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REPORT

## Electric Fields Elicit Ballooning in Spiders

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### ▼ Highlights

- Spiders detect electric fields at levels found under natural atmospheric conditions
- Ballooning behavior is triggered by such electric fields
- Trichobothria mechanically respond to such electric fields, as well as to air flow
- Electric field and air flow stimuli elicit distinct displacements of trichobothria

### ▼ Summary

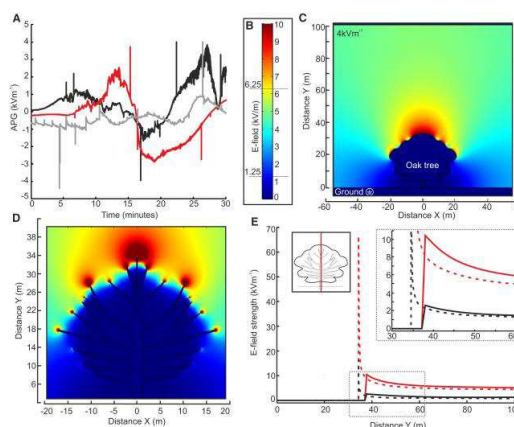
When one thinks of airborne organisms, spiders do not usually come to mind. However, these wingless arthropods have been found 4 km up in the sky [1], dispersing hundreds of kilometers [2]. To disperse, spiders “balloon,” whereby they climb to the top of a prominence, let out silk, and float away. The prevailing view is that drag forces from light wind allow spiders to become airborne [3], yet ballooning mechanisms are not fully explained by current aerodynamic models [4, 5]. The global atmospheric electric circuit and the resulting atmospheric potential gradient (APG) [6] provide an additional force that has been proposed to explain ballooning [7]. Here, we test the hypothesis that electric fields (e-fields) commensurate with the APG can be detected by spiders and are sufficient to stimulate ballooning. We find that the presence of a vertical e-field elicits ballooning behavior and takeoff in spiders. We also investigate the mechanical response of putative sensory receivers in response to both e-field and air-flow stimuli, showing that spider mechanosensory hairs are mechanically activated by weak e-fields. Altogether, the evidence gathered reveals an electric driving force that is sufficient for ballooning. These results also suggest that the APG, as additional meteorological information, can reveal the auspicious time to engage in ballooning. We propose that atmospheric electricity adds key information to our understanding and predictive capability of the ecologically important mass migration patterns of arthropod fauna [8].

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### ▼ Results and Discussion

In the early 1800s, two competing hypotheses were proposed to explain how ballooning animals become airborne, invoking (1) the aerodynamic drag from wind acting on the silk or (2) atmospheric electrostatic forces [9]. Aware of the prevailing arguments, Charles Darwin mused over how thermals might provide the forces required for ballooning as he watched hundreds of spiders alight on the Beagle on a calm day out at sea [10]. Darwin’s observation, however, did not provide further evidence in support of either hypothesis. The physical force required for ballooning has since been attributed to aerodynamic drag at low wind speeds ( $<3 \text{ ms}^{-1}$ ) [4, 5, 11], yet the involvement of electrostatic forces in ballooning has never been tested. Several issues have emerged when models using aerodynamic drag alone are employed to explain ballooning dispersal. For example, many spiders balloon using multiple strands of silk that splay out in a fan-like shape. Instead of tangling and meandering in light air currents, each silk strand is kept separate, pointing to the action of a repelling electrostatic force [12]. Questions also arise as to how spiders are able to rapidly emit ballooning silk into the air with the low wind speeds observed in ballooning; the mechanics of silk production requires sufficient external forces to pull silk from spinnerets during spinning [13]. And, how do low wind speeds provide the high initial accelerations seen in ballooning takeoff [10]? Attempts to find weather

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 Figure 1

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**Figure 1**

Quantifying Electric Fields in Nature

(A) Atmospheric potential gradient (APG) measured for 30 min periods across 3 days using a field mill (Chillworth JCI131) at the University of Bristol School of Veterinary Sciences, Langford. Colors depict recordings from different days in June 2016.

(B) Scale bar for (C) and (D).

