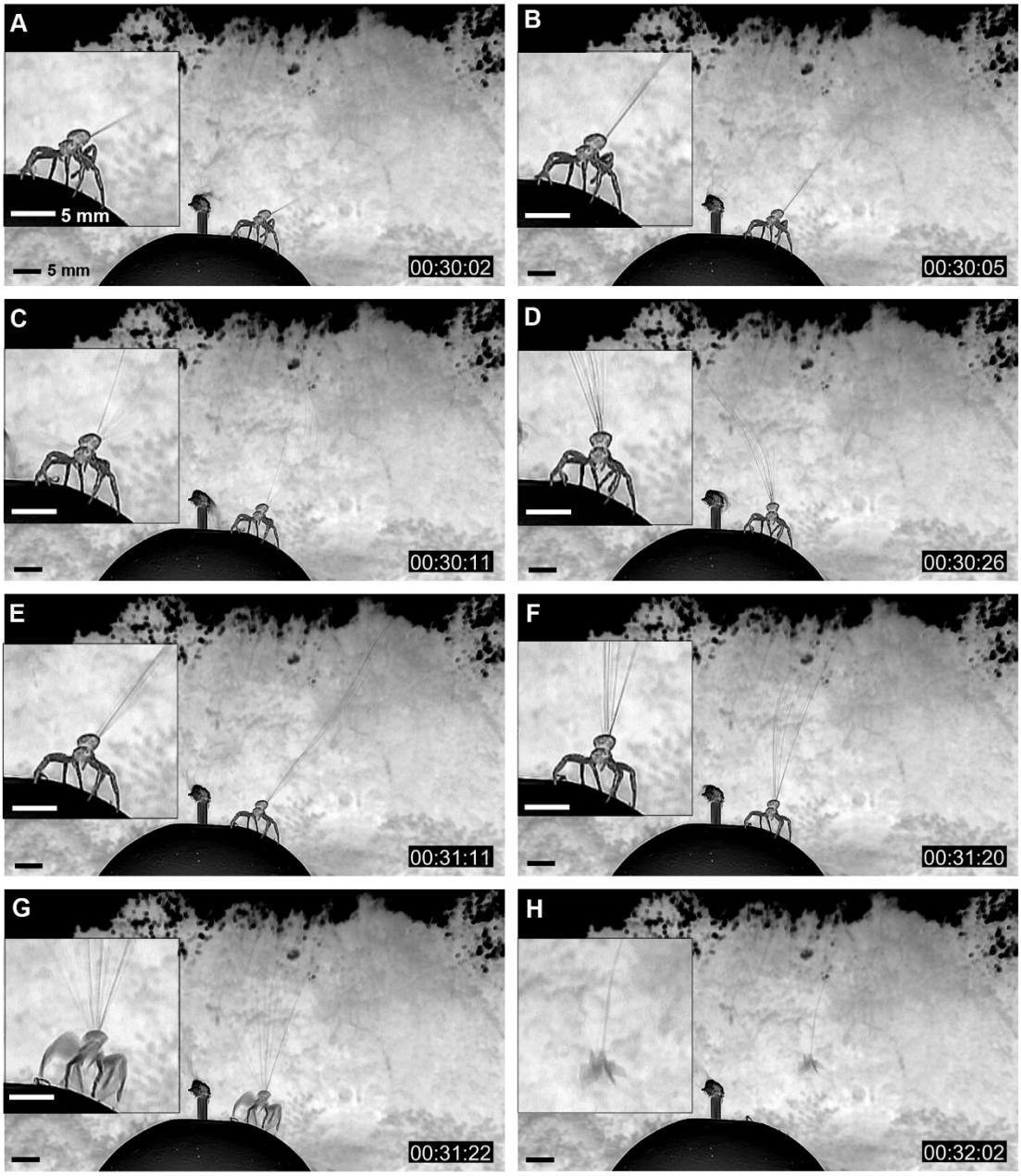

Fig 3. A crab spider's ballooning process (Images were converted to negative images to visualize ballooning lines). (A, B) Initial phase of spinning ballooning lines; (C, D, E, F) Fluttering of a bundle of ballooning lines. Because of turbulent flows in wind, the ballooning threads fluttered unsteadily; (G) Takeoff moment; (H) Airborne state of a ballooning spider. (Original video: see the movie in supporting information)

'Rafting' pre-ballooning behavior could also be observed. On September 26 and 28, 2015, the wind speed was 6 ms^{-1} (gust: 16 ms^{-1}) and the temperature was 16°C, measured by the Dahlem weather station. The local weather condition was a little bit colder and windier than on September 24, 2015. Crab spiders were not active on that day. As soon as they were set on the platform, they showed either one of two behaviors. Either they hid on the opposite side of the platform to avoid the wind, or they quickly retreated downwards about 0.4 to 1.1 m relying on their

drag lines, and spun their multiple ballooning fibres downstream of the wind. During this process, the spiders also postured all its front legs and second legs outwards and backwards, so that they hung and directed their bellies in an upwards direction of the wind. The backward (downstream) spun threads slowly curved upwards and the spiders' body also slowly moved upwards. At some point, when the threads had generated enough drag and lift, the drag lines near the spinnerets were cut and the spider finally ballooned.

This detailed behavior of ballooning was evaluated statistically. The fourteen crab spiders were set 25 times onto the mushroom shaped platform. If they did not tend to balloon and hid for about five minutes, they were recollected. Once a spider raised one or both front legs and then put them back again on the platform, this was considered to be an active sensing motion, and was counted as one behavior. 'Tip-toe' motion, raising abdomen and putting down again was also counted as one motion. Duration was also measured. However silk spinning duration could not be measured because it was not visible.

