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Ballooning dispersal in arthropod taxa with convergent behaviours: dynamic properties of ballooning silk in turbulent flows

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We present a new model of ballooning behaviour in arthropods in which draglines are regarded as being extendible and completely flexible. Our numerical simulations reveal that silk draglines within turbulent flows can become twisted and stretched into highly contorted shapes. Ballooners are therefore predicted to have little control over their aerodynamic drag and their dispersal within the atmospheric boundary layer. Dragline length is crucial only at lift-off. This prediction runs counter to that of Humphrey who suggested that the length of *rigid* draglines can be used to control dispersal. In contrast with Humphrey's model, the new model accounts naturally for the large distances travelled by some ballooners.

Keywords: ballooning; dispersal; silk; arthropods

1. INTRODUCTION

A large number of economically and ecologically important small invertebrate species use secreted strands of silk (draglines) as a kind of parachute for dispersal on the wind (ballooning). Representatives from the spiders (Araneae), spider mites (Acari) and the larvae of moths (Lepidoptera) all employ dragline ballooning as their primary mode of dispersal, using it to colonize new habitats and emigrate from unfavourable conditions (Bell *et al.* 2005*a*). Ballooning is the primary mechanism by which spiders can re-colonize many agro-ecosystems, thereby impacting upon prey populations and influencing crop production.

For the majority of ballooners, the distance of dispersal is probably of the order of a few metres. But, for some, dispersal distances of many tens of kilometres may be inferred from anecdotal information and ballooning spiders have been found many hundreds of kilometres out at sea on boats (Bristowe 1939). The lengths of silk draglines range from one to several metres (Bell *et al.* 2005*a*) and it is conceivable that draglines well below 1 m are possible although these would be difficult to observe and measure in the field. Humphrey's (1987) seminal theoretical study together with two subsequent empirical investigations (Suter 1991, 1992) still provides the conceptual framework used to support investigations of the physical constraints under which ballooning operates. Humphrey regarded ballooners as being comprised of spherical bodies attached to rigid and straight draglines of constant length.

Ballooners have some control over when to balloon (Bell *et al.* 2005*a*), and presumably selection has acted to initiate ballooning behaviours under environmental conditions that would maximize the probability of successful dispersal. What is not clear is whether ballooners have any control over their dispersal distance, since the atmospheric boundary layer is spatially and temporally unpredictable (Suter 1999). Humphrey's (1987) model of ballooning suggests that ballooners can exercise some control over their dispersal distance by producing particular lengths of silk dragline. The time that a ballooner remains airborne and so the distance over which it can travel are intimately related to its terminal velocity. Humphrey's (1987) model predicts correctly the dependency of the terminal velocities of ballooners in still air and in laminar airflows, on the mass of the ballooner and the length of the silk dragline. Terminal velocities decrease (and so dispersal ranges increase) with increasing length of the silk dragline.

The physical basis for Humphrey's (1987) model is, however, questionable. Silk draglines are not rigid and when carried within the atmospheric boundary layer may become twisted and stretched into highly contorted shapes by turbulence. Such effects will dramatically reduce the ability of ballooners to control their dispersal, as the aerodynamic drag acting upon the silk dragline is dependent on the *unpredictable* shape of the silk dragline itself. In this paper, a new model of ballooning is presented in which silk draglines are regarded as being completely flexible and extendible. Using numerical simulations, we compare the expectations of our new model with those of Humphrey's (1987) model. We predict the distribution of terminal velocities, the expected conformation of the silk dragline in a turbulent flow and the distribution of 'effective' dragline lengths during a ballooning flight. The effective dragline length is the straight-line distance between the centre of the ballooners' body and the end of the silk dragline. Our model predictions are that ballooners have little control over their distance of dispersal within turbulent flows such as the atmospheric boundary layer.

2. MODEL FORMULATION AND MODEL PREDICTIONS

Humphrey's (1987) model predicts correctly the terminal velocities of ballooners in still air. Terminal velocities are attained when the aerodynamic drag exactly balances buoyancy forces, i.e. when

$$F = -m\tau^{-1}v - m_s\tau_s^{-1}v + (m + m_s - m_a)g = 0. \tag{2.1}$$

Here, v is the terminal velocity of the ballooner, m and m_s are the masses of the ballooner's body and the attached silk dragline, τ and τ_s are the associated aerodynamic response times, m_a is the mass of air displaced by the ballooner and the dragline, and g is acceleration due to gravity. When the dragline makes the dominant contribution to the drag force so that $m_s\tau_s^{-1}v \gg m\tau^{-1}v$, equation (2.1) reduces to

$$v \approx m\tau_s g/m_s \propto m/L, \tag{2.2}$$

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in accordance with recent experimental studies (Bell *et al.* 2005*b*). Humphrey's expression for the terminal velocity, $v=(m_s g/\alpha)^{1/2}$ (given here with the typographical error corrected) stems from more complicated and less transparent governing equations in which the total aerodynamic drag on the spider and the attached dragline is represented by a single nonlinear term, $-\alpha v|v|$.

