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SHORT COMMUNICATION

Disentangling the roles of electric fields and wind in spider dispersal experiments

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Abstract. Observations of spiders' pre-dispersal behavior can be used to answer various ecological and evolutionary questions. So far, dispersal experiments have often used air currents as a stimulating factor. Effects of electric fields on the pre-dispersal behavior of spiders have recently been discovered. Electric fields may lead to unexplained variation in results and limit comparability between previous studies. Here we aim to disentangle the roles of wind and electric fields on the passive aerial dispersal of three linyphiid spider species. Our results confirm that strong electric fields in the air elicit pre-dispersal behavior, and in combination with a light wind, facilitate dispersal (take-off). Nevertheless, even the strong electric fields employed here played a rather supplementary role in spiders' dispersal with wind remaining the most influential factor. We recommend that studies of passive aerial dispersal should control for electric field strength but otherwise use wind as the primary stimulating factor.

Keywords: Araneae, atmospheric electricity, ballooning, Linyphiidae, tiptoe behavior

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Dispersal is a widespread feature of animal life (Sheldon et al. 2017). Numerous species from at least 29 spider families disperse passively as aerial plankton (Bell et al. 2005). Such airborne migrants are largely dependent on atmospheric forces and have very little ability to control their flight. However, the take-off is mostly initiated by the organism, and individuals usually enter the airstream actively by performing pre-dispersal behavior (Reynolds & Reynolds 2009).

In spiders, dispersal over a long distance is called "ballooning", where individuals become airborne by emitting threads of silk in the air. Spiders also disperse over short distances by "rappelling", when the thread attaches to nearby substrate and is then used by the spider as a bridge to climb along. Prior to ballooning and rappelling, a spider performs a pre-dispersal behavior called "tiptoeing". It shows a motivation to disperse by climbing to an elevated position, straightening its legs, lifting its abdomen and releasing silk threads into the air. Apart from dispersal behavior, tiptoeing is important for ecological and evolutionary studies since it indicates spiders' willingness to disperse (Weyman 1993; but see Lubin & Suter 2013).

Multiple environmental conditions can influence spider ballooning behavior, including temperature, humidity and wind speed (Bonte et al. 2007; Simonneau et al. 2016; Postiglioni et al. 2017). Hitherto, most experiments addressing evolutionary and ecological questions around spider ballooning have used air currents (< 3 m/s) as stimulating factors and driving forces for aerial dispersal (e.g., Greenstone 1982; Weyman 1995; Bonte et al. 2007; Entling et al. 2011; Mestre et al. 2014; Wolz et al. 2020). However, a role of atmospheric electric fields in passive aerial dispersal was hypothesized and discussed already in the 19th century (Loudon et al. 1830). It was recently demonstrated that electric fields (e-fields) in the air elicit pre-dispersal behavior in linyphiid spiders and that spiders can sense e-fields with their trichobothria (Morley & Robert 2018). Consequently, the lack of control on the presence of e-fields during earlier ballooning experiments could lead to unexplained variation in the results and limit comparability between studies.

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Here we aim to disentangle the roles of wind and e-fields for passive aerial dispersal using three spider species from the family Linyphiidae, which are frequent aeronauts (Blandenier 2009). We study the single and combined effects of e-fields and wind on tiptoe behavior and aerial dispersal (take-off).

We collected three spider species from the family Linyphiidae, namely *Agyneta rurestris* (C. L. Koch, 1836), *Erigone dentipalpis* (Wilder, 1834) and *Mermessus trilobatus* (Emerton, 1882) from hay meadows in southwest Germany and northeast France between June and August 2019 using a vacuum sampler (modified STIHL SH86 blower; Stihl, Waiblingen, Germany). *Agyneta rurestris* and *E. dentipalpis* were selected because they were most abundant in the sampled grasslands. *Mermessus trilobatus*, which is native to North America, was included because we were planning a more detailed study on the evolution of its dispersal during its invasion process in Europe (Narimanov et al. 2021). We transferred all individuals into glass jars (100 ml) with a 1 cm layer of plaster of Paris to create a humid environment for housing and kept them inside climate cabinets under standard conditions (25°C, RH = ~100%, L:D =16:8). We fed all spiders *ad libitum* with springtails (*Sinella curviseta*).