When the weather conditions for ballooning were appropriate, the spiders showed 67 active sensing motions with their leg I. 44 of these sensing motions were connected to 'tip-toe' pre-ballooning motions. A total of 6 spiders had ballooned successfully after their 'tip-toe' pose. They also dropped down 8 times relying on their drag lines. Three of them showed a 'Rafting' takeoff (Table 1).

Table 1 Ballooning behaviors on the artificial platform

Date (2015)	Temp. [℃]	Wind (mean /gust) [ms^{-1}]	Number of specimens	Number of tests	Sensing motion	Tip-toeing		Rafting		Total Ballooned Spiders	Escape (Fall down)
						Tried	Ballooned	Drop & Climb	Ballooned		
9.24 (13:00-14:30)	19	6/17	7	13	48	31	4	1	0	4	3
9.26 (13:00-15:30)	16±1	7/14	5	10	19	13	2	5	1	3	2
9.28 (12:00-12:30)	16	6/16	2	2	0	0	0	2	2	2	0
Total			14	25	67	44	6	8	3	9	5

The duration of each "tip-toe" behavior was measured and their frequencies were analyzed. Short period "tip-toe" poses, which lasted for less than 5 sec, were the most frequent. The longest "tip-toe" event lasted 65 sec. Successful ballooning takeoffs were not biased in relation to "tip-toe" duration (Fig 4).

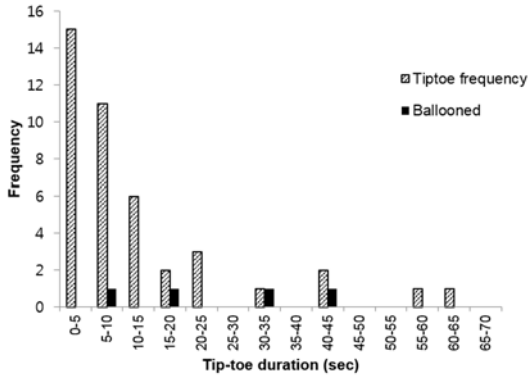

Fig 4. Frequency diagram of "tip-toe" behaviors according to "tip-toe" duration (N = 42). Black columns are the "tip-toe" behaviors which were connected to the successful ballooning takeoffs (N = 4).

3.1.2 Gliding

On October 3, 2016 over thirty gliding spiders were observed at the Teltow canal. Most of them were horizontally transported along the channel at about 1-8 m above the water surface. They drifted passively due to light wind, but rarely fell down. With the naked eye about 2 to 5 threads could be observed. Some of them were inclined downstream. The others were inclined upstream. The shape of the threads during flight could not be photographed nor recorded as a video, because only limited parts of the ballooning threads were reflected by the sun rays. However the movement and shape of the threads could be recognized with the naked eye and these shapes were quickly sketched by hand.

A total of 32 floating threads was sketched. Two of them were just threads alone without a spider. The number of observed threads was one to five. However, as not all threads were visible with the naked eye, some may have been the multiple threads, which stuck together, although they seemed to be a single thread. Some of them may not have been seen, because of their inappropriate angles and positions in relation to the sun. Most of the spiders positioned at the lower end of their threads. This means that the body of the spiders played the role of a weight and constrained the motion of one end of the spider's threads in the wind. Although the threads showed different numbers and shapes, they were usually laid diagonally (Fig 5).

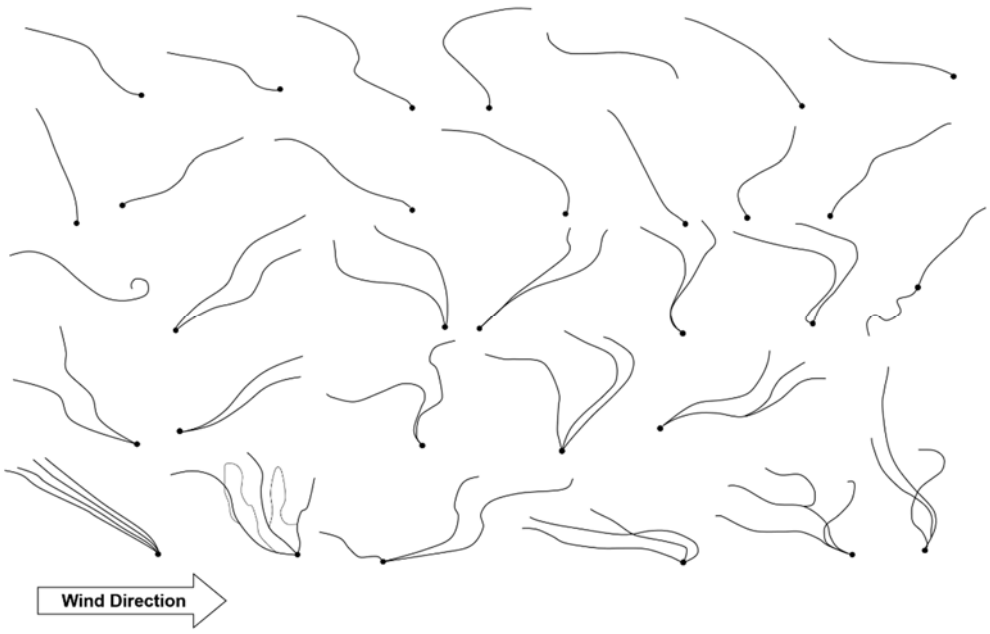

Fig 5. Sketches of ballooning structures (body + ballooning threads). These structures were observed above the water surface, at heights of 1-8 m. Wind was blowing from left to right. Therefore, these structures were transported in the same direction as the wind. Black and thick points represent spider's body. Black lines represent ballooning threads.