The predictive value of dragline length and the validity of Humphrey's rigid dragline model are, however questionable, for ballooners airborne within the atmospheric boundary layer. This is because silk draglines are not rigid and are likely to become twisted and stretched into highly contorted shapes by turbulent vortices. Here, we elucidated this possibility through the analysis of an idealized model in which ballooners are regarded as comprising spherical bodies attached to extendible, but completely flexible draglines. That is, the draglines are assumed to offer no resistance to bending. Ballooners, along with their flexible draglines, are modelled by a chain of N spheres attached by springs and acted upon by aerodynamic drag and elastic restoring forces. The governing equations are

$$\boldsymbol{F}_i = m_i\tau_s^{-1}(\boldsymbol{u}_i-\boldsymbol{v}_i)+K(\boldsymbol{p}_{i,i-1}s_{i,i-1}+\boldsymbol{p}_{i,i+1}s_{i,i+1}) + m_0\boldsymbol{g}\delta_{i,0}, \qquad (2.3)$$

where $\boldsymbol{u}$ is the local air velocity. The ballooner with mass $m_0=m$ and velocity $\boldsymbol{v}_0$ is located at node $i=0$ and the chain of spheres with masses $m_i=m_s/N$ and velocities $\boldsymbol{v}_i$ representing the dragline extends from node $i=1$ to node $i=N$. Differences between the actual separation and the equilibrium separation, s_{eq}, of the ith and $i+1$th from the spheres are denoted by $s_{i,i+1}$. The quantities $p_{i,i+1}$ are unit vectors orientated along the lines joining the ith sphere to the $i+1$th sphere. The model with just one link in the chain ($N=1$) is a modified form of Humphrey's model in which silk draglines can be stretched but not twisted or folded.

The dispersion of modelled ballooners in statistically stationary, isotropic and homogeneous turbulence was studied in kinematic simulations (Kraichnan 1970). These turbulent characteristics approximate to those of the atmospheric boundary layer well above the surface layer (i.e. several metres above the ground) when the mean wind speed exceeds several metres per second and are sufficient to determine the predictive value of dragline length. In the kinematic simulations, incompressible turbulence having a Kraichnan energy spectrum is represented by sets of unsteady random Fourier modes. Such simulations are known to reproduce accurately many aspects of turbulent dispersion (Fung *et al.* 1992). In the current application, wavenumbers and frequencies are chosen to encompass the spatial scales and aerodynamic response times, s_{eq}, L, τ and τ_s of the ballooner and the attached dragline.

Figure 1 illustrates how completely flexible draglines can become highly distorted within turbulent flows. As a consequence, the distance between the ballooner's body and the end of the dragline is not sharply defined, but broadly distributed around a mean value that is less than the equilibrium length of the dragline. This is

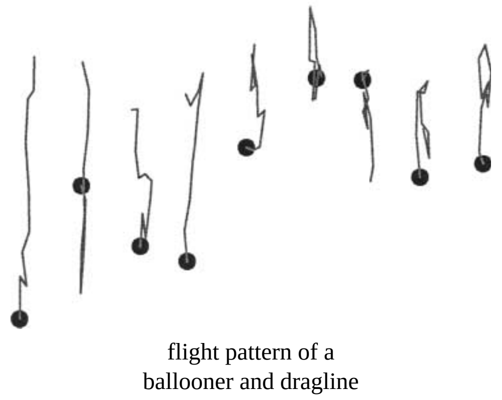

Figure 1. Snapshots of model predictions for displacements of a ballooner (filled circle) and the shape of a dragline within isotropic, homogeneous turbulence. The turbulence has Kraichnan energy spectrum that is a maximum when the wavenumber $k=k_0$. The simulated turbulence comprises 10 random Fourier modes which on average contain equal proportions of the total specific turbulent kinetic energy, $1/2u_0^2$. The frequencies of these modes are drawn from a Gaussian distribution with mean 0 and standard derivation, $\sigma=0.4ku_0$. Wavenumbers range from $k_{min}=0.1k_0$ to $k_{max}=10k_0$. Predictions are shown for draglines modelled as $N=10$ spheres with aerodynamic response times $\tau=(k_0u_0)^{-1}$ and connected by springs having specific elasticity $K/m_i=(k_0u_0)^2$ and equilibrium lengths, $s_{eq}k_0=10$. The size of the largest simulated turbulent eddy structures, $2\pi/k$, is comparable to the equilibrium length of the silk dragline, Ns_{eq}. Smaller rather than larger turbulent eddies make the dominate contribution to the twisting and folding of the silk dragline. The mass of the ballooner's body is a hundred times greater than that of the dragline. Qualitatively similar behaviours are obtained for much larger ratios of the body mass to dragline mass. Acceleration due to gravity, $g=-1/2k_0^{-1}u_0^2$. The ballooner with a vertically orientated dragline was released from rest. The time interval between successive snapshots corresponds to the eddy-turnover time, $k_0u_0^{-1}$.

