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SHORT COMMUNICATION

Dispersal behavior in agrobiont spiders (Linyphiidae) — differential response to a wind chamber

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Abstract. Two species of common, farmland-inhabiting money/dwarf spider, *Erigone atra* Blackwall, 1833 and *Oedothorax fuscus* (Blackwall, 1834), were exposed to light wind conditions within a wind chamber to determine their propensity to exhibit dispersal behaviors over a nine-month period. A novel design of wind chamber, incorporating two tangential fans, produced a wide outflow thereby allowing behaviors to be expressed over a relatively large test area (1 m × 0.65 m). Sticks placed at 3 cm intervals in an undulating foam surface structurally mimicked a natural field setting. Whereas the majority of *E. atra* expressed dispersal and related behaviors (tiptoe and drop posture and ballooning) in every month testing occurred, corresponding behaviors were rarely recorded in *O. fuscus*. Results are discussed in relation to knowledge of the dispersal activity of *O. fuscus* in the field and factors which may influence dispersal frequency and initiation.

Keywords: Ballooning, *Erigone*, *Oedothorax*

Erigone atra Blackwall, 1833 and *Oedothorax fuscus* (Blackwall, 1834) are two common species of money/dwarf spider (Linyphiidae) occurring in abundance on agricultural land in the British Isles. The survival of agrobiont spiders in the disturbed farmland environment is relevant from an agro-ecological perspective as evidence suggests that pest populations may be suppressed by farmland inhabiting linyphiids (Nyffeler & Sunderland 2003). Dispersal through the air by means of silk (ballooning) is thought to promote survival by spreading the risk of mortality-causing disturbance and by enabling spiders to quickly relocate should habitat quality decline (Weyman et al. 1994; Thomas & Jepson 1999). Although *E. atra* and *O. fuscus* are known to balloon, data from field studies suggests that *E. atra* is a more frequent disperser than *O. fuscus* (Weyman et al. 2002). In this study, spiders collected from the field over the course of nine months were exposed to light air currents within a wind chamber to determine: i) the proportion of spiders expressing dispersal behavior (ballooning and related behaviors) in a controlled environment; and ii) whether seasonal influence on dispersal motivation is a factor in the duration spent in dispersal behaviors and latency (i.e., the time taken to express dispersal behavior). The study was carried out at the former Seale-Hayne Faculty of Agriculture, Food and Land Use, Plymouth University, Devon, UK (now owned by the Dame Hannah Rodgers Trust).

The novel design of the wind chamber incorporated a large test area relative to a vertical air flow design (Weyman 1995), together with naturalistic structure with the intention of eliciting the fullest range of natural behaviors in test subjects. The wind chamber (Fig. 1) comprised a box made from 4 mm clear acrylic sheeting measuring 29 cm in height, 65 cm in width and 100 cm in length. An air flow was generated by two tangential (cross-flow) fans mounted at one end (total fan length 60 cm, fan diameter 6 cm). This type of fan was chosen because the outflow of the air was even across the width of the fan's surface. Each fan was driven by an AC single-phase induction motor which allowed for a triac (triode for AC) based speed control. A domestic lighting dimmer switch was adequate for this purpose, enabling a wide degree of speed control down to very low fan speeds (the resistance rating being high enough for the inductive loading of the motor). The fans' outflow across the sticks (see below) produced a light, turbulent wind current throughout the chamber. A hot-wire anemometer recorded wind speeds 15 cm from the fan fluctuating between 0.10-0.46 m s^{-1}, and 15 cm from outflow end, between 0.09-0.42 m s^{-1}. Wind speeds also fluctuated between the top and bottom of the sticks with no clear differentiation in strength. On the floor of the wind chamber, a layer of 'egg-box' foam was fitted, into which sticks, 16 cm and 5 cm in length, were placed alternately at the top of each prominence. This created a lattice arrangement with a distance between each stick of 3 cm. The regular undulating surface allowed spiders on the ground to locate a stick at any point by following the surface inclines. The foam was raised slightly at the outflow end to preserve the direction of airflow over the back wall.

