

## BALLOONING: DATA FROM SPIDERS IN FREEFALL INDICATE THE IMPORTANCE OF POSTURE

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**ABSTRACT.** Ballooning, the aerial displacement of a spider caused by friction between air and the spider with its silk, has considerable ecological importance but remains poorly understood as a mechanical process. The studies reported here provide insight into the mechanics of ballooning by way of experiments involving (1) stroboscopic measurement of the rates of fall of spiders slowed by known lengths of silk and (2) direct measurement of the drag generated by moving air at the surface of spiders as those spiders change their postures. The terminal velocities of spiders trailing silk, derived from their rates of fall at known distances from release, were remarkably variable. The variability could not be attributed entirely to silk length and spider mass, and in some cases silk length was not even statistically correlated with terminal velocity. Drag measurements made on living spiders revealed that the variability in terminal velocities could be explained by variability in posture.

Some spiders, particularly small ones, travel great distances by ballooning. The ecological circumstances under which ballooning occurs are now well-documented (e.g., Richter 1970, Vugts & Van Wingerden 1976), and data derived from newly developed techniques (Greenstone et al. 1985) should increase our understanding of the temporal, spatial, and geographical parameters of ballooning. The physics of ballooning, in a theoretical sense, has also been well elucidated, both very generally (Vogel 1981) and in considerable detail (Humphrey 1987). In contrast, our empirical information about the physics of ballooning has been limited to deductions from micrometeorological, behavioral, and morphometric observations of ballooning (e.g., Dean & Sterling 1985, Eberhard 1987, Greenstone et al. 1987), and a single experimental study (Suter 1991).

In that earlier paper, I reported on the drag produced by silk and by whole spiders under the laminar flow conditions of a wind tunnel. The most useful results of the study were a set of equations relating the weights of spiders and the lengths of their ballooning silks to their terminal velocities and to the velocities of rising air necessary to make them airborne. Because the experiments involved spiders of several families, many sizes, and a variety of shapes, the results were quite general and therefore directly applicable, in a sense, only to spiders of average shape and a particular posture. Nevertheless, for a living spider of a particular weight, the equations

allowed one to predict roughly its terminal velocity at any known length of ballooning silk (Suter 1991).

The experiments reported below constitute an extension of that work, by testing the true terminal velocities of falling spiders against the predictions generated in the earlier work.

### METHODS

**Spiders.**—The great majority of ballooning spiders have masses below 2 mg (Greenstone et al. 1985, 1987), although much larger spiders are found among the aerial plankton (Coyle et al. 1985). Because of that size distribution, only small spiders were used in this study. In freefall trials, five spiders were subjects: three were unidentified hatchling theridiids (0.18, 0.18, and 0.2 mg), one was an unidentified immature theridiid (1.8 mg) and one was an immature *Uloborus glommosus* (Walckenaer) (Uloboridae) (1.0 mg). In the drag measurement trials, both subjects were unidentified theridiids, one a hatchling (0.18 mg) and one an immature (7.2 mg). The spiders were captured from their webs in August and September 1991 and were maintained in plastic vials at 100% R. H. for the few hours to few days between capture and testing. They were not fed during their captivity and were weighed within 24 hours of testing.

**Freefall.**—Figure 1 shows the apparatus used to measure the acceleration and velocity of spiders falling through still air in a dark room. In each trial, a spider was induced to attach its drag-