3.1.3 Landing of ballooner

The landing of a crab spider on the water surface was observed at the Teltow canal on the afternoon of November 2, 2015, at a temperature of about 12-13°C. Although the temperature was relatively cold, the sun was shining and there was a light breeze (0.3-1.5 ms^{-1} by the Beaufort wind speed scale). The ballooning lines of this spider were 4 to 5 m long and consisted of 5 to 6 threads. The threads were tangled at a couple of points and were inclined about 35 degrees from the horizontal surface (Fig S4A). The landed spider didn't sink. It floated on the water surface, supported by the water surface tension and its ballooning silks were hung on the bank of the canal. The spider did not move for over 30 min and did not show any sailing pose (not like that which was recently observed by Hayashi; Hayashi et al. 2015). The spider was rescued and identified as a female with a weight of 12.9 mg. Another landing was observed on the same day. The air movement was very calm, about 0-0.3 ms^{-1} (by the Beaufort wind speed scale). A silk about 10 m long floated horizontally at a heights of 2-3 m above the water surface. One end of the silk was connected to the crab spider, which was floating on the water surface. Another 6-8 m threads were floating opposite the 10 m thread. A light wind pulled these threads towards the bank and hung them on it (Fig S4B). There were two crab spiders (one large and one small), with weights of 23.8 mg and 6.6 mg, respectively. For about 5 min the large spider didn't show a sailing posture, nor any movement; then it started to wind up its thread in order to climb up from the water surface. Both spiders were females.

3.2 Identification of Ballooning Fibres

For the quantitative study, the production of ballooning silks was induced in front of an open jet wind tunnel in the laboratory. The spinning behaviors that led to the ballooning silks was observed precisely. The anchored drag line

was connected to the anterior spinnerets and ballooning fibres were spun from either one or both posterior or/and median spinnerets (Fig S5). The length of the ballooning fibres from 16-20 mg spiders was finally measured, 3.22 ± 1.31 m (N = 22) (Fig 6). The maximum length of the spun ballooning lines was 6.2 m.

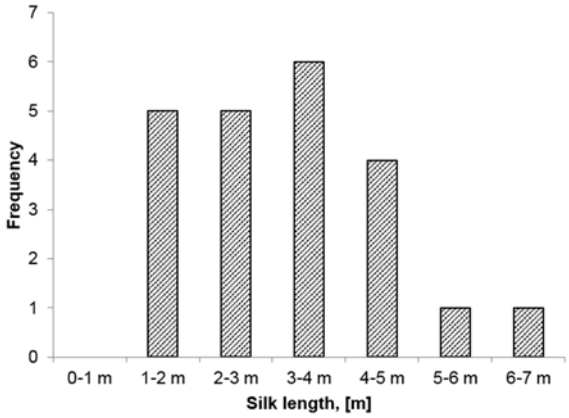

Fig 6. Distribution of the length of ballooning lines (N = 22).

The successfully collected ballooning fibres of both *Xysticus cristatus* and *Xysticus* spec. were observed with the FESEM. Ballooning fibres consist of two thick nanoscale fibres and many thin nanoscale fibres. The two adult spiders, *Xysticus* spec., spun, 48 to 58 thin nano-fibres and 2 thick nano-fibres that were attached together (Table 2). The thickness of the thin nano-fibres ranged from 121 to 323 nm with an average of 211.7 ± 45.2 nm (N = 40). The thickness of the thick nano-fibres was 698 to 768 nm with an average of 722.2 ± 32.5 nm (N = 4) (Fig 7). These thin nanoscale fibres seemed aciniform fibres (wrapping silk) from median/poster spinnerets and the thick nanoscale fibres seemed minor ampullate silks from median spinnerets. The initially spun fibre which was regarded as a single fibre consisted of a group of nano-fibres that had a diameter of 1.761 μm (Fig 7D). The next fibres were separated independently (Fig 7A,B,C). On the other hand, drag lines consist of one pairs of fibres (sometimes two pairs, from left and right) which were spun from the major ampullate glands on the anterior spinnerets. One pair of a drag fibres (safety line), which were attached together, was observed. The thickness of these major ampullate silks was about 790 nm for *Xysticus cristatus* and 493 nm for *Xysticus audax* respectively (Fig 7E,F).

Table 2 Identification of the number and thickness of ballooning fibres through FESEM

	Species	Weight	Thin nanoscale fibres		Thick nanoscale fibres	
			Number of fibres	Thickness of fibres	Number of fibres	Thickness of fibres
Spider 1	*Xysticus spec. (f.)*	20.8 mg	58	192.3 ± 36.3 nm (N = 20)	2	734.0 ± 48.1 nm (N = 2)
Spider 2	*Xysticus cristatus (f.)*	18 mg	48	231.1 ± 45.6 nm (N = 20)	2	710.5 ± 17.7 nm (N = 2)
Average	-	-	53 ± 7.1 (N = 2)	211.7 ± 45.2 nm (N = 40)	2 (N = 2)	722.2 ± 32.5 nm (N = 4)