Spiders were collected from nearby fields using a modified garden vacuum suction sampler (Flymo BVL-320, Husqvarna) between February and October 2005. Species were identified and placed separately into clear plastic pots 46 mm in height and 90 mm in diameter. The bottom of each pot contained a 10 mm layer of moist Plaster of Paris to prevent dehydration. Spiders were kept outside in a sheltered area and were brought into the laboratory for testing within two days of collection.

Individual spiders were released onto the upper portion of the same stick, situated near the mid line of the chamber, approximately 20 cm from the outflow end. The duration of expressed behaviors were recorded over a three-minute period using *Etholog*, a behavioral transcription program (Ottoni 1999). The behavioral states recorded were as follows: i) tiptoe: spider rears up on the ends of the tarsi in a 'tiptoe stance', a precursor to the release of ballooning silk; ii) drop: spider drops on a short length of silk, a precursor to the release of ballooning silk; iii) non tiptoe/drop: release of silk when not in the previous positions; iv) balloon: spider becomes airborne after releasing silk; v) rig: spider traverses silk between sticks above the ground; vi) haul: silk released by the spider (or other spiders) is gathered by the forelegs while the spider is above the ground; vii) climb: spider climbs vertically up or down sticks; viii) lower: spider lowers itself on a length of silk but does not assume the 'drop' posture and continues to the ground; ix) ground active: spider is active on the ground; x) inactive: spider is inactive either above or on the ground; xi) groom: spider displays grooming behavior, usually while stationary.

The average number of spiders tested each month was 22.1 ± 6.1 *E. atra* females ($n = 161$), 20.6 ± 7.2 *E. atra* males ($n = 103$), 17.9 ± 1.1 *O. fuscus* females ($n = 143$) and 14.6 ± 3.1 *O. fuscus* males ($n = 44$). Insufficient numbers for testing ($n \leq 5$) were collected in some

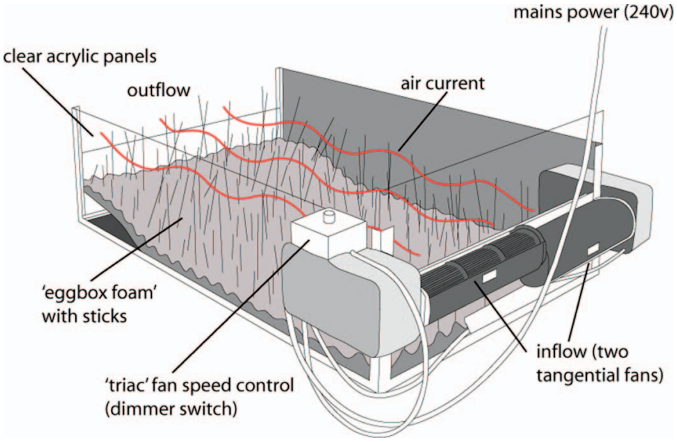

Figure 1.—Diagram of the wind chamber depicting tangential fans and the test area with egg-box foam and wooden sticks positioned at the top of each prominence. The intakes of the fans are reversed (one up, one down) to allow the fans to abut. The motors being on the same side prevented this arrangement when the intakes were in the same direction.

months. Between February and October *E. atra* females were not tested in April and August, *E. atra* males were not tested in March, April, May and August, and *O. fuscus* females were not tested in August. Males of *O. fuscus* were collected infrequently and only tested in February, July and October.

Dispersal behavior (tiptoe, drop, non-tiptoe drop and balloon) was recorded in all months for *E. atra* females and males. The total proportion of *E. atra* exhibiting dispersal behavior was 83% for females and 69% for males. Average time spent in dispersal behavior for *E. atra* females was higher for specimens collected in July, September and October than in earlier months. A Tukey HSD test revealed significant differences between March and July ($Q = 4.966$, $P < 0.001$), March and September ($Q = 4.906$, $P < 0.001$), May and July ($Q = 4.616$, $P = 0.019$) and May and September ($Q = 4.556$, $P = 0.022$). A significantly lower latency was recorded in October compared to May ($Q = 4.362$, $P = 0.033$). For *E. atra* males, average time spent in dispersal behavior was not significantly different between individual months although a one-way ANOVA (Welch's test for unequal variances) was significant for all months ($F = 2.576_{102}$, $P = 0.042$). Similarly, latency was not significantly different between individual months although a one-way ANOVA (Welch's test for unequal variances) was significant for all months ($F = 3.292_{41.28}$, $P = 0.02$).

