PHYSICAL REVIEW E **72**, 041928 (2005)

Scale-free movement patterns arising from olfactory-driven foraging

A. M. Reynolds*
Rothamsted Research, Harpenden, Hertfordshire, AL5 2JQ, United Kingdom

(Received 11 March 2005; revised manuscript received 2 August 2005; published 26 October 2005)

The scale-free movement patterns of some foragers has aroused considerable excitement because they are known to optimize the success of random searches when target sites are randomly and sparsely distributed. Here it is shown that scale-free movement patterns can arise from a naive response of foragers to scent concentrations within turbulent plume structures.

DOI: 10.1103/PhysRevE.72.041928 PACS number(s): 87.19.Bb, 05.10.Gg, 05.40.Fb, 47.27.Eq

I. INTRODUCTION

The movement patterns of bumblebees and some other foragers exhibit a scale-free characteristic [1–3]. These scale-free movement patterns (Lévy walks) have aroused considerable excitement because they are known to optimize the success of random searches when target sites are randomly and sparsely distributed [4]. Lévy walks have also been associated with advantageous collective foraging strategies [5,6] and with scale invariant properties of the underlying ecosystem [3]. The association of Lévy walks with optimum or advantageous behaviour does, however, fail to acknowledge that foragers tend to move within scent plumes undergoing turbulent dispersion within the atmospheric boundary layer. Here, it is shown that simple olfactory-driven searching strategies can account for the observed scale-free movement patterns of bumblebees [1]. This finding calls into question interpretations of scale-free movement patterns in terms of optimal or advantageous searching strategies.

The movement patterns of bumblebees are simulated numerically by combining models of olfactory response with a stochastic model for the turbulent fluctuations in scent concentration experienced by bumblebees along their planar-trajectories [7] in three-dimensional scent plumes. The model replicates faithfully many of the observed properties of scent fluctuations in turbulent air flows, including: distributions of scent concentration; intermittency factors (i.e., probabilities of observing nonzero scent concentrations); power-law distributions of durations between peak scent concentrations; threshold concentration up-crossing rates and; the conditional dependency of temporal gradients in scent concentration upon scent concentration [8–11]. The occurrence of scale-free foraging patterns is predicted to be largely insensitive to the distribution of scent sources and the chemical composition of scents.

II. MODELING SCENT PLUMES

Experimental studies of plumes dispersing in the atmospheric boundary layer have revealed that probability distribution functions (pdf) for within-plume scent concentration fluctuations (i.e., for scent concentration fluctuations with the intermittent periods of zero concentrations removed) are well represented by log-normal forms,

$$P(\phi) = \frac{1}{\sqrt{2\pi}\sigma_l \phi} \exp\left(-\frac{\ln^2 \phi}{2\sigma_l^2}\right), \tag{1}$$

where $\phi = c/c_{50}$ is the dimensionless scent concentration and c is the instantaneous scent concentration with median c_{50} [9]. The mean C, root-mean-square σ_c, and the intensity, $i_p = \sigma_c / C$, of within-plume scent concentration fluctuations, are determined by c_{50} and σ_l, the root-mean-square value of $\ln \phi$. Here following Hilderman and Wilson [10], Eq. (1) is extended to account for intermittency arising from plume meander. In this approach, the within-plume scent concentrations c are related to intermittent scent concentration fluctuations, c_i, by $c_i = c - c_{base}$ if $c \geqslant c_{base}$ and by $c_i = 0$ if $c < c_{base}$. The value of c_{base} is chosen to ensure that the probability of a non-zero scent concentration is equal to the intermittency factor γ and the probability of obtaining a zero scent concentration is $(1-\gamma)$. This results in a pdf with a delta function at zero scent concentration. Underlying this shifted log normal distribution is the notion that nonzero fluctuations in scent concentration and intermittent periods of zero concentration are produced by the same physical mixing process. Namely, that turbulent eddies carrying scent result in nonzero fluctuations in scent concentration whilst turbulent eddies carrying clean air result in intermittent periods of zero scent concentration.