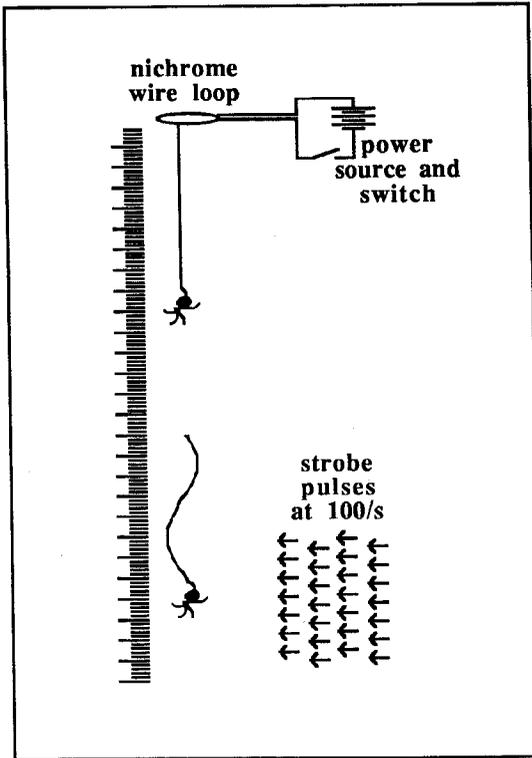


Figure 1.—Apparatus used to measure the velocity of a spider falling through still air while trailing a known length of dragline silk. Electrical current applied to the nichrome wire loop at the top released the silk and spider. The falling spider, illuminated by stroboscope flashes at 100/s, was photographed as it fell past the stroboscope and camera (not shown). The nichrome wire loop could be adjusted to any height, allowing experimental manipulation of the distance the spider fell before being photographed.

line to a small nichrome wire loop (diameter: 0.5 cm). At some point during its subsequent descent, electrical current was fed to the wire loop which incandescenced rapidly and released the spider trailing its dragline (a hot-wire anemometer indicated no measurable air flow, at 1 cm below the wire loop, during the first 0.5 s after the loop was energized). Dim light focused on a ruler near the path of the dangling and then falling spider allowed an observer to note and record the length of silk with which the spider had been suspended just prior to its release. A camera with its shutter open, mounted so that it focused on both the ruler and the path of the falling spider, recorded the position of the spider during each flash of a strobe (set at 100 flashes/s). Because of the very brief duration of each flash, high speed film (Ko-

dak TMAX 3200) was used to record the spider's motion. The height of the nichrome wire loop was adjustable, which made it possible to alter the distance a spider fell before it appeared in front of the camera.

Each spider in these trials was tested repeatedly, at different silk lengths and at different distances from its release. The resulting velocity vs. distance lines were plotted together with theoretical curves derived from drag measurements made on spiders and their silk in wind tunnel experiments reported elsewhere (Suter 1991). Many of the velocity vs. distance lines were long enough to confirm that their shapes conformed to the theoretical curves (e.g., Figs. 3–5). I therefore assumed that all of the lines represented segments of similarly shaped curves, and estimated the terminal velocities by extrapolation in cases in which the final three data points did not indicate relatively constant velocity (e.g., Figs. 6–7).

**Drag measurement.**—Data derived from the freefall trials suggested that variation in spider posture strongly influenced the rates of fall of spiders trailing draglines. Because posture was difficult to ascertain from the images produced during freefall trials, I designed the apparatus shown in Fig. 2 to allow direct observation of posture and simultaneous measurement of drag. The apparatus constituted a miniature wind tunnel in which air near the aperture was in laminar flow and had velocity (measured by a hot wire anemometer) that could be closely controlled (at air speeds less than 0.2 m/s, velocities varied less than 0.008 m/s). The tests reported here took place at an air velocity of 0.07 m/s.

Each spider in these trials was attached at the posterior surface of the abdomen (with cyanoacrylate glue) to the end of a wire 1.4 cm long (diameter: 17.8  $\mu$ m). The other end of this wire was connected with paraffin to the end of a galvanometer needle (see Fig. 2). An opaque plastic target (1.2  $\times$  2.0 mm) mounted on the galvanometer needle partially interrupted the beam of a HeNe laser, so that very small movements of the needle were detected as changes in the amount of light falling upon a photodetector. DC output from the photodetector was converted to a frequency modulated signal by passing it through a voltage-controlled oscillator circuit, and the FM signal was recorded on one audio channel of the videotape that was recording the activities of the spider.