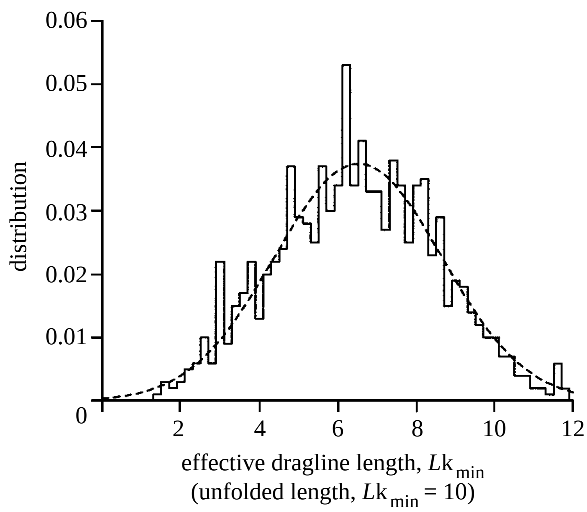

Figure 2. Predicted equilibrium distribution of distances between the body of a ballooner and the end of the dragline. Also shown is a Gaussian distribution with equivalent mean and variance (dashed line). Gaussian distributions of effective dragline lengths are obtained for other choices of the model parameters. Model parameters are given in the caption for figure 1.

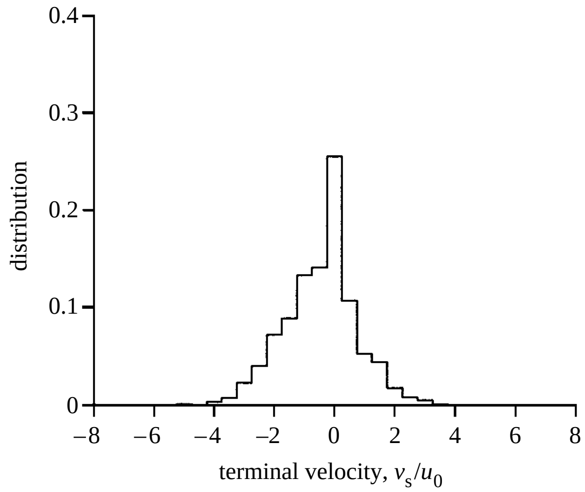

Figure 3. Predicted equilibrium distribution of terminal velocities, v_s, of ballooners with completely flexible draglines. A negative velocity corresponds to a downward displacement. Model parameters are given in the caption for figure 1. The simulated turbulent flow has specific turbulent kinetic energy, $1/2u_0^2$.

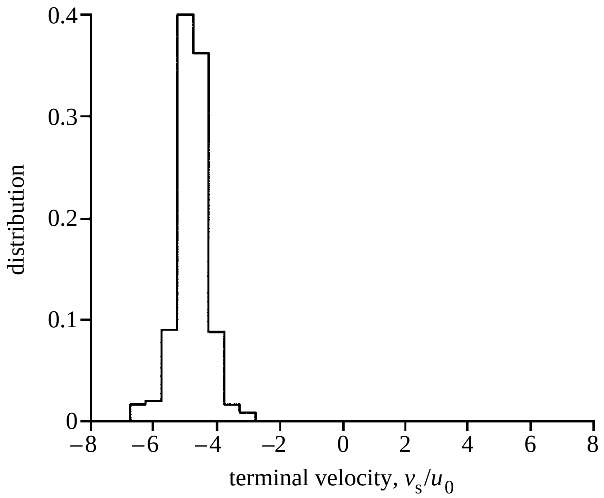

Figure 4. Predicted equilibrium distribution of terminal velocities, v_s, of ballooners with inflexible draglines. The draglines are modelled as a single spheres attached to the ballooners by springs ($N=1$). This model is effectively Humphrey's (1987) model with the rigidity condition, but not the inflexibility condition relaxed. Predictions can be compared directly with those shown in figure 3 for completely flexible draglines because the inflexible and flexible draglines have same equilibrium lengths, masses and total aerodynamic response times. Model parameters are given in the caption for figure 1. The simulated turbulent flow has specific turbulent kinetic energy, $1/2u_0^2$.

quantified in figure 2. Figures 3 and 4 show that predicted terminal velocities are broadly distributed and typically much smaller than those predicted by a simple extension of Humphrey's rigid dragline model. These relatively small terminal velocities arise because completely flexible draglines, unlike rigid draglines, can by twisting and stretching, adapt to and follow turbulent flow structures. This ability to follow the flow of air promotes long-range dispersal.

3. CONCLUSIONS

We presented a new model of ballooning, where individuals are regarded as being comprised of spherical bodies attached to extendible, but completely flexible draglines. Our simulation data suggest that turbulent dispersion does not depend sensitively upon the length of a dragline and that as a consequence, the length of a dragline will be of little value when determining dispersal distance. In contrast with Humphrey's model, the new model accounts naturally for the large distances travelled by some ballooners (Bristowe 1939). The range of terminal velocities expected with rigid draglines is narrower than for flexible and extendible silk. Some velocities from our model are also positive, suggesting that ballooners using flexible, extendible draglines will rise in an air column when otherwise similar rigid silk ballooners would not.

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