The scent concentration fluctuations, c, at time t and at position $\mathbf{x}$ along the trajectory of a bumblebee are modeled as a first order Markov process,

$$dc = a(c,x,t)dt + b(c,x,t)d\xi, \tag{2}$$

where $d\xi$ is an incremental Wiener process with mean zero and variance dt. Such models are known to represent well, measurements of temporal derivatives in scent concentration and threshold concentration up-crossing rates made at fixed points within plumes in turbulent boundary layers [10,11]. Simulated scent concentrations are exactly compatible with (1) when

$$a = \frac{(C-c)}{T_c} + cu_i\left(\frac{\partial \ln \sigma_l}{\partial x_i} \ln(c/c_{50}) + \frac{\partial \ln c_{50}}{\partial x_i}\right) \tag{3}$$

and

---

*FAX: +44(0)1582 760981. Email address: andy.reynolds@bbsrc.ac.uk

$$b^2 = \frac{\sqrt{2\pi}\sigma_l C c}{T_c} \exp\left(\frac{\ln^2(c/c_{50})}{2\sigma_l^2}\right)\left[\mathrm{erf}\left(\frac{\ln(c/c_{50})}{\sqrt{2}\sigma_l}\right) - \mathrm{erf}\left(\frac{\ln(c/c_{50})-\sigma_l^2}{\sqrt{2}\sigma_l}\right)\right], \tag{4}$$

where T_c is a decorrelation time and where u is the velocity of a bumblebee. For spatially homogeneous plumes (4) reduces to the model of Hilderman and Wilson [10].

Unless stated otherwise, attention is focused upon the foraging characteristics of bumblebees downwind of a single compact source. Mean within-plume scent concentrations at the source height are taken to have a Gaussian form,

$$C = \frac{Q}{2\pi U \sigma_y^2} \exp\left(-\frac{y^2}{2\sigma_y^2}\right), \tag{5}$$

where Q is the mass flux of scent, y is the cross-wind position measured relative to the source position, and U is the mean streamwise velocity. Such mean scent concentrations are well established and form the basis for the much used Gaussian-plume models. The mean-square plume width is given by

$$\sigma_y^2 = \frac{2k}{U}x + \sigma_s^2, \tag{6}$$

where k is the turbulent diffusivity, x is the distance downwind from the source, and σ_s^2 is the mean-square source size.

The intensity of within-plume scent concentration fluctuations is $i_p \approx 1$ for all locations within the plume [12]. Near the source, $x < x_0$, where the plume width is less than the spatial extent of the plume meander, plume width grows as $x^{3/2}$ and the spatial extent of plume meander grows as x. As a consequence the fraction of time that the plume covers the plume centre-line (i.e. the intermittency factor) grows as $x^{1/2}$. In the far field $\gamma \rightarrow 1$ on the plume centreline. These limiting cases are encapsulated within

$$\gamma \sim \left(\frac{x}{x+x_0}\right)^{1/2} \exp\left(-\frac{y^2}{2\sigma_y^2}\right). \tag{7}$$

Perhaps the simplest olfactory response is a "passive" one in which a bumblebee advances upwind (i.e., in the negative x direction) if the scent concentration, c_i, in its immediate vicinity exceeds some threshold value, $c_{\text{threshold}}$, otherwise it makes random traverses in the crosswind (y) direction. That is, the upwind and crosswind advancement of a bumblebee evolves according to

$$x \rightarrow x - \Delta x \quad \text{and } y \rightarrow y \quad \text{if } c_i > c_{threshold},$$

$$y \rightarrow y \pm \Delta y \quad \text{and } x \rightarrow x \quad \text{if } c_i \leqslant c_{threshold}, \tag{8}$$

during response times of duration Δt. The functional form of the predicted distribution of flight lengths, presented below, does not depend upon the sizes of the incremental steps, Δx and Δy. The inherent inefficiency of this "passive" search rule is related to the small probability of encountering scent concentrations above the threshold concentration; a problem that is particularly acute when the location of the bumblebee falls well outside of the parabola (5) defining the mean plume structure. Active searches overcome this limitation by restricting search activity to regions for which the probability of finding the source is greater than some small constant, p_c [13]. If a scent concentration fluctuation above the threshold concentration is detected at some location x_i, y_i, then this search region is approximately defined by

$$(y-y_i)^2 \leqslant \frac{4k}{U}(x-x_i)\ln\left(4\pi p_c \frac{k}{U}(x_i - x)\right) \tag{9}$$

