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Ballooning dispersal in arthropod taxa: conditions at take-off

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We have solved a long-standing and seemingly paradoxical set of questions that relate to the conditions which govern spider ballooning. We show that observations of spider ballooning excursions are best explained by meteorological conditions which maximize dispersal. Dispersal is predicted to be most effective in terms of distance when the stability of the atmosphere is non-ideally convective and is less effective during purely convective or neutrally stable conditions. Ballooners are most likely to travel a few hundred metres, but dispersal distances of several hundred kilometres are possible.

Keywords: spider ballooning; colonization; dispersal; Araneae; Linyphiidae

1. INTRODUCTION

Passive airborne dispersal, in which the direction and distance of travel is largely determined by the structure of the wind, affects pathogenic organisms, pollen and seeds of many plants as well as vast numbers of ballooning mites, caterpillars and spiders (Bell *et al.* 2005; Nathan *et al.* 2005). Despite a disparate phylogeny, all passive dispersing organisms are now being considered under a unified theory that can explain observed dispersal distances (Nathan *et al.* 2002, 2005). However, at least for mites, caterpillars and spiders, there is some controversy, as simulation modelling approaches have shown that ballooning organisms might be passive or active, depending upon the assumptions adopted.

Humphrey (1987) modelled spiders as a solid spherical body attached to a rigid rod which emulated the silk line that was responsible for dragging the individual into the air. Humphrey found that this 'spider' could indeed balloon under computer simulation, and his theory predicted that the silk dragline accounted for up to 70% of the drag of the model spider. This led others to suggest that by modifying the length of the dragline, a spider aeronaut might exert 'active' control over the distance and duration of a flight (Reynolds *et al.* 2006). Later, Reynolds *et al.* (2006) developed a model for spiders that appeared, superficially, to be similar to that of Humphrey's theory, but modified the properties of the silken rod, allowing it to be extensible and completely flexible. It was found that the silk dragline would contort with the air and, consequently, the

length of the silk had little predictive value for the distance and duration of a ballooning excursion.

Other controversies are also apparent. Biologists agree that take-off occurs when the air is rising and that ballooning is strongly correlated with meteorological conditions (Richter 1970; Vugts & van Wingerden 1976; Greenstone 1982), but recent research is puzzling. Greenstone (1990) found that ballooning was strongly correlated with the proportion of sky covered by clouds such that numbers of ballooners decreased with increasing proportions of sunshine. Suter (1999) observed that take-offs fall markedly when wind speed exceeds approximately 3 ms^{-1}. These observations are puzzling because solar heating and wind shear drive the production of updrafts that enable the ballooners to become airborne. Here, we resolve this apparent paradox by showing that ballooners select meteorological conditions which maximize dispersal. This is done by extending the approach of Reynolds *et al.* (2006) to numerical simulations using Lagrangian stochastic (LS) models (Rotach *et al.* 1996) that accurately simulate the trajectories of passively advected bodies, such as spiders, within convective boundaries with wind shear.

2. MATERIAL AND METHODS

Passive dispersal within the complex non-Gaussian turbulent flows like the atmospheric boundary layer is best predicted by LS models because other approaches such as diffusion models or similarity scaling are either inappropriate or invalid (Thomson 1989). LS models for the evolution of the velocity (u) and position (x) of a passive body in high Reynolds number turbulence take the general form

$$du_i = a_i(\mathbf{x}, \mathbf{u}, t)dt + \sqrt{C_0 \varepsilon}d\xi_i, \qquad (2.1)$$

$$d\mathbf{x} = \mathbf{u}\,dt,$$

where bold quantities denote vectors; the indices denote Cartesian components; $C_0 = 5$ is the Kolmogorov's Lagrangian velocity structure constant; t is the time; and ε is the mean rate of dissipation of turbulent kinetic energy divided by the density of air (Thomson 1989). The quantities $d\xi_i$ are increments of a Wiener (white noise) process and have mean zero and variance equal to the time increment, dt. The model is, by construction, compatible with Kolmogorov's similarity theory, a scaling widely observed in atmospheric flows. The well-mixed condition (Thomson 1989) currently constitutes the most rigorously correct theoretical framework for the formulation of LS models like equation (2.1). It guarantees that the velocity statistics of simulated dispersing bodies are compatible with prescribed Eulerian (fixed-point) velocity statistics which characterize the turbulent flow and which are used as model inputs. Mathematically, it requires that the function $a_i(\mathbf{x}, \mathbf{u}, t)$ be a solution of the Fokker–Planck equation.