We adapted our experimental setup from the experiments of Morley & Robert (2018). The setup was comprised of a wooden frame holding two horizontal 0.8×0.8 m^2 metal electrodes, 0.8 m above each another. We used a high voltage power supply (PHYWE Systeme GmbH und Co. KG; Göttingen, Germany; Product number: 13671-93) to create an electric field in the area between the electrodes. To match natural conditions, where the lower electrode acts as the negatively charged grounded earth surface and the area above as the atmospheric potential gradient, we charged the upper electrode positively relative to the grounded lower electrode. We used the field strength of 6.25 kV/m by applying 5 kV over the distance of 0.8 m between the electrodes. The value is quite high and represents the e-fields in the atmosphere during disturbed weather. The value was chosen because it revealed clear responses in a previous study (Morley & Robert 2018). We placed the dispersal platforms in the middle of the lower electrode. To provide an elevated point, the dispersal platform consisted of a 7-cm tall

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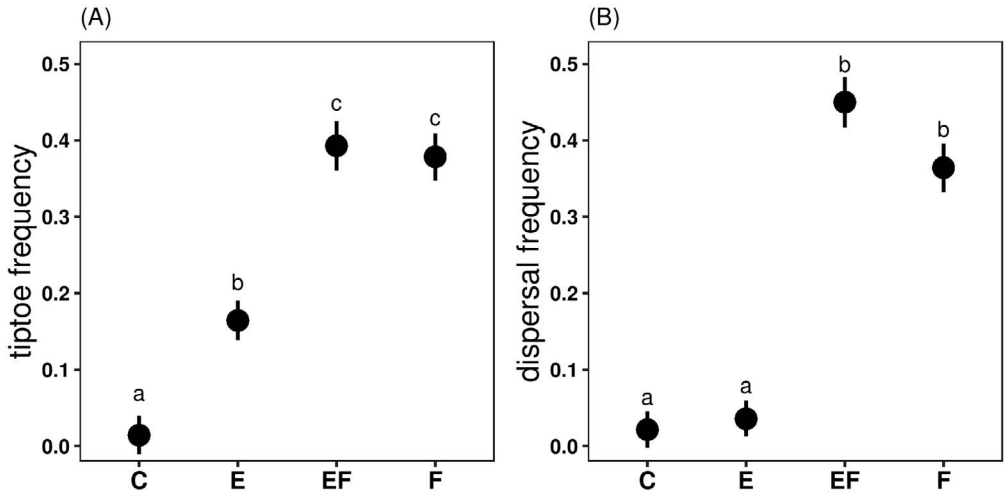


Figure 1.—Effect of treatments (C = control; E = e-fields; EF = e-fields and fan; F = fan) on tiptoe (A; presence/absence) and dispersal behavior (B; presence/absence). Means ± SE are presented. Differences between the treatment groups are illustrated with letters based on the results from the Tukey contrast test.

wooden stick pointed vertically upwards in a 2.5 cm diameter disk made of plaster of Paris. We prevented spiders from escaping by placing the platforms in the middle of a 7-cm petri dish filled with water. The plaster was saturated with water, and a wire grounded it to the lower electrode. We placed a table fan (diam. = 23 cm, 30 W) approx. 1 m beside the arena at the level of the lower electrode to provide a suitable wind with a range of 1.3 m/s – 2.3 m/s (Simonneau et al. 2016). Before the experiments, we measured the wind velocity at the position of the arena, in the middle of the bottom electrode, using a cup anemometer (PCE – A420). For control and wind treatments, no voltage was applied, and the interconnected electrodes were electrically grounded in order to shield the arena against possible e-fields existing in the room. We used a vertically oriented textile mesh at a horizontal distance of 1.5 – 2 m downwind from the arena to capture dispersing individuals.

We had four treatments, namely control (C), e-fields (E), fan (F), and the combination of e-fields and fan (EF) to test the roles of the wind and e-fields, as well as a combination of both on dispersal behavior. We subjected each spider to all treatments in a randomized order during consecutive days; one treatment a day. In each trial, we placed a spider on the dispersal platform and observed it for up to 10 minutes. We stopped experiments after 10 minutes or once the spider dispersed. We washed and wiped the dispersal platforms between the trials to remove silk and possible chemical cues left by the previous spider. All individuals were offered no food for at least three days before the experiment to standardize starvation levels and to increase the likelihood of dispersal (Weyman et al. 1994). We used 140 adult individuals in total (40 *A. rurestris*; 36 *E. dentipalpis*; 64 *M. trilobatus*) for dispersal assays. We recorded the presence of tiptoe behavior and dispersal events (take-off) during the 10 minutes of observation.