[13] [see also Eqs. (5) and (6)]. In an active search a bumblebee continually advances upwind while simultaneously passing within a distance L (scent correlation length-scale, set by the height above the ground) of all points within the cone (9) in order not to miss the source. This advancement is achieved in two steps: (1) detect scent at x_i, y_i; (2) (re)start crosswind counter-rotating flights so that the upwind advancement per turn is L and so that the transverse amplitude grows as $\sqrt{4k/U(x_i - x)}$. These crosswind motions prevent bumblebees from becoming trapped in regions where the probability of encountering scent concentrations is small, thereby increasing the rate at which scent concentration fluctuations above the threshold concentration are detected. The resultant transverse motion is biased toward the plume centerline where large scent concentration fluctuations are least frequent. The relentless upwind advancement arising from both the passive and active searches prevents back and forth movements between neighboring sources. Active searches mimic the scent-modulated optomotor anemotaxis adopted by moths [14] and other insects.

Typical predictions for the trajectories of bumblebees downwind of a compact area source, along with a corresponding prediction for the history of scent concentrations experienced by a bumblebee, are shown in Fig. 1 for the case of passive searching. These predictions were obtained by numerically integrating the stochastic model (2) for the evolution of scent concentrations whilst simultaneously updating the bumblebee's location using the passive searching strategy (8). The random crosswind motions that arise in the absence of a scent signal are replaced by counterturning crosswind motions and upwind advancement when the searching is active rather than passive. As expected bumblebees in the immediate vicinity of the source are predicted to experience highly intermittent scent concentration fluctuations and consequently undergo pronounced casting. This high intermittency arises because the plume width becomes less than the spatial extent of the plume meander. In practice the large casting events in the vicinity of the source may be curtailed by visual identification of the target or by other processes. Baker *et al.* [15] suggested that the cessation of upwind progress by insects that occurs near scent sources might be triggered by fusing of the receptor output when the receptor system can no longer resolve the individual odour pulses. The ability of an insect to resolve individual pulses is dependent upon the characteristics of the odor-detection system. In the case of attractant scents, it is widely believed that odour molecules enter through pores on the olfactory sensilla and then bind to receptor proteins on the surface of the sensory dendrites. Graded potentials arising from the dendrites