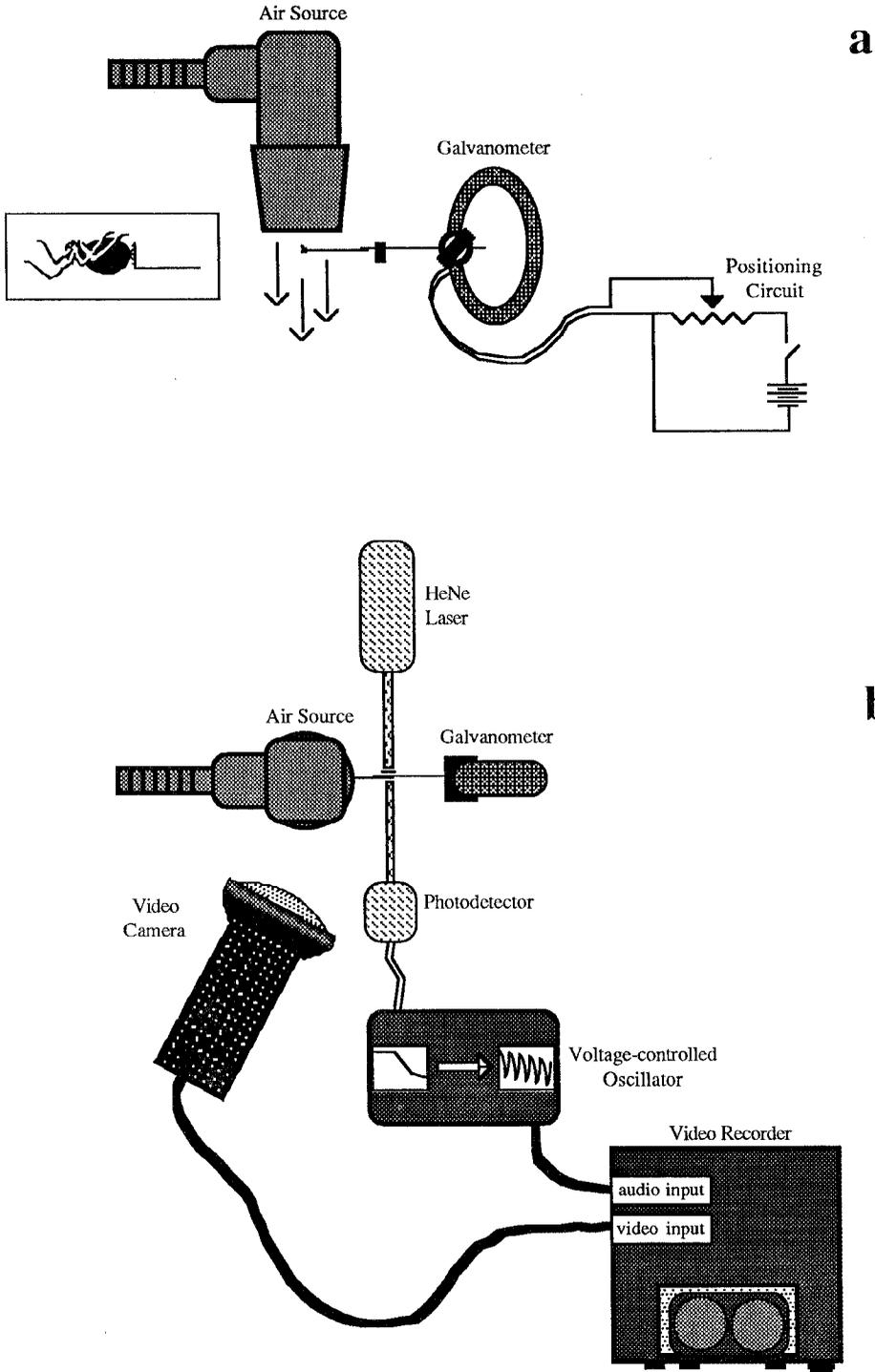
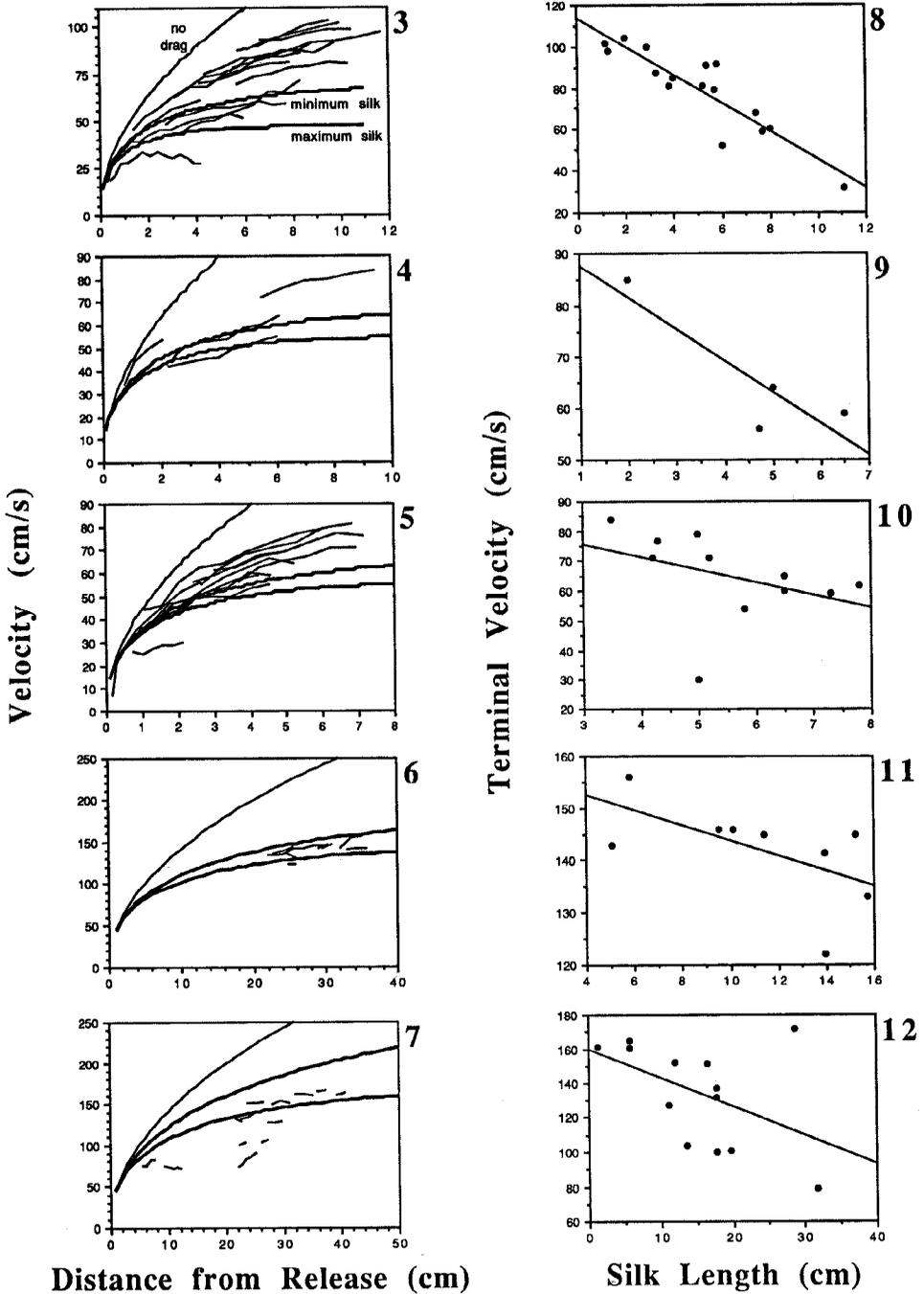