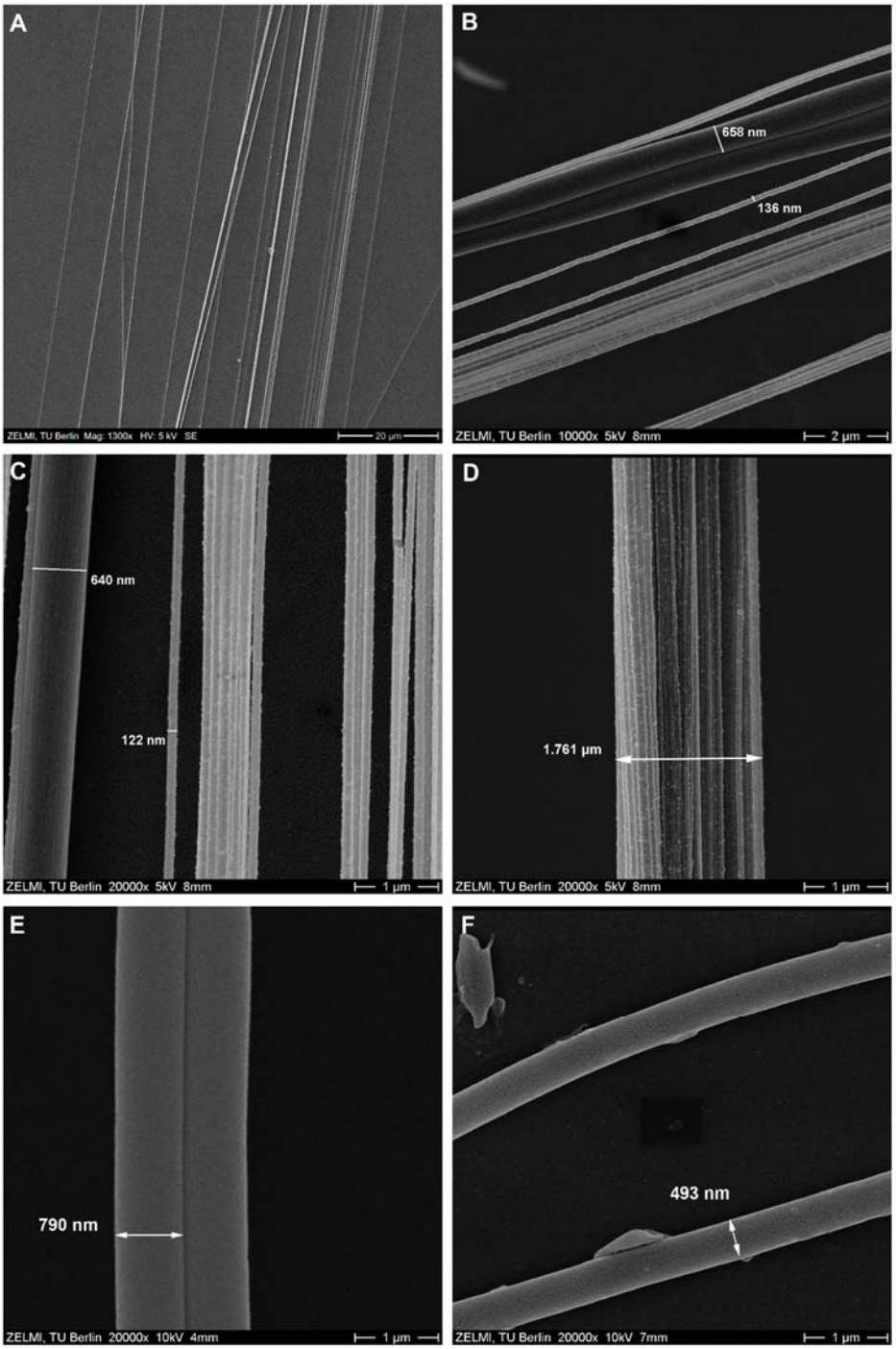

Fig 7. (A) Ballooning fibres of *Xysticus cristatus*. (1300×). (B) Ballooning fibres of *Xysticus audax* (10000×). (C) Middle part of ballooning fibres of *Xysticus audax* (20000×). (D) A bundle of ballooning fibres of *Xysticus audax* at the end of threads (20000×). (E) Drag lines of *Xysticus cristatus* (a weight of 18 mg) (20000×). (F) Partially separated drag lines of *Xysticus audax* (a weight of 16.4 mg) (20000×).

4. Discussion

Spider's active sensing motion of the wind condition

How spiders actively evaluate meteorological conditions in order to balloon was first observed and interpreted in the present study. Normally ballooning behavior is first triggered either by a warm ambient temperature or by a rapid increase of ambient temperature (Richter 1971, Vugts and Van Wingerden 1976).

Additionally, if they are exposed to a wind which is slower than 3 ms^{-1}, they show 'tip-toe' behavior. Until now it had been known that spiders sense the wind speed passively through the sensory hair (Trichobothria) on their legs (Palmgren 1936, Vugts and Van Wingerden 1976, Humphrey 1987). However, the present observations show **that spiders sense the aerodynamic condition of wind not just passively, but rather actively, raising their leg I high and shaking it.** This spider's active sensing motion of the wind tells us two important things. **First, in spiders ballooning, aerodynamic force maybe be a dominant factor.** One hypothesis claims that an electrostatic charge on ballooning silks could generate lifting forces in the Earth's vertical atmospheric electrostatic field (Gorham 2013). But the leg raising behavior indicates that, from the spider's viewpoint, airflow is an important factor for its ballooning. This behavior can be interpreted as follows: the spider enhances the sensibility of its sensory hairs, by raising its legs upward in the outer region of the boundary layer, where airflows are faster than near the substrate. The first instars of the *coccid Pulvinariella mesembryanthemi* show a similar behavior by standing on their hind legs to increase their body drag for their aerial dispersal (Washburn and Washburn 1984). **Second, the spiders do not simply rely on the random condition of the wind, but they intellectually sense, evaluate, the condition of the wind and decide the right moment for their takeoff.** The sequential process of ballooning behaviors that link active sensing motion, tip-toe behavior and takeoff, strongly supports the above hypothesis. The active sensing motion reduces the number of takeoff failures. This is a distinct feature of spiders' ballooning in contrast to other passive aerial dispersal, like that of seeds or aero-planktons.