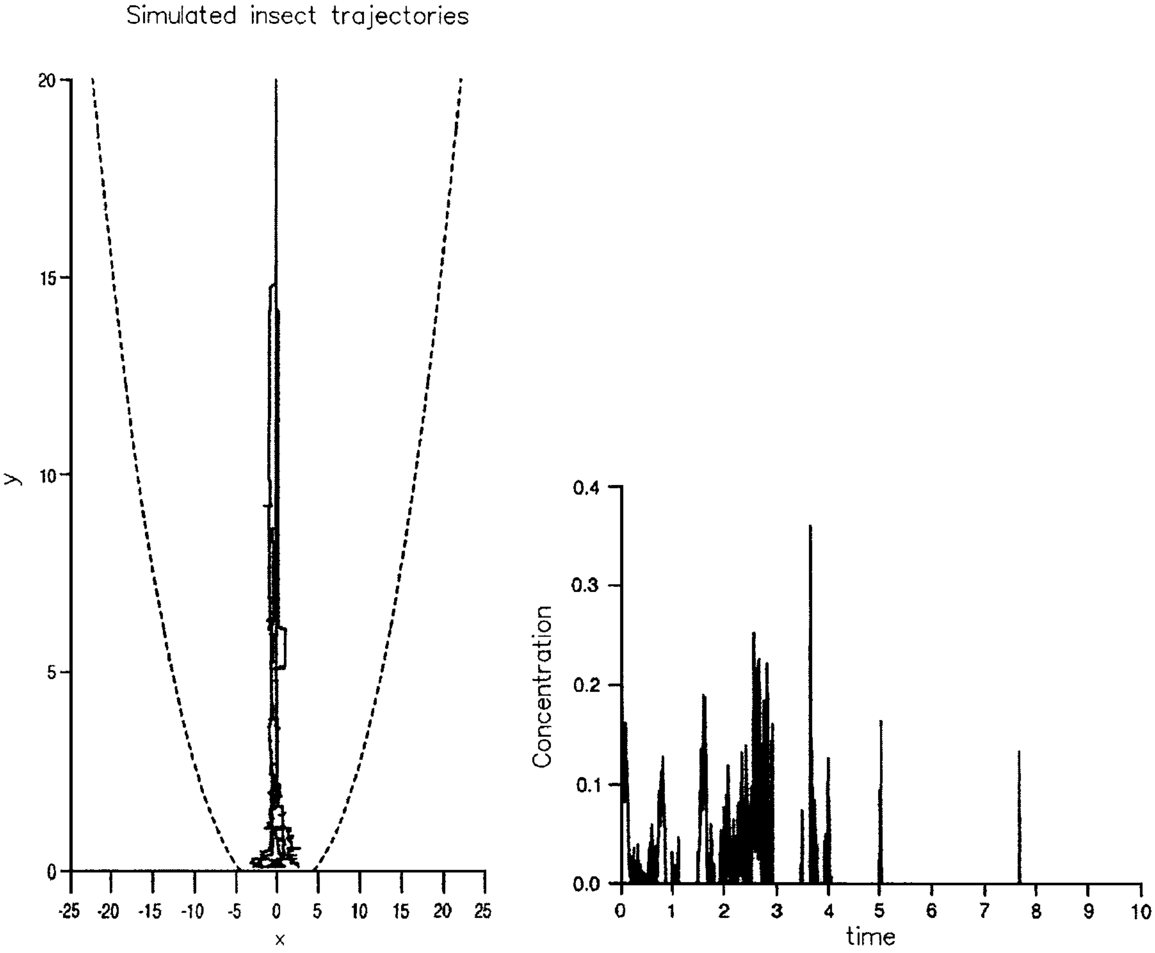

FIG. 1. The left panel shows some typical predictions (solid lines) for the trajectories of bumblebees undertaking passive searching downwind of a single compact scent-source located at $x=0$ and $y=0$. The locations where the mean scent concentration is equivalent to the detection threshold concentration are indicated (dashed line). The units are arbitrary. The right panel shows a corresponding predicted history of scent concentrations experienced by a bumblebee. Time and lengths have been non-dimensionalized using the mean wind speed, U, and the correlation time scale, T_c. Figure 2 presents non-dimension quantities.

are transmitted into trains of action potentials that propagate along the sensory axon to the central nervous system. The frequency of such action potentials is proportional to the odor intensity. This is largest in the vicinity of the source.

The predicted distribution of journey times, $P_t(t)$, from a single point of release located directly downwind of a scent source to arrival at the source is sensitively dependent upon whether the searching is passive or active. For passive searching the distribution is exceeding broad $P_t(t) \sim t^{-1}$ whilst for active searching the distribution of arrival times is strongly peaked around a well-defined mean arrival time. Predicted basins of attraction typically extend to distances that are more than ten times the distances at which the mean scent concentration equals the detection threshold concentration.

III. PREDICTED FLIGHT LENGTHS OF FORAGING BUMBLEBEES

The model approach pertains to bumblebee flights between previously unvisited florets. It precludes scent-trigger associative recall [16].

Bumblebees are assumed to land when the scent concentration exceeds some threshold value that is greater than the threshold utilized in the passive and active searches for search-locating manoeuvres. This is in accordance with the notion that there is, in practice, a cessation of upwind progress in the vicinity of nectar source, triggered perhaps by the fusing of the receptor output when the receptor system can no longer resolve the individual odor pulses. During the time between descent and returning to the location at which scent concentration spike was detected, simulated scent concentrations continue to evolve. When considering the experiments of Heinrich [1] the neglect of visual cues is perhaps not unreasonable because the visual appearance of clover florets unlike their scent does not depend significantly upon nectar content.