By invoking the well-mixed condition, Rotach *et al.* (1996) formulated an LS model for the simulation of passive body dispersal in atmospheric boundary layers with stabilities ranging from ideally neutral to fully convective. Model predictions are in good agreement with the data collected in the laboratory-scale experiments and in the field (Willis & Deardorff 1976; Gryning & Lyck 1984). A detailed description of this LS model, its numerical implementation and the accompanying parametrization of required meteorological inputs can be found in Rotach *et al.* (1996). Here, we adopt this model for the simulation of spider ballooning dispersal. Underlying the approach is the assumption that the dragline is critical only at lift-off and is used to sense the current wind conditions. It is assumed that spiders, whether through cognition or reflex, launch into updrafts and that once airborne, they are passively advected by the air currents. Model predictions for the mean distances travelled by ballooning spiders and for the distribution of their landing sites were obtained by simulating the trajectories of 100 000 spiders under a range of atmospheric conditions.

3. RESULTS AND DISCUSSION

Predictions for the distribution of distances travelled by ballooners within a purely convective boundary
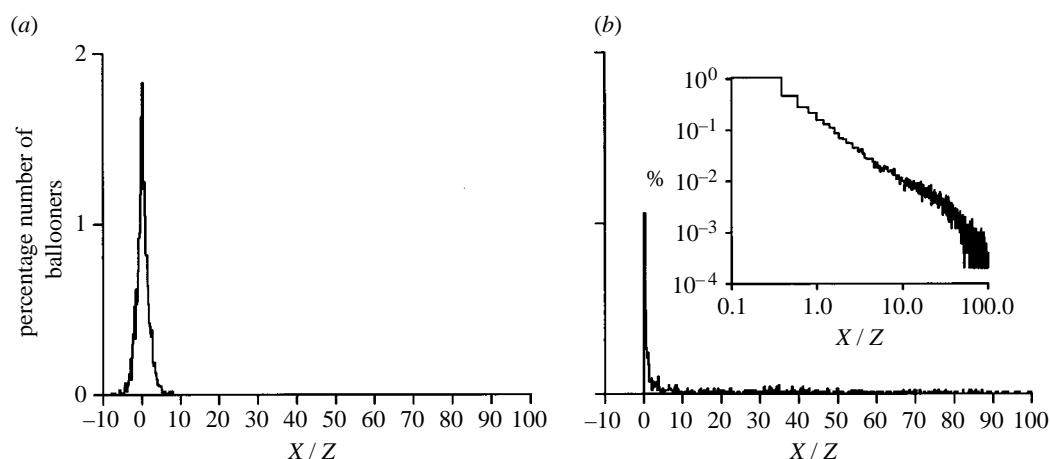
Figure 1. Percentage number of ballooners that are predicted to travel a distance, X, within a (a) purely convective boundary layer with convection velocity scale $w_* = 1 \text{ ms}^{-1}$ and (b) boundary layer of near neutral stability (convective boundary layer with wind shear with friction velocity, $u_* = 1 \text{ ms}^{-1}$, and convective velocity scale, $w_* = 1 \text{ ms}^{-1}$). Predictions are shown on linear–linear and on log–log scales (inset). Ballooners launch into thermals from a height $0.001Z$ (height of the surface roughness) into boundary layers of depth $Z = 1000$ m. The convective velocity scale $w_* = (-H_* Z)^{1/3}$, and consequently $w_* = 1 \text{ ms}^{-1}$, corresponds to a small surface heat flux, H_*, of approximately $30 \text{ J m}^{-2}\text{s}^{-1}$ (buoyancy flux $-10^3 \text{ m}^2\text{s}^{-3}$). $u_* = w_* = 1 \text{ ms}^{-1}$ corresponds to a mean wind speed (average over the boundary layer) of approximately 12.9 ms^{-1}.
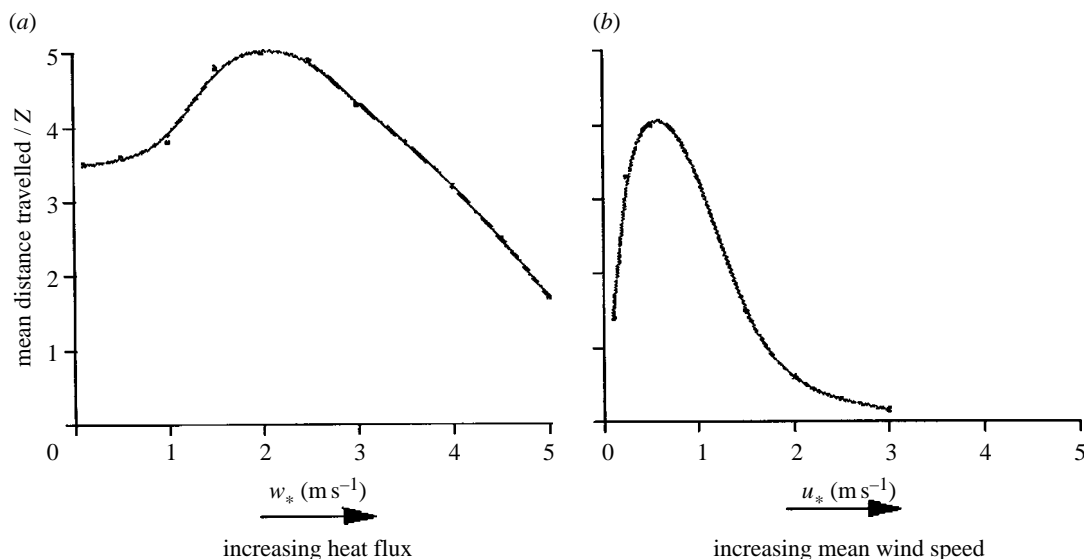