(C) Finite element analysis (FEA) model of electric field (e-field) enhancement around a geometrically domed oak tree in an APG strength of  $4 \text{ kV m}^{-1}$ .

(D) FEA model detailing the e-field around geometrically sharp tree branches in an APG strength of  $4 \text{ kV m}^{-1}$ .

(E) Two-dimensional plot of the e-field along cut lines (red; left inset) of (C) oak modeled as geometrically domed (solid) and (D) branches (dashed) in an APG of  $4 \text{ kV m}^{-1}$  (red) and  $1 \text{ kV m}^{-1}$  (black). Inset: detail of area indicated by the gray box.

 See also [Figure S1](#).

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patterns that predict the prevalence of ballooning have been made, but results remain inconsistent [14]. Mass ballooning events occur sporadically, and weather conditions on days with abundant aeronauts cannot be readily distinguished from days void of them. Although reports claim thermal air currents and temperature gradients on fair-weather days are the driving force [15, 16, 17, 18], ballooning can be observed when skies are overcast, as well as in rainy conditions ([14, 15] and E.L.M, unpublished data). Humidity is potentially an important predictor [19, 20], but causal and testable explanations are lacking. One consistent predictor of ballooning is wind speed; spiders only take flight when wind speed is below  $3 \text{ ms}^{-1}$  [11, 15, 17, 19, 20, 21], a very light breeze, but models show that these conditions should not allow large spiders to balloon, despite observation to the contrary [12].

In the early 20<sup>th</sup> century, atmospheric electricity was intensively studied, establishing the ubiquity of the atmospheric potential gradient (APG) [6]; from fair to stormy weather, an APG is always present, varying in strength and polarity with local meteorological conditions. Over a flat field on a day with clear skies, the APG is approximately  $120 \text{ Vm}^{-1}$  (Figure S1). In more unsettled meteorological conditions, charged clouds passing overhead modify the APG, with rainclouds, storm clouds, and mist or fog generating APGs of several kilovolts per meter [6, 22, 23] (Figure 1A). Any electrically grounded, geometrically sharp structure protruding from this flat field will cause a substantial enhancement of local electric fields (e-fields) [24] (Figures 1C and 1D). Fundamentally, this is why lightning rods work to channel a safe, predictable, path for lightning to reach ground. Because they are rooted in the earth and contain a high proportion of water and electrolytes, plants tend to equalize to ground potential [25, 26], and the electric field strength surrounding leaves and branches, due to their sharp geometry, can reach many kilovolts per meter [25, 26, 27] (Figures 1B–1E). For example, in mildly unsettled weather (APG of  $1 \text{ kVm}^{-1}$ ), the electric field  $\sim 10 \text{ m}$  above the canopy of a 35-m-tall tree can exceed  $2 \text{ kVm}^{-1}$  (Figures 1B–1E and S1). Closer to the tree, around sharp leaf, needle, and branch tips, e-fields easily reach tens of kilovolts per meter (Figures 1B–1E and S1). Local e-fields can become very high under observed atmospheric conditions; the potential difference between a grounded plant and the surrounding air is often high enough to initiate ion emission by corona discharge [26, 28, 29, 30, 31].

APGs and the e-fields surrounding all matter are relevant to biological systems; for example, bumblebees can detect e-fields arising between themselves and flowers [27], and honeybees can use their charge to communicate within the hive [32]. But beyond bees, how widespread is the ability to detect and use electrostatic forces in terrestrial organisms? Spider silk has long been known as an effective electrical insulator; indeed, it was used in the first quantitative measurements of electrostatic charge by Michael Faraday and is positioned at the bottom of the triboelectric series, where it accumulates a net negative charge [33]. Previous theoretical considerations have proposed that when silk is charged, the APG can provide sufficient coulomb force to enable ballooning and aerial suspension using electrostatic forces alone [7]. Quite surprisingly, APG is rarely invoked, let alone quantified, in conventional weather descriptors and parameters collected by weather stations. As the APG plays a role in defining e-fields surrounding vegetation, it is reasonable to surmise that if e-fields are ecologically relevant, spiders should be able to detect and respond to an e-field by changing their behavior to engage in ballooning. Here, we presented adult Linyphiid spiders (*Erigone*) with e-fields quantitatively commensurate with atmospheric conditions. Spiders were placed on a vertical strip of cardboard in the center of a polycarbonate box, limiting air movement. This box also served as an APG simulator in the form of a parallel-plate capacitor. This entire setup was situated within an acoustic isolation and Faraday cage room ( $3 \text{ m} \times 2.8 \text{ m} \times 2.25 \text{ m}$ ). In their natural environment, ballooning spiders take off from protruding branches, leaves, or fences. We used a non-conductive, glue-free cardboard to construct a triboelectrically neutral takeoff site. This takeoff site generates a spatially uniform and moderate e-field within the arena (Figure 2A). Vertical e-field strengths across the arena were either  $0 \text{ Vm}^{-1}$  control conditions,  $1.25 \text{ kVm}^{-1}$ , or  $6.25 \text{ kVm}^{-1}$ , encompassing APG values observed in overcast, misty, and stormy weather [23], as well as e-fields around grounded trees, grasses, and flowers [6, 25, 30] (Figure 1).