Distribution functions of flight lengths (distances between successive landing sites, l), $P(l)$, were obtained by ensemble averaging over many simulated bumblebee flights. Model predictions for the functional form of the distribution of flight lengths are determined by the simulated dynamics underlying the modelled scent concentration fluctuations and

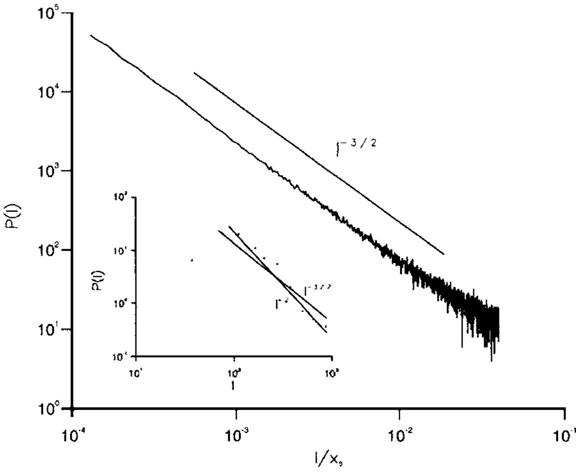

FIG. 2. Distribution, $P(l)$, of simulated flight lengths, l, of bumblebees undergoing active searches downwind of a compact scent source. The bumblebees are initially located at a distance x_s downwind of the source. The inset shows (symbols) the distribution of observed bumblebee flights of length, l (cm) [1]. The predicted and observed $l^{-3/2}$ scaling is indicated (solid lines). Also indicated in the inset is the l^{-2} scaling of the observational data advocated by Viswanathan *et al.* [4] (solid line).

by the searching strategies. It is not dependent upon model parameter values. Distributions of simulated flight lengths associated with both passive and active searches have the form $P(l) \sim l^{-3/2}$, for lengths l much less than the distance, x_s, between the initial location of the bees and the scent source. For much longer lengths, the power-law scaling, $P(l) \sim l^{-3/2}$, is not attained because many simulated flights converge on the source, as illustrated in Fig. 1, and because flights not terminating at the source will not progress beyond the source location in the downwind direction into the region where scent concentrations vanish. As a consequence, the first moment of $P(l)$ (i.e., the mean length flight l) is a convergent quantity. Figure 2 shows that the predicted power-law scaling, $P(l) \sim l^{-3/2}$, is compatible with the observational data of Heinrich [1].

The prediction of a scaling exponent less than 2 is not unprecedented within the context of foraging and has been reported on previously by Viswanathan *et al.* [4]. Viswanathan *et al.* [4] considered scale-free random searching processes comprising of sequences of uncorrelated, randomly orientated, segments with lengths drawn from a power-law distribution with a characteristic exponent μ where $1 < \mu \leq 3$. They showed that when foragers have no prior knowledge of the distribution of target sites and when targets sites are sparsely and randomly distributed and can revisited any number of times (nondestructive foraging), $\mu = 2$ is an optimal searching strategy. When target sites are destroyed by the forager and so become unavailable in subsequent flights (destructive foraging), $\mu \rightarrow 1$ is an optimal searching strategy. As $\mu \rightarrow 1$ the fraction of flights with lengths less than the mean spacing between target sites becomes negligible and foragers effectively move along straight lines until they detect a target site. Numerical simulations (not presented) reveal that $\mu = 3/2$ can constitute an optimal scale-free searching strategy. This can arise, for instance, when flight directions are orientated in the upwind direction if the local scent concentration exceeds some threshold concentration but are otherwise randomly orientated. The scaling exponent characterizing the optimal such scale-free searching strategy is found to decrease monotonically as the relative proportion of upwind flights increases.

The prediction of a Lévy-like distribution of flight-lengths is robust and does not change when, for instance, the time spent on the ground is randomly distributed. Nor does it change when the spectra of simulated scent concentration fluctuations is changed, following the approach of Reynolds and Lo Iacono [17], from the Markovian form, $S \propto \omega^{-2}$, to $S \propto \omega^{-5/3}$ which is consistent with Kolmogorov-Obukhov-Corrsin scaling for high Reynolds number turbulence. A Lévy distribution of flight lengths is predicted to arise when the scent plume consists of a two independent components not necessarily having the same correlation time scales (i.e., same Prandtl numbers). This is the case when the olfactory responses are determined by linear combinations of component scent concentrations exceeding some threshold value and when olfactory responses are determined by individual component scent concentrations simultaneously exceeding threshold values. Levy distributions of flight lengths are also predicted to arise in the far field of independent overlapping plumes from multiple sources. Only when bumblebees are released in the immediate vicinity of a source do the high tails of the distribution of flight lengths have an exponential rather than a power-law form.