There are still other questions that can be asked. What type of information do spiders need for their decision to balloon? From previous studies and the author's observations, we can deduce a couple of factors. (i) Wind speed: A spider does not show 'tip-toe' behavior under conditions of high wind speed, over 3 ms^{-1} (Richter 1971, Vugts and Van Wingerden 1976, Lee et al. 2015). (ii) A vertical wind speed: Favorable condition for ballooning, usually vertical acceleration of wind, persisting only for a few seconds. Under such a condition the spider spins its silk fibres in wind rapidly and releases its substrate (Richter 1971, Suter 1999). (iii) Wind direction: From our observation, spiders rotate their body to the wind direction, as soon as they have evaluated the wind condition. Therefore at least spider perceives, not only elevation (Suter 1999), but also direction of the wind. (iv) Wind fluctuation: For drop and swing dispersal, spiders were particularly more incentive with turbulent flows (Barth 1991). This means that spiders can perceive the fluctuation of a turbulent flow. Suter showed that the ballooning site is usually laid within chaotic air flows (Suter 1999). Reynolds showed that the chaotic motion of turbulent flow reduces the terminal speed of ballooners and that this feature enables long permanence in the air (Reynolds et al. 2006). Therefore, it can be deduced that spiders may sense the fluctuation of wind.

Nanoscale multi-fibres and ballooning flight

While the ballooning of small spiders, which are lighter than 2.0 mg, was investigated by calculation (Humphrey 1987), experiments (Suter 1991) and observation (Suter 1999), the plausibility of a large spider's ballooning was so far not explained (Humphrey 1987, Henschel 1995). **The mysterious flying behavior of large spiders can be explained by their nanoscale multi-fibres.** From our wind tunnel test, we found that the *Xysticus* genus uses tens of nano fibres (diameters of 121 to 323nm) for their aerial dispersal. The number of ballooning fibres and their lengths were identified. Based on these measured values, the required updraft speed for the ballooning takeoff was calculated using modified Humphrey's and Suter's equations (equation (1)-(5); Humphrey 1987, Suter 1991) (Fig 7A-D, Table 2). **For a crab spider weighing 10 to 25 mg, the required vertical wind velocities, according to Humphrey's theoretical formula 0.08-0.20 ms^{-1}, and according to Suter's empirical formula, are 0.04-0.09 ms^{-1}.** These values are much smaller than the values, 9.2 – 21.6 ms^{-1}, which were calculated for *Stegodyphus* species (Wicker and Seibt 1986, Henschel 1995). Humphrey's chart cannot explain the ballooning of large spider, weighing over 9 mg (Humphrey 1987). Our results show plausibility for the large spider's flight at low wind speeds regime (2-3 ms^{-1}), that can intermittently produce 0.1-0.5 ms^{-1} updraft. Our results also quantitatively prove Schneider's observation that adult females of the *Stegodyphus* genus balloon with at least tens to hundreds of threads (Schneider et al. 2001). From our experiments, *Xysticus* species. spun maximally 60 nanoscale fibres.

The ballooning silks, exposed to the air, experiences a low Reynolds number flow (Stokes flow, their Reynolds number is smaller than 1). The upper limit of the Reynolds number is about 0.04 ($Re = \rho V d/\mu$; Air density: 1.225kgm^{-3}, maximum possible velocity: 3 m^{-1}, thickness of spider silk: 211 nm, dynamic viscosity of air: 1.837 x 10^{-5} $kgm^{-1}s^{-1}$). The maximum possible speed, that the thread experiences, is assumed to be 3m/s, because a spider seldom flies above this wind speed. The maximum relative wind speed between spider silk and air also occurs at its takeoff phase, when the spider silk is point-fixed to its substrate. Once a spider is airborne, the relative speed of air with respect to the silk is reduced. Therefore, the Reynolds number of spiders' silks during their flight is much smaller than 0.04. Therefore, a spider's flight is connected to this micro-fluid mechanics (Purcell, 1977). They collect the microscopic drags using their high tensile strength nanoscale fibres to support their macro-scale bodies. This kind of silk-soaring is a special passive flight in comparison with other insects' flight that mostly use membrane-like wings.

$$D_H = \sum_{i=1}^{n} \frac{2\pi \cdot \mu \cdot U \cdot l_i}{ln(2l_i/d_i) - 0.72} \quad (1)$$

$$D_S = \sum_{i=1}^{n} 11.5 \cdot l_i \cdot U \cdot W_{eq,i}^{0.094} \times 10^{-6} \quad (2)$$

$$U_H = \frac{W}{\sum_{i=1}^{n} \frac{2\pi \cdot \mu \cdot l_i}{ln(2l_i/d_i) - 0.72} + 1.94 \cdot W^{0.366} \times 10^{-6}} \quad (3)$$

$$U_S = \frac{W}{\left(\sum_{i=1}^{n} 11.5 \cdot l_i \cdot W_{eq,i}^{0.094} + 1.94 \cdot W^{0.366}\right) \times 10^{-6}} \quad (4)$$

$$W_{eq,i} = \frac{\pi(d_i \times 10^6)^2 + 0.184}{0.0277} \quad (5)$$

D_H: Drag of multiple spider silks by Humphrey's equation in N.

D_S: Drag of multiple spider silks by Suter's equation in N.