There are two behavioral proxies for ballooning in spiders: the upward extension of the opisthosoma and silk extrusion, referred to as tiptoeing (Figure 2A), and dropping on a silk dragline followed by extrusion of ballooning silk [3]. Although both behaviors allow spiders to become airborne, tiptoeing exclusively precedes ballooning and is an established predictor of ballooning propensity [2]. The occurrence of these behaviors was video recorded under the different experimental treatments and subsequent analysis scored blind.

Spiders show a significant increase in ballooning in the presence of e-fields (tiptoes  $\Delta\text{AIC}$  [Akaike information criterion] between full and null model 42.1, AIC 153.1 versus 195.2, d.f. = 2,  $p < 10^{-6}$ ; dragline drops  $\Delta\text{AIC}$  between full and null model 28.1, AIC 310.5 versus 282.4, d.f. = 2,  $p < 10^{-6}$ ; Figures 2C and 2D). Significantly more dragline drops are elicited at  $1.25 \text{ kVm}^{-1}$  ( $Z = 2.95$ ;  $p = 0.003$ ) and  $6.25 \text{ kVm}^{-1}$  ( $Z = 4.87$ ;  $p < 10^{-6}$ ), and there is a significant increase in the number of tiptoes at  $6.25 \text{ kVm}^{-1}$  ( $Z = 4.03$ ;  $p < 10^{-6}$ ) (Table S1). The observed change in spider behavior establishes that they can detect APG-like e-fields. Moreover, the spider's unlearned response to e-fields is to engage in ballooning, and, on becoming airborne, switching the e-field on and off results in the spider moving upward (on) or downward (off) (Video S1).

**Video S1. Video of Spider Ballooning in an E-Field, Related to Figure 2**

Switching the field on and off results in the spider moving up and down in the arena.

The behavioral experiments demonstrate that spiders can detect e-fields, but what is the sensory basis of spider e-field detection? In bumblebees, mechanosensory hairs are the putative electroreceptors sensitive to e-fields [34]. Arachnids have mechanosensory hairs known as trichobothria (Figures 3A and 3B). Much is known about their mechanical and neural response to medium flows (air and water) [35, 36]; they are exquisitely sensitive, detecting air motion close to thermal noise [37], they detect sound [38], and they are omnidirectional [39]. Early studies using electrostatic actuation as a tool to investigate trichobothria mechanics indicate that they may also be sensitive to e-fields [39, 40, 41].

We tested the mechanical response of trichobothria on the front metatarsus to both air flow ( $0.5 \text{ ms}^{-1}$ ) and e-fields using laser Doppler vibrometry (LDV). Pseudo-direct current (DC) electrical stimuli with 0.1 Hz and 0.01 Hz square waves were used to simulate a static deflection and rapid change in e-field, as happens when charged clouds pass overhead (Figure 1). Also, a 1 Hz sine wave was used to investigate the response to slowly changing e-fields. The response to air flow, a stimulus long established to deflect trichobothria, was also measured for comparison.