Figure 2.—Side view (a) and top view (b) of the apparatus used to measure drag generated by a living spider in a laminar air flow while recording changes in its posture. Changes in the posture of the spider (above the middle arrow in *a*, and inset) caused changes in friction between the moving air and the spider's surface, and that change in drag caused movement of the needle. The change in position of the needle was detected as an altered amount of light falling on the photodetector (in *b*). Both the FM-encoded signal bearing drag information and the video signal bearing posture information were recorded for later analysis.



Figures 3–12. — Each graph on the left contains data pertaining to a different spider as it fell, repeatedly, through still air. In each graph, the top curve represents the velocity of an object falling through a vacuum; the other two curves represent velocities calculated from Suter (1991) of a spider of the same mass as the test spider and with the shortest length of trailing silk used in the tests shown (middle curve) or the longest length of trailing silk (bottom curve). The shorter curves in each graph represent the velocities of the test spider in separate freefalls: because of the experimental setup (see text and Fig. 1), curve segments originating nearer to the origin are from trials in which a relatively long length of silk acted as the balloon, and segments originating at longer distances from release are from trials with shorter silk lengths. Each graph on the right shows the relationship between silk length and terminal velocity of each test spider in Figs. 3–7. The test spider identities, masses, and

I calibrated the apparatus at the end of each trial by first turning off the air flow and then giving the spider a series of coils of very fine nichrome wire (diameter:  $2.5 \mu\text{m}$ ), each of measured length (and therefore of known weight). Fortunately the spiders were very cooperative: each grabbed and held on to each wire coil, manipulating it for several seconds then dropping it, allowing me to record (as above) the effect of each weight on the output of the photodetector. Because output from the photodetector was recorded on the same tape that carried postural information in the form of a video signal, subsequent analysis of the relationship between drag and posture was facilitated.