U_H: Required vertical wind speed for ballooning using Humphrey's equation in ms^{-1}

(Body drag is used from Suter's equation).

U_S: Required vertical wind speed for ballooning using Suter's equation in ms^{-1}.

μ: Dynamic viscosity of the air at 20℃ ($1.837 \times 10^{-5} kg \cdot m^{-1} s^{-1}$).

U: Velocity of the air in ms^{-1}.

l_i: Length of i-th silk fibre in m.

d_i: Diameter of i-th silk fibre in m.

W: Weight of the spider body in N.

$W_{eq,i}$: Equivalent weight of the spider body corresponding to the diameter of a ballooning fibre in μN.

Shear flow and the spider's posture

From our observed facts, the following hypothesis is deduced: **The spiders' outstretching motion of its legs during flight may be intended to increase the influence of the horizontal shear flows in the wind on its ballooning structure (silks + body) which is thus able to reduce terminal speed of this structure.**

If a ballooning structure lies in a horizontal shear flow, its ballooning silks are stretched horizontally forming diagonally inclined shape because of the spider body weight (Fig S6). This diagonally lying shape of the spider's ballooning fibres was observed in our field observations in the Teltow canal (Fig 5). It showed an irregular shape of its fibres, that Reynolds postulated the tangled shape of ballooning fibres due to his simulation of the ballooning structure in a homogeneous turbulence (Reynolds et al. 2006). However, our observation showed a greater

tendency for those silk fibres to be stretched diagonally. This difference between our observation and Reynolds' simulation is caused by the fact that while Reynolds introduced homogeneous turbulence in his simulation, the real turbulence near the surface boundary layer includes instantaneous horizontal wind shears which are mostly induced by vertical differences in wind speed (Grass 1971, Dennis 2015). Here we could have the question why some of the ballooning structures inclined upstream (not downstream), indicating that the upper end of the threads directs upstream and the spider body directs downstream? If we consider the positive gradient of a mean wind profile, the upper end of the threads should direct downstream. This question give us a somewhat important key idea about the ballooning phenomenon in which the instantaneous horizontal shear flow is indirectly induced by a coherent structure in the atmospheric boundary layer, that is generated by the vertical wind profile. This will be discussed later.

From Suter's empirical formular, spiders' (weighing 10 to 25 mg) body drags per unit velocity, which are 10.4-14.5 $\mu\mathrm{N} \cdot m^{-1}s$, are just 0.4-0.56% of the whole drag (silks + body) per unit velocity, 2593-2608 $\mu\mathrm{N} \cdot m^{-1}s$. Although spiders stretch their legs outwards, the percentage of body drag is still 2-2.8% (5-fold change is applied. from Suter's research) (Suter 1991, 1992). Despite such a small drag, spiders stretch their legs outwards during flight (Fig S4C,D). Therefore, it could be questioned, what type of role do the stretched legs play in ballooning flight. Suter concluded that when a spider uses a relatively short length of silk, the influence of posture on its terminal speed is greater than when the silk is very long (Suter 1992). As was shown from our wind tunnel experiment and calculation, the crab spider spins an abundant number of silks, length, which indicates that the influence of posture may be small. Here, we hypothesize that a spider intends to increase its body drag using its legs, not vertically, but horizontally, to enlarge the influence of shear flow on the ballooning structure. This intention induces diagonally laid shape of ballooning structure and then finally reduces its terminal speed indirectly, because horizontally stretched silks produce more drag than vertically distributed shapes of silk, because of an anisotropic drag of silks in a low Reynolds number flow (Childress 1981). This hypothesis should be proved by studying the effect of shear flow on ballooning flight. The wind gradient is suspected to be an influential factor on ballooning dispersal in Greenstone's study (Greenstone 1990).

Low wind velocity and Turbulence

In line with previous research on turbulent flow in the atmospheric boundary layer, we hypothesize that the reason why spiders show their pre-ballooning behavior at a low wind speed regime (smaller than 3 ms^{-1}) is because they use the "ejection" regimes in turbulent flow, which contain updraft components and are induced by a "coherent structure" near the surface boundary layer. Many studies agree with that spiders do

their ballooning only when the wind speed is lower than 3 ms^{-1} (Richter 1971, Vugts and Van Wingerden 1976, Lee et al. 2015). Why do spiders fly mostly in this low wind regime? The answer could be found in the previous studies about turbulent flow in the atmospheric boundary layer. A shear flow on a planted field, a meadow, or relatively short plants, forms an organized structure called the "coherent structure" (possibly "hairpin vortex" or "horseshoe vortex", Fig 8A,B) (Theodorsen 1952, Adrian et al. 2000, Hommema and Adrian 2003, Adrian 2007, Finnigan et al. 2009, Dennis 2015). These structures intermittently produce up- and downdrafts (Adrian et al., 2000, Adrian 2007, Finnigan et al., 2009). The interesting point is that these updrafts are highly correlated with a decrease of wind speed, which is categorized as Q2 ($u' < 0$ and $v' > 0$), an "ejection" region in a quadrant analysis (Adrian 2007, Steiner et al. 2011, Zhu et al. 2007). u' and v' respectively mean streamwise fluctuating velocity and vertical fluctuating velocity, which are equal to the subtracted values of the actual values of velocity minus the mean values of wind speed. Therefore, the phenomenon that spiders usually balloon in the low wind speed regime (lower than 3 ms^{-1}) could be explained with this organized structure in atmospheric turbulent flows above the ground. These organized structures appear in nature as 'hairpin vortex packets' or 'dual hairpin vortex structures' over relatively short plants or planted field (Fig 8C,D). The hairpin vortex packet is the three dimensional space which is surrounded by various hairpin vortices (hairpins or cane-type vortices). This region grows upwards from the wall and creates a streamwise low momentum and upward flow. The turbulent flow over a planted field builds a dual hairpin vortex, which consists of a head-up hairpin vortex and a head-down hairpin vortex. This dual hairpin vortex is developed as follows: If there is a wind gradient on a plant field, its shape is like the wind gradient of a free shear flow (Finnigan et al. 2009). This wind gradient initially produces transversely laid Helmholtz vortex tubes. If the shear increases, the vortex tubes are stretched in the main flow direction. When the head of the vortex tubes is laid at the top, there is an updraft region. If the head of the vortex tubes is laid at the bottom, there is a downdraft region. These upwards flow regions in both 'hairpin vortex packets' and 'head-up hairpin vortices' can be used for the spiders takeoff.