Trichobothria are displaced in different ways by DC air flow and DC e-fields (Figures 3C–3F). In response to air flow, trichobothria are statically displaced for the duration of stimulus presentation, a tonic response. In contrast, displacement to e-fields is maximal at the transient switch in voltage, decreasing back to the baseline over a period of around 30 s, a phasi-tonic response. Here, the direction of trichobothria displacement is independent of stimulus polarity; both positive-to-negative and negative-to-positive stimulus transitions produce displacement in the same direction, a response indicative of induction charging where forces are always attractive regardless of stimulus polarity. Notably, the different types of mechanical response generated by air movement and e-fields suggest that wind and electric field detection can be differentiated despite sharing a common peripheral receptor.

The trichobothrium is also displaced in response to a 1 Hz sine wave (Figures 3G and 3H), showing that they mechanically respond to slowly varying e-fields, as well as to rapid changes in potential. Here, the frequency response of the trichobothrium is twice that of the stimulus (Figures 4E and 4F); each zero crossing of the stimulus generates a change in the direction of displacement of the trichobothrium, providing additional evidence of electrostatic induction. The response of trichobothria, measured as the number of times the velocity spikes (Figure 4A), scales linearly with e-field strength within the range measured ( $3.6\text{--}0.4 \text{ kVm}^{-1}$ ). No response above instrumentation noise (typically 2–10 pm) was elicited from spines (Figures 4B and 4C). The measurement of tibial spines is a useful control allowing the exclusion of non-stimulus specific air motion, electrical crosstalk, or the motion of the entire animal as potential drivers of the responses measured from trichobothria. Hence, the trichobothria's mechanical response can be considered to result from forces applied to them by the electric field. Such sensitivity to ambient e-field strength is compatible with the notion that spider trichobothria can work as electromechanical receptors. The neuroethology of trichobothria in response to e-fields needs further characterization, to add to the detailed knowledge of their response to medium flows.

This is the first demonstration of aerial electroreception in spiders and in arthropods beyond Apidae. The phylogenetic distance between spiders and bees indicates that aerial electroreception could be widespread among the Arthropoda. Consequently, the electromechanical sensitivity of hair structures present in bumblebees and spiders indicates a possible dual function, as medium flow sensors and electroreceptors. The hypothesis thus emerges that the mechanosensory hairs of many arthropod species may exhibit the additional function of aerial electroreception.

The present evidence shows that the APG and resulting electrostatic forces are sufficient to elicit ballooning, yet they may not always be necessary. Aerodynamic drag associated with light wind and electrostatic forces can work in synergy to facilitate ballooning. As a result of this work, we propose that the APG serves at least three functions: an indicator of meteorological conditions, an informational trigger, and a physical driving force enabling ballooning. Several mechanistic questions now emerge, pertaining to the dielectric characteristics of ballooning silk and whether altitude control and navigation take place. Future work needs to disentangle the complex interplay between animal behavior and variations in the APG. Inclusion of the APG as a meteorological parameter has the potential to provide better predictions of dispersal events and the distribution of spider populations.

Understanding the mechanisms that underpin dispersal is crucial for describing biomass and gene flow, population dynamics, species distributions, and ecological resilience to stochastic changes. It is therefore of great importance for global ecology. Spiders are a powerful source of biological control, consuming 400–800 million tons of biomass globally each year [42], significantly impacting the composition and diversity of ecosystems [43]. The terrestrial biological world has evolved within the APG and the use of e-fields in dispersal could extend beyond ballooning spiders to those species of caterpillar (Lepidoptera) and spider mite (Trombidiformes) that also disperse aerially [2], as well as plant propagules. As ballooning arthropods constitute a proportion of significant seasonal bioflows [8], studying the role of atmospheric electricity and its detection by arthropods has

implications for predicting the transport of nutrients, pathogens, agricultural pests [44, 45, 46], and their predators between ecosystems and biomes [8].

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## ▼ Author Contributions

Conceptualization, E.L.M.; Methodology, E.L.M. and D.R.; Investigation, E.L.M.; Writing – Original Draft, E.L.M.; Writing – Review & Editing, E.L.M. and D.R.; Resources, D.R.

## ▼ Declaration of Interests

The authors declare no competing interests.

## ▼ Supplemental Information

### Document S1. Figure S1 and Table S1

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