### RESULTS

Spiders with trailing silk draglines passed the camera lens at velocities that were in part dependent on how far they had fallen. Figures 3–7 show the velocities of these falling spiders as functions of distance from the release point (i.e., the elevation of the spider when its fall began). Each figure presents the data from multiple releases of the same spider, all plotted against three theoretical curves. Those theoretical curves represent (1) the velocity of a spider falling in a vacuum (no drag), (2) the velocity of a spider of the same mass as the test animal, trailing the minimum length of silk used by the test spider during the trials (drag calculated from Suter 1991), and (3) the velocity of a spider of the same mass as the test animal, trailing the maximum length of silk used by the test spider during the trials (drag calculated from Suter 1991). Of the five spiders tested in this study, only the immature uloborid produced data that consistently corresponded closely with expectations derived from the wind tunnel experiments.

Because the distance from release varied inversely with silk length, individual curves near the origins of Figs. 3–7 represent spiders with relatively long draglines and curves far from the origins represent spiders trailing relatively short lengths of silk. Sometimes a spider fell more slowly when trailing a longer dragline than when trailing shorter draglines, but this relationship

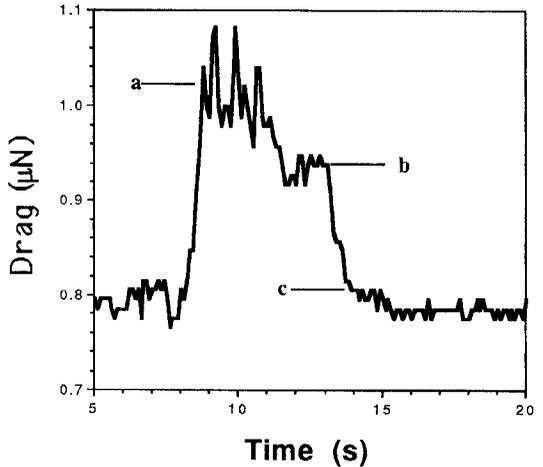


Figure 13.—Drag generated on the surfaces of a theridiid hatchling (0.18 mg). The horizontal lines indicate drag at different postures: (a) all legs extended and waving; (b) all legs loosely held against the body; (c) all legs tightly held against the body. Note that a very small change in posture (from b to c) resulted in a substantial reduction in drag.

was by no means perfect. Significant inverse relationships between silk length and terminal velocity were found for both of the 0.18 mg theridiid spiderlings (Figs. 8, 9) but not for the other three test animals (Figs. 10–12), all of which were larger. The substantial deviations from the expected relationship led to the tentative conclusion that posture must play a prominent role in influencing terminal velocity.

Measurements of drag on spiders mounted in a laminar air stream are shown in Figs. 13, 14. Relatively small changes in posture for both very small and somewhat larger spiders caused as much as a 10-fold change in drag, even at the very low air velocity used in this test.

### DISCUSSION

A spider falling through still air accelerates until the drag produced by air flowing past its body and trailing silk just equals the pull of gravity: at that point, acceleration is zero and the spider is at its terminal velocity. Thus terminal velocity is a function of the mass of the spider and various

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velocity vs. silk length relationships were as follows: Figs. 3 & 8, hatchling theridiid, 0.18 mg,  $R = 0.90$ ,  $P < 0.01$ ; Figs. 4 & 9, hatchling theridiid, 0.18 mg,  $R = 0.88$ ,  $P < 0.05$ ; Figs. 5 & 10, hatchling theridiid, 0.20 mg,  $R = 0.39$ ,  $P > 0.05$ ; Figs. 6 & 11, *U. glomus*, 1.0 mg,  $R = 0.59$ ,  $P > 0.05$ ; Figs. 7 & 12, immature theridiid, 1.8 mg,  $R = 0.49$ ,  $P > 0.05$ .