Figure 2. (a) Model predictions for the mean distance travelled by ballooners after launching themselves into thermals from a height $0.001Z$ and before landing as a function of the convective velocity scale, w_*. Predictions are shown for a friction velocity scale $u_* = 0.5 \text{ ms}^{-1}$, which corresponds to mean wind speeds (averaged over the depth of the boundary layer, $Z = 1000$ m) ranging from $6.9 \text{ ms}^{-1} (w_* = 0 \text{ ms}^{-1})$ to $2.2 \text{ ms}^{-1} (w_* = 5 \text{ ms}^{-1})$. (b) Model predictions for the mean distance travelled by ballooners after lift-off into thermals from a height $0.001Z$ (height of the surface roughness) and before landing as a function of the friction velocity, u_*. Predictions are shown for a convective velocity scale $w_* = 1 \text{ ms}^{-1}$. The predicted mean distance travelled is a maximum when $u_* \approx 0.5 \text{ ms}^{-1}$.

layer (no wind shear) and within a boundary layer of near neutral stability (convective boundary layer with wind shear) are shown in figure 1. For the majority of ballooners, the distance traversed between take-off and landing is less than a few hundred metres. But for some ballooners, dispersing within convective boundary layers with wind shear, dispersal distances of tens or even hundreds of kilometres are possible. This prediction is consistent with the observations of long-ranged ballooner dispersal (Bell *et al.* 2005), and suggests that a spider's sensing of local wind conditions has almost no predictive value for the subsequent distance of travel and can only contribute to a spider's behaviour in a statistical sense (Suter 1999).