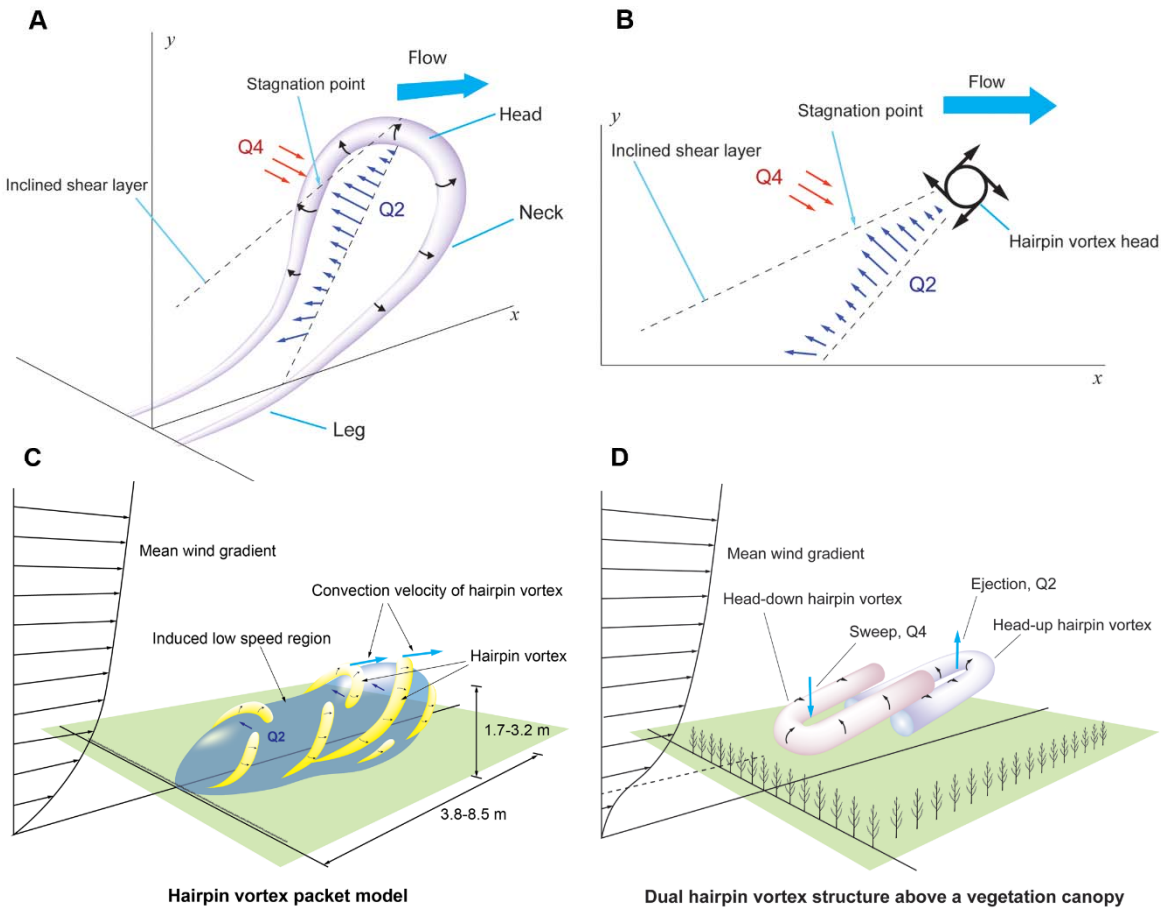

Fig 8. (A) Schematic diagram of a single hairpin vortex in the wall boundary layer. Q2 is an "ejection" region whose velocity vectors are u' < 0 and v' > 0. Q4 is a "sweep" region whose velocity vectors are u' > 0 and v' < 0. (B) Cross-section of the x-y plane of the hairpin vortex. (C) Schematic diagram of the hairpin vortex packet. Yellow colors mean hairpins or cane-type vortices. Blue region means low momentum region, which contains upward air currents. (D) Coherent structure, "dual hairpin vortex", on the plant field. Head-down hairpin vortex produces "sweep" event. Head-up hairpin vortex produces "ejection" event. (A, B) Redrawn from [Adrian et al. 2000] (C) Redrawn from [Adrian et al. 2000, Hommema and Adrian 2003] (D) Redrawn from [Finnigan et al. 2009]