The total proportion of *O. fuscus* exhibiting dispersal behavior was 1.4% for females and 11.4% for males. Dispersal behavior was recorded in five *O. fuscus* males, two in July and three in October. Only two spiders, both in October, displayed sustained dispersal-related activity (over one minute), with others showing very brief activity (less than ten seconds). Two *O. fuscus* females displayed very brief dispersal activity (less than ten seconds). Further statistical analysis between months was not performed owing to the small number of individuals expressing dispersal behavior.

Differences in time spent expressing behaviors between *E. atra* and *O. fuscus* was analysed for the behaviors, tiptoe, drop, balloon, climb and ground active. A General Linear Mixed Model (GLMM) analysis was performed using SAS/STAT® software using the 'GLIMMIX' procedure with 'Month' selected as a random factor. A negative binomial distribution was selected for the response distribution. Fit statistics (AIC) were comparable to those for the Tweedie distribution commonly fitted to data with a high proportion of zero counts (but not available in GLIMMIX). Time spent in 'tiptoe' was significantly higher for *E. atra* than *O. fuscus* ($F = 277.42\ _{448}$, $P < 0.001$), time spent in 'drop' was significantly higher for *E. atra* than *O. fuscus* ($F = 48.16\ _{448}$, $P < 0.001$), time spent in 'balloon' was significantly higher for *E. atra* than *O. fuscus* ($F = 15.79\ _{448}$, $P < 0.001$), time spent in 'climb' was non-significant ($F = 0.91\ _{448}$, $P = 0.34$) and time spent in 'ground active' was significantly higher for *O. fuscus* than *E. atra* ($F = 37.56\ _{448}$, $P < 0.001$).

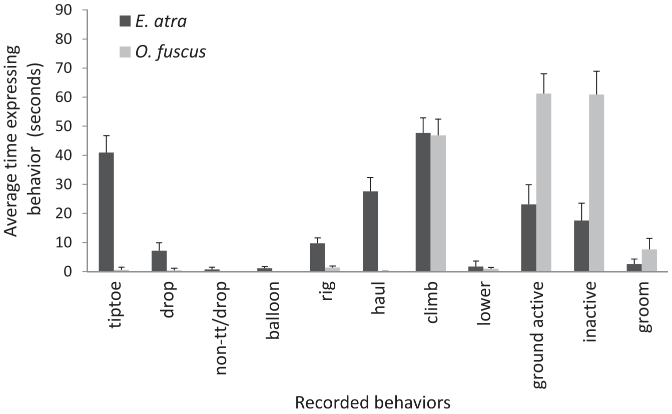

Figure 2.—Average time expressing recorded behaviors for *E. atra* ($n = 270$) and *O. fuscus* ($n = 188$) collected between February and October 2005. Error bars are 95% confidence intervals.

Whereas dispersal related behaviors made up almost a third of all activity in *E. atra* females, these behaviors were almost absent in *O. fuscus* females. The majority of *O. fuscus* males were similarly unresponsive compared to *E. atra* males. 'Inactive' averaged one third of total time in *O. fuscus*, however, approximately 60% of total time was spent in active behaviors (Fig. 2). Spiders which were active tended to move along the ground but also frequently climbed to the top of sticks before rapidly descending and moving to another. In this manner, some *O. fuscus* climbed numerous sticks in the three minute period. The act of climbing is seen as a prelude to ballooning behavior (Weyman 1995), however, the lack of ballooning related activity, even in individuals that climbed, suggests that a different set of prerequisite conditions are necessary to elicit ballooning compared to *E. atra*. Possible explanations for the lack of dispersal related activity would appear to exclude seasonal influence, none of which was observed for *O. fuscus* (although this cannot be discounted until the appropriate conditions to initiate dispersal are known). Light wind conditions simulated by the wind chamber were within the 3 $m\ s^{-1}$ threshold above which ballooning is limited (Vugts & Van Wingerden 1976). The character of the airflow was also investigated with spiders being placed in a chamber similar to that used by Weyman et al. (1995) with a vertical airflow. Dispersal behavior was also not elicited under these conditions (C. Woolley, unpublished data). Some indication as to the nature of the necessary conditions comes from dispersal activity monitored in the field. Females of *O. fuscus* were found to disperse in large numbers during sustained light wind conditions (lasting several days) associated with the passage of high pressure systems in autumn and winter (Woolley et al. 2016). Covariation under such conditions makes it difficult to implicate a specific variable as the cause (should just one exist). Changes in temperature, light, humidity, wind, vibration and atmospheric pressure, as has been found initiating dispersal in the twospotted spider mite (Li & Margolies 1994), have been suggested as possible stimuli (Weyman 1993); duration of conditions and rate of change may also be relevant.