Convective boundary layers with wind shear can be characterized by two velocity scales: the friction velocity u_* (square root of the surface stress divided by the density of the air) and the convective velocity scale $w_* = (-H_* Z)^{1/3}$, where H_* is the surface buoyancy flux and Z is the boundary layer height. The relative importance of thermal convection and surface shearing forces can be quantified in terms of the gradient Richardson number, R_i. Over quite a wide range of stability, $R_i \approx -\kappa w_*^3/u_*^3$, where $\kappa \approx 0.4$ is the von Kármán constant (Businger 1988).

Figure 2 shows that the mean distance travelled by a simulated ballooner does not increase monotonically with increasing values of the convective velocity

scale (i.e. increasing surface heat flux). Instead, the mean distance travelled increases with increasing values of the convective velocity scale when $w_*/u_* < 2$, but decreases with increasing convective velocity scale when $w_*/u_* > 2$ This may account for the strong correlation between numbers of spiders trapped as a result of ballooning activity and variations in the gradient Richardson number (Vugts & Wingerden 1976). The condition for maximal dispersal, $w_*/u_* = 2$, corresponds to a gradient Richardson number of approximately -3.2. This prediction compares favourably with the experimental study by Vugts & van Wingerden (1976). On the day selected by Vugts & Wingerden (1976), numbers of trapped ballooners peaked when the gradient Richardson number peaked at around -2.5. The model predictions are readily understood. Increasing the surface heat flux promotes thermals that in turn promote successful lift-off. However, when $w_*/u_* > 2$, the dispersion properties of convective boundary layers with wind shear are close to those of a purely convective boundary layer (Mason 1992). As a consequence, most ballooners would tend to rise and fall within a column of air above the launch site, rather than disperse in a downwind direction. Ballooning dispersal is therefore predicted to be most effective in terms of distance when the stability of the atmosphere is non-ideally convective (a condition attained in warm ambient temperatures and a light breeze). Figure 2 also shows that the dispersal of ballooners increases with increasing friction velocity (mean wind speed) when $u_* < w_*$, but decreases with increasing friction velocity when $u_* > w_*$. The suppression of dispersion can be attributed to the suppression of thermals that occurs when $u_* > w_*$. This may account for the observed decline in ballooning activity when the mean wind speed exceeds approximately 3 ms^{-1} (Suter 1999). The observed reduction may also stem, at least in part, from selection acting against hazardous ballooning excursions at high wind speeds or by the inhibition of ballooning by wind-induced oscillations of the substratum upon which the spider rests (Humphrey 1987).

The meteorological conditions that produce non-ideal convection and the greatest dispersal distances are typically attained in conditions of warm ambient temperatures and light breezes, such as that might occur in the spring and autumn of temperate latitudes. Ballooning dispersal is expected to be less effective when atmospheric conditions are purely convective (hot ambient temperatures and no breeze) or neutrally stable (cool ambient temperatures and strong winds) resulting in ballooners travelling shorter distances. Our findings are, therefore, not entirely supportive of Toft's (1995) hypothesis that summer dispersal is for long-range ballooning and spring and autumn for short-range movements. The theory also predicts the observed decrease in ballooning activity with increasing direct sunlight (Greenstone 1990) and with increasing mean wind speed when the mean wind speed exceeds approximately 3 ms^{-1}.

In conclusion, we show for the first time that optimal conditions for ballooning distance also explain the observed patterns of spider take-off events. Our theory for spider ballooning, which allies the flexible silk model of Reynolds *et al.* (2006) to the turbulent modelling presented here, would suggest that spider ballooning is constrained to the meteorological conditions required for non-ideal convection. However, our theory for spider ballooning remains to be tested experimentally. Soon, by examining the null hypothesis that dispersal distance is unrelated to silk length, we shall observe deposition patterns of ballooning spiders in replicated field experiments. We would expect that the results of these tests might have some generality for other biological entities such as pathogens (Aylor & Flesch 2001; Brown & Hovmoller 2002), seeds (Nathan *et al.* 2002, 2005) and pollen (Burrows 1986), which are all determined by unstable flows.

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