Triangular sheet of ballooning fibres and electrostatic force

Here we postulate that the possible cause of triangle fan shaped ballooning silks is turbulent flows. The shape of multiple ballooning silks during pre-ballooning behavior is like a triangular sheet that flutters (Fig 3). A similar shape was observed by Schneider, triangular sheet (1 m length and 1 m width) (Schneider et al. 2001). From our observation, the vertex angle of this triangle sheet varied from 5 to 35 degrees, which is smaller than Schneider's value (about 60 degrees). Darwin and Schneider thought that such a fan shape might be due to electrostatic forces on ballooning fibres. However, if it is true, it can be questioned, why these silk fibres scatter forming a 2-dimensional sheet, and not a 3-dimensional conical shape? The 2-dimensional fluttering sheet can be explained by the fluctuating airflow. If a bundle of ballooning threads is fixed to the spider's spinnerets and the rest floats in a fluctuating air flow, normally the tension forces in the silks near the spider's spinnerets are larger than the tension

forces in the silks which are far from the spinnerets. The larger tension plays a role as a constraint for the movement of fibres. Therefore, the segments near the spinnerets drift relatively little against the wind fluctuation. The smaller tension forces in the silks, which are far from the spinnerets, result in the lager drifts by the wind fluctuation. If we consider the continuity of fluid, the tension forces in the fibres near the spinnerets should be changed in series. These serial differences of tension forces determine the consequential series of fibre positions. This can be the reason why a bundle of ballooning fibres builds a two-dimensional fluttering sheet in turbulent wind. From our observations in both, field and wind tunnel experiments, the silks mostly diverged two dimensionally building a surface which fluttered against the flow fluctuation. However, if the threads are exposed to steady uniform flows, a bundle of silks merged into one thread.

5. Conclusion and outlook

To find the clues which can elucidate the physical mechanism of spider's ballooning, the adult and sub-adult crab spider's ballooning behavior was observed in the field and in a laboratory. A couple of important features in ballooning behavior were observed and identified. From these features we conclude that

(1) Fluid-dynamic (aerodynamic) force is a major force, which rules the ballooning phenomenon, from spider's behavioral evidence, active sensing motion of wind condition.

(2) Spiders do not rely on the randomness of wind condition. To reduce failures in their takeoff, they intellectually sense, evaluate the condition of the wind and decide the right moment to takeoff.

(3) The physical values of ballooning silks were identified by tests in a wind tunnel. *Xysticus* spider's ballooning lines consist of 2 ± 0 thick nanoscale fibres (N = 2), 722.2 ± 32.5 nm (N = 4), and 53 ± 7.07 thin nanoscale fibres (N = 2), 211.7 ± 45.2 nm (N = 40). The length of the ballooning silks was 3.22 ± 1.31 m (N = 22). These values show that large spiders produce abundant ballooning fibres for their flight and they can perform soaring flight with a light updraft of air of 0.1-0.5 ms^{-1}. Therefore, the ballooning of large spiders is not mysterious, but possible from the aerodynamic viewpoint.

(4) The glands for ballooning silks are inferred from the observation in the wind tunnel test. The crab spiders seem to produce ballooning fibres through either one or both their median or/and posterior spinnerets, which contain minor ampullate glands and aciniform glands.

(5) From observed shape of silks during spiders' gliding, the instantaneous horizontal shear flow in the atmospheric boundary layer may be the main influential factor on spider's ballooning, rather than turbulent flow.

(6) Spiders stretch their legs outwards during their flight. Considering the small percentage of body drag in

comparison to the whole drag (body drag + silk drag), the drag maximizing posture may be intended to increase the spiders body dag horizontally, not vertically, in order to increase the influence of shear flow on their ballooning structure.

(7) In line with previous research on turbulent flow in the atmospheric boundary layer, we hypothesize that the reason why spiders show their pre-ballooning behavior at a low wind speed regime (under 3 ms^{-1}) is due to the use of the "ejection" regimes ($u' < 0$ and $v' > 0$) in turbulent flow. In the "ejection" region, the low speed region is usually highly correlated with updraft wind components.

In future work, the influence of a shear flow on a ballooning structure and the possible updraft condition in the atmosphere for spiders' ballooning flight will be studied.

6. Supporting Information

Fig S1. Ballooning behavior of a male crab spider. The spider shows the tip-toe behavior and spins ballooning silks.

Fig S2. Tidying motion of spider's safety line (anchored line) with leg IV before spinning of ballooning lines.

Fig S3. (A, B) An anchored line was found during a "tip-toe" takeoff. As soon as spiders were airborne, they stretched the legs outwards. (C) To ensure the behavior of outstretched legs during flight, the pose of a spider was observed during its gliding phase. (D) The spider kept its legs outstretched.

Fig S4. (A) Sketches of landing of 12.9 mg female crab spider, Xysticus spec. (B) Sketches of landing of 23.8 mg and 6.6 mg crab spiders, Xysticus spec. (C) 12.9 mg female crab spider on the water surface. (D) 23.8 mg and 6.6 mg crab spiders on the water surface.

Fig S5. (A) Spinning motion of ballooning silks in front of the open jet wind tunnel. Ballooning lines were spun from either or both of a median or/and posterior spinnerets. (B) Spinnerets of *Xysticus cristatus* through FESEM.

Fig S6. (A) Ballooning structure in a shear flow. (B) Drift of a ballooning structure along with wind. The upper and lower parts of a silk are exposed to the flow fields which exert to the other directions. (C) The ballooning structure exposed in a shear flow is stretched horizontally. If the drag of a body increases, the structure is stretched more horizontally. (V_{wG}: Wind speed profile relative to ground, V_D: Drift speed of a ballooning structure, V_{wR}: Wind speed profile relative to a ballooning structure, D_S: Horizontal component of drag on the spider's body, h : height)

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8. Competing interest

No competing interests declared.

9. Author contributions

MS.C. designed the study, performed the experiments and wrote the script. I.R. and P.N. supervised the design of the study and contributed to the writing of the script. MS.C and C.F. executed the FESEM observation. All authors gave final approval for publication.

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