IV. SUMMARY

The foraging characteristics of bumblebees have been studied in numerical simulations by combining a stochastic model for the fluctuations in scent experienced by bumblebees with simple models of olfactory-driven searches. In the far field of a scent source, foraging patterns are, in accordance with observations [1], predicted to be scale free. It was shown that this scale-free characteristic arises directly from simple responses [11] of bumblebees to the complex histories of scent concentration fluctuations experienced along their flight paths. This result calls into question interpretations of scale-free foraging patterns in terms of optimal or advantageous searching strategies [4–6]. This is because the scale-free distributions of flight lengths arising from naive olfactory-driven searching and from optimal or advantageous searching strategies fit existing experimental data equally well [1]. Olfactory-driven searching does, however, result in biased Levy walks with motions tending to be directed either towards or along the plume centreline whilst optimal or advantageous searching produces free-ranging paths with a uniform distribution of turning angles.

Potential practical applications of the modeling approach include the following: determining insect population densities from observed trap counts and meteorology conditions;

quantifying uncertainties in trap counts for low population density; the prediction of insect flight disruption due to modification of background scent concentrations; and the determination of capture domains.

ACKNOWLEDGMENTS

This work was funded by the BBSRC through a core strategic grant. I thank Juliet Osborne for many stimulating discussions about bumblebee flight patterns.

---

[1] R. Heinrich, Oecologia **40**, 235 (1979).
[2] R. P. D. Atkinson, C. J. Rhodes, D. W. MacDonald, and R. M. Anderson, Oikos **98**, 134 (2002).
[3] G. M. Viswanathan, V. Afanasyev, S. V. Buldyrev, E. J. Murphy, P. A. Prince, and H. E. Stanley, Nature (London) **381**, 413 (1996).
[4] G. M. Viswanathan, S. V. Buldyrev, S. Havlin, M. G. E. da Luz, E. P. Raposo, and H. E. Stanley, Nature (London) **401**, 911 (1999).
[5] M. Levandowsky, J. Klafter, and B. S. White, Bull. Mar. Sci. **43**, 758 (1988).
[6] F. L. Schuster and M. Levandowsky, J. Eukaryot Microbiol. **43**, 150 (1996).
[7] J. R. Riley, D. R. Reynolds, A. D. Smith, A. S. Edwards, J. L. Osborne, I. H. Williams, and H. A. McCartney, Nature (London) **400**, 126 (1999).
[8] E. Yee, P. R. Kosteniuk, G. M. Chandler, C. A. Biltoft, and J. F. Bowers, Boundary-Layer Meteorol. **66**, 127 (1993).
[9] B. L. Sawford, Boundary-Layer Meteorol. **38**, 209 (1987).
[10] T. L. Hilderman and D. J. Wilson, Boundary-Layer Meteorol. **91**, 451 (1999).
[11] S. Du, D. J. Wilson, and E. Yee, Boundary-Layer Meteorol. **92**, 229 (1999).
[12] D. J. Wilson, A. G. Robins, and J. E. Frackrell, Atmos. Environ. **19**, 1053 (1985).
[13] E. Balkovsky and B. I. Shraiman, Proc. Natl. Acad. Sci. U.S.A. **99**, 12589 (2002).
[14] A. Mafra-Neto and R. T. Cardé, Nature (London) **369**, 142 (1994).
[15] T. S. Baker, M. A. Willis, K. F. Haynes, and P. L. Phelan, Physiol. Entomology **10**, 257 (1985).
[16] J. Reinhard, M. V. Srinivasan, and S. Zhang, Nature (London) **427**, 411 (2004).
[17] A. M. Reynolds and G. Lo Iacono, Phys. Fluids **16**, 4353 (2004).