We modelled tiptoe and dispersal behavior (presence/absence) by fitting generalized linear mixed-effects models (GLMM) for a binomial response from the lme4 package (Bates et al. 2015) in R 3.6.1 (R Core Team 2019). We analysed the explanatory variables, namely treatment (C, E, EF, F), species (*A. rurestris, E. dentipalpis, M. trilobatus*) and also the interaction (treatment × species) as fixed predictors by ANOVA χ^2- test from the R package car (Fox & Weisberg 2019) on logistic regression (glmer). We used a Tukey contrast test to illustrate the difference between the treatments by using the glht function from the multcomp package in R (Hothorn et al. 2008). We included individual ID as a random factor for the within-subject design. Data are available from *Figshare*, online at: https://doi.org/10.6084/m9.figshare.13116509.v1

Both tiptoe ($\chi^2 = 38.21$, d.f. = 3, $P < 0.0001$) and dispersal behavior ($\chi^2 = 49.78$, d.f. = 3, $P < 0.0001$) were strongly influenced by the experimental treatments. E-fields alone significantly increased the spiders' tiptoe behavior, but the effect of wind was more than twice as strong (Fig. 1A). By contrast, spiders' dispersal did not increase under the e-fields but was dependent exclusively on the presence of wind (Fig. 1B). Highest rates of tiptoe behavior and dispersal were observed when the e-fields and wind were combined, but the difference from wind alone was not significant (Fig. 1). There were also significant differences in behavior among species, both in tiptoe ($\chi^2 = 47.8$, d.f. = 2, $P < 0.0001$) and dispersal ($\chi^2 = 32.76$, d.f. = 2, $P < 0.0001$) (Fig. S1 in supplementary material, online at: http:// doi.org/10.1636/JoA-S-20-063.s1). The highest number of tiptoe events were performed by *E. dentipalpis* (60%), followed by *A. rurestris* (23%) and *M. trilobatus* (17%). Also, dispersal frequencies were higher in *A. rurestris* (47%) and *E. dentipalpis* (42%) than in *M. trilobatus* (11%). The interaction of treatment and species was not significant (tiptoe: $\chi^2 = 6.95$, d.f. = 6, $P > 0.05$; dispersal: $\chi^2 = 10.13$, d.f. = 6, $P > 0.05$), indicating a similar response to the treatments among the tested species.

To our knowledge, this is the first empirical study testing the single and combined effects of e-fields and wind on passive aerial dispersal. Our study confirms that e-fields motivate linyphiid spiders' dispersal by eliciting a higher frequency of tiptoe behavior. However, linyphiids become airborne more frequently in the presence of wind. There was only a single case among the trials where the e-field alone was sufficient to lift the spider in the absence of wind. Interestingly, 80% (4 out of 5) of all dispersal events with the e-field treatment was performed by rappelling. Thus, the forces provided by e-fields in isolation were sufficient to drag and lift a negatively charged thread (Hawthorn & Opell 2002) but not to bring the spider aloft within our experimental setup. However, as the upper electrode limited the vertical room of our setup to 0.8 m, investigations in setups that provide more vertical space or even field studies would be needed to appropriately test if spiders can get airborne with electric fields alone. As e-fields were not required to motivate high tiptoe or dispersal events in our study, future experiments could work with air currents only. Still, the setups should be shielding experimental arenas from

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the ambient e-fields to avoid any uncontrolled variation that these may cause in spider behavior. Alternatively, e-fields could be measured and statistically controlled for. However, as the measurement of static e-fields requires specialized equipment, shielding the experiment from the ambient field will usually be the more pragmatic solution.

The values of e-fields used here are relatively high, typical for exposed positions such as tree crowns in so-called disturbed weather (Bennett & Harrison 2007). By contrast, spider ballooning has widely been reported in fair weather conditions when the values of e-fields are much lower (Vugts & Van Wingerden 1976). Moreover, the studied linyphiid species are grassland spiders that prevalently balloon from the tip of grass or any other elevated position in open habitats. The strengths of e-fields in open habitats can vary between +0.05 and +0.3 kV/m (Bennett & Harrison 2007) with simulated values at the tip of grass blade reaching up to 1 kV/m (Morley & Gorham 2020). In contrast to the 6.25 kV/m applied here, e-fields of 1.25 kV/m had no significant effect on the tiptoe behavior of *Erigone* spp. in Morley & Robert (2018). Hence, the effects of even weaker e-fields appear unlikely. Still, to explore the roles of e-fields in less extreme situations, experiments implementing a wider range of e-fields strengths are needed. For example, the e-fields equivalent to the strength often found in grassland with the inclusion of a combination of different wind speeds.

The present study confirms that strong electric fields in the air motivate linyphiid spiders to disperse by eliciting higher tiptoe behavior, and in combination with a light wind, facilitate dispersal (take-off). Nevertheless, even the strong e-fields employed here played a rather supplementary role in linyphiid spiders' dispersal with air current remaining the most influential factor. Thus, e-fields could function as initial cues to initiate movement, but their potential roles for take-off requires study in more realistic situations. Considering also the higher technical effort to create electric fields compared to airflow, we recommend that ecological and evolutionary studies of passive aerial dispersal should control for electric fields strength but should otherwise use wind as a primary stimulating factor.

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SUPPLEMENTAL MATERIAL

Figure S1, available online at http://doi.org/10.1636/JoA-S-20-063.s1

Data are available from Figshare, online at: https://doi.org/10.6084/m9.figshare.13116509.v1

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