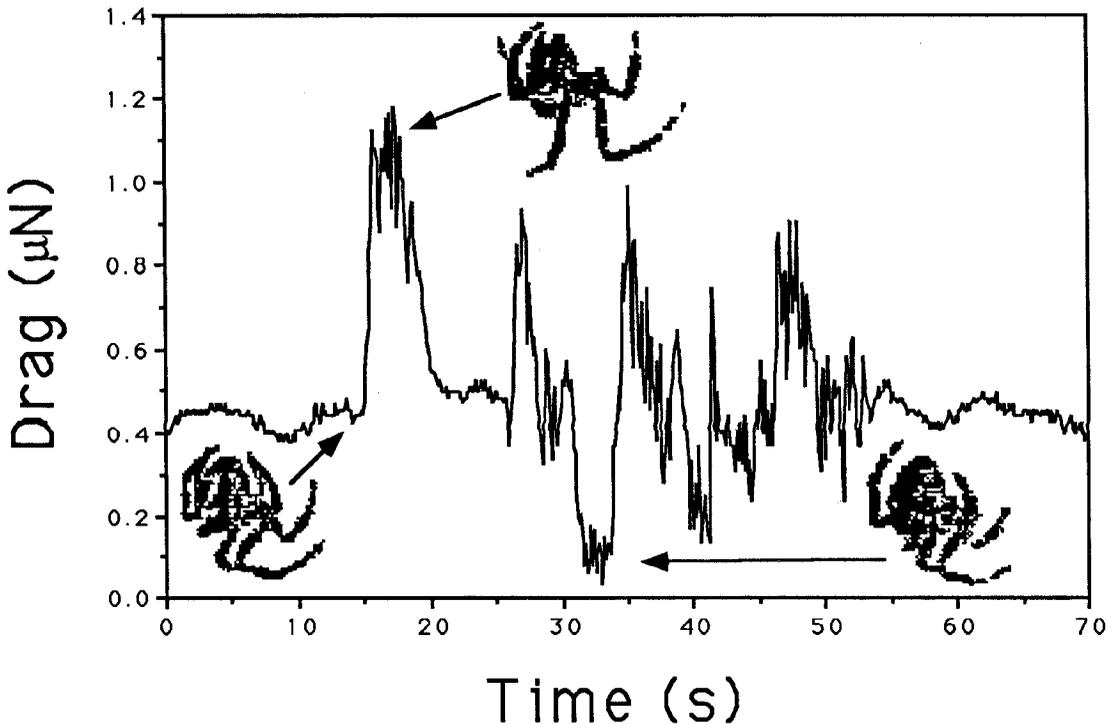


Figure 14.—Drag generated on the surfaces of a 7.2 mg theridiid. The postures shown at three points in the graph are computer-enhanced images from individual video frames.

characteristics of the surfaces of the spider itself and its silk. The relevant characteristics of the surfaces have been discussed in theory by Humphrey (1987), and I have discussed elsewhere (Suter 1991) their relative importances as deduced from wind tunnel experiments. Both I and Humphrey acknowledged a role of posture in determining drag, but both of us considered its role to be secondary, Humphrey because simplifying assumptions needed to be made to make the calculations tractable, and I because of my use of dead spiders in the wind tunnel experiments. The results reported here make clear the need to reassess the role of posture in ballooning.

Figures 3–7 show that individual spiders trailing silk sometimes fall much faster and sometimes much slower than predicted. Because these large differences can occur between trials of a single spider (e.g., Figs. 3, 7), they cannot be attributed to differences in morphology. All of the silk used by the spiders was dragline, the structure of which is known and relatively invariant (Suter 1991), so that the differences in velocities cannot be attributed to variations in silk structure either. Finally, although silk length

is sometimes a significant component in the determination of terminal velocity (Figs. 8, 9), it by no means acts alone: even at a single silk length in an individual spider, terminal velocity can vary by a factor of 2.6 (e.g., Fig. 10: at 5 cm, 78 vs. 29 cm/s). This variability must arise, therefore, from the single uncontrolled variable in this system, the posture of the falling spider relative to the direction of motion.

The influence of posture on the drag developed by a spider in a moving air stream is clearly evident in Figs. 13, 14. Even what appears to be a small change, pulling the legs tightly to the body from a posture where the legs are slightly more loosely held, can result in a reduction in drag of  $0.17 \mu\text{N}$  at a very low air velocity (0.07 m/s), and that is for a spider with a weight of  $1.76 \mu\text{N}$ . At much higher air velocities like those reached by a falling spider of the same size (e.g., from Fig. 3, 50 cm/s), the effect of this postural change would be much greater [using Equation 4 from Suter (1991), the reduction in drag due to a comparable postural change at 50 cm/s would be  $1.19 \mu\text{N}$ ] and would easily account for the terminal velocity differences seen in Figs. 8–12.

The importance of posture as an influence on terminal velocity in ballooning spiders must, of course, vary with the amount of silk that is used: when a spider uses only a short length of silk, the influence of posture will be greater than when silk is very long and little of the drag on the silk/spider system is developed by the spider's body and appendages. Unfortunately, almost nothing is known about the amount of silk actually used by ballooning spiders. That absence of data means that the importance of posture in the travels of ballooning spiders (even in their ability to control their elevation) cannot yet be assessed.

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