Certain aspects of behavior and physiology appear to correspond with differences in dispersal frequency. The cursorial hunting habit observed for *O. fuscus* (Thornhill 1983) could compensate for local variations in prey density, reducing the need to balloon to higher density patches. Egg-guarding by female *O. fuscus* (Baarlen et al. 1994) could be inhibitory to dispersal, although male spiders would not be similarly restricted. Interestingly, 'male-only' dispersal activity has been observed in autumn (Woolley et al. 2016) which may be related to reproductive activity and could account for the only sustained dispersal activity observed for *O. fuscus* males in October. For *E. atra*, where egg-guarding behavior is limited or does not occur (Baarlen et al. 1994), frequent dispersal could allow eggsacs to be dispersed over a wider area thereby reducing the probability that all eggsacs succumb to parasitism by spreading the risk across multiple locations. The physiology of *E. atra* also appears better adapted to perturbations in prey intake (De Keer & Maelfait 1988) which may be a consequence of frequent passive dispersal and greater exposure to habitats of varying quality.

In the locality where *O. fuscus* was collected, the population was found to be heavily female dominated. This could be the result of infection by a sex-ratio altering endosymbiont such as *Wolbachia,* which is known to manipulate sex ratios in congener *O. gibbosus* (Blackwall, 1841) (Vanthournout 2012). Individuals of *E. atra* infected by the endosymbiont *Rickettsia* have been shown to exhibit lower dispersal motivation compared with those receiving antibiotic treatment (Goodacre et al. 2009). Life history traits outlined above might suggest that endosymbiont infection is not a major determinant in dispersal frequency, at least not to the extent that it might account for the lack of dispersal motivation compared to *E. atra*. It has been suggested though that species which display pronounced phenotypic effects might be 'deeply modified organisms' (Thomas et al. 2005), with multiple traits arising under the influence of infection.

Compared to the findings of Weyman et al. (1995), *E. atra* females did not show a seasonally consistent ballooning response over the study period. More time spent in pre-ballooning behavior and lower latencies (although these variables are not independent) were observed in later months, although no clear pattern was discernible for males. That spiders were kept outside in a sheltered area could be of significance. Without radiative warming by the sun, spiders may not have been sufficiently warmed before being placed in the wind chamber. In warmer months, spiders were consequently more active which may have resulted in a greater propensity to display dispersal behavior.

Weyman et al. (2002), in their review of the evolution and mechanisms of ballooning, recognised the difficulty in unravelling the potential factors responsible for its initiation. With evidence that *O. fuscus* displays pronounced, although infrequent, dispersal in the field, this study suggests that *O. fuscus*, or one of its congeners (e.g., *O. apicatus* (Blackwall, 1850), a common agrobiont species which also shows infrequent dispersal (Blandenier 2009; Thomas et al. 1990), may be worthy of further investigation into ballooning initiation. Discovering the parameters under which *Oedothorax* spp. will disperse may have relevance to long-standing questions regarding conditions which give rise to the large and congruent dispersal of spiders, so called 'mass dispersal events' (Bennett 2003). Models to determine population persistence in the agricultural environment (Halley et al. 1996) may also benefit from such data.

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