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Fluctuating environments drive insect swarms into a new state that is robust to perturbations

Short title: Fluctuating environments drive insect swarms into a robust new state

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In contrast with laboratory insect swarms, wild insect swarms display significant coordinated behaviour. Here it is hypothesised that the presence of a fluctuating environment drives the formation of transient, local order (synchronized subgroups), and that this local order pushes the swarm as a whole into a new state that is robust to environmental perturbations. The hypothesis finds support in a theoretical analysis and in an analysis of pre-existing telemetry data for swarming mosquitoes. I suggest that local order is sufficient to make swarms fault-tolerant and that the swarm state and structure may be tuneable with environmental noise as a control parameter. The new theory opens a window onto thermodynamic descriptions of swarm behaviours and extends a long-standing analogy with self-gravitating systems.

In contrast with bird flocks, fish schools and animal herds, insect swarms maintain cohesion but do not possess global order [1-11]. This has prompted the search for more nuanced ways to characterize collective motions in animal aggregates that go beyond the identification of global ordering or patterning [5-8]. These studies vividly demonstrate that an aggregates' properties cannot be determined by passive observations of its quiescent state alone; instead the aggregate must be perturbed [12]. In contrast with laboratory insect swarms [1-8], wild insect swarms [9-11] contend with temperature gradients, air flows, and other dynamic perturbations. Understanding how and why laboratory and wild swarms differ may therefore lead to a better understanding of collective motion and to why collectives possess enhanced properties relative to individual animals.

Insects within laboratory swarms appear somewhat paradoxically to be tightly bound to the swarm whilst at the same time weakly coupled inside it [2]. This is quite different from wild swarms which display very strong correlations associated with the intermittent presence of synchronized subgroups [9-11]. Here I account for the difference in observed correlations between the two data sets. I show how the presence of transient synchronized subgroups can push the swarm as a whole into a new state that is robust to environmental perturbations. The new theory predicts that the aerial density profiles of wild swarms can be accurately characterized by q-Gaussians. Support for this distinctive prediction is found in an analysis of pre-existing telemetry data for swarming mosquitoes [11]. The occurrence of q-Gaussians is shown to sharpen much-exploited similarities between insect swarms and self-gravitating systems [1,13-16].

In wild swarms, subgroups of synchronized individuals form momentarily [11]. These subgroups predominantly consist of pairs of individuals flying in parallel. For illustrative purposes I begin by considering wild swarms that consist exclusively of individuals and coordinated pairs. In the long-time limit, the dynamics of such swarms can be described 'thermodynamically' and so without direct reference to specific individuals by a pair of coupled reaction-diffusion equations

$$\frac{\partial N_1}{\partial t} = -\alpha N_1^2 + 2\beta N_2 + k\frac{\partial}{\partial x}(xN_1) + D_1\frac{\partial^2 N_1}{\partial x^2}$$

$$\frac{\partial N_2}{\partial t} = \frac{1}{2}\alpha N_1^2 - \beta N_2 + k\frac{\partial}{\partial x}(xN_2) + D_2\frac{\partial^2 N_2}{\partial x^2}$$

(1)

where N_1 and N_2 are the spatio-temporal distributions of individuals and coordinated pairs

60   [17]. The first two terms on the right hand sides of Eq. (1), the fusion-fission terms, describe the continuous formation and break-up of pairs. The third terms account for the attraction to the swarm centre. [The results that follow apply irrespective of whether or not pairs are attracted to the swarm centre]. Taken together the first, third and fourth terms are the Eulerian, long-time equivalent of the Lagrangian models of Obuko [1] and Reynolds et al

65   [13,14] which encapsulate many of the microscopic and emergent macroscopic properties of laboratory swarms. Here in accordance with observations [11] it is assumed that: (1) $N_1 \gg N_2$; (2) $D_2 \gg D_1$ (i.e., co-moving pairs have higher motility); (3) reaction dynamics are fast so that $\alpha N_1^2 - 2\beta N_2 \approx 0$ which is consistent with the membership of synchronized pairs changing rapidly over time. Under these assumptions, Eqn. 1 reduces to the non-linear

70   diffusion equation

$$\frac{\partial N}{\partial t} = k \frac{\partial}{\partial x}(xN) + D_2' \frac{\partial^2 N^2}{\partial x^2} \tag{2}$$

where $N = N_1 + N_2$, $D_2' = \frac{\alpha}{2\beta} D_2$ and $N_2 = \frac{\alpha}{2\beta} N_1^2 \approx \frac{\alpha}{2\beta} N^2$

The stationary solution of Eqn. 2 is a q-Gaussian with *q=0*

$$N = \frac{3}{4\sigma}\left(1 - \frac{x^2}{\sigma^2}\right) \ for \ |x| < \sigma = \left(D_2'/k\right)^{1/2}$$
$$= 0 \ for \ |x| > \sigma \tag{3}$$

75   Laboratory swarms, on the other hand, have Gaussian density profiles with long tails [2]. These are predicted by the model, Eqn. 1, when fission-fusion processes are absent. Given enough time an insect in a laboratory swarm can explore the whole of its potential well, whereas an insect in a wild swarm never can. Confinement in wild swarms arises because Eqn. 2 corresponds to a density-dependent random walk model

80   $$dx = -kxdt + \sqrt{2DN(x)}d\xi \tag{4}$$

where $d\xi$ is a white noise process with mean zero and variance *dt* [18]. The intensity of the driving noise depends on the probability distribution, $N(x)$, and vanishes at the edges of the swarm. As a consequence, wild swarms are predicted to be more tightly bound together than are laboratory swarms where individual movements at long-times are described by

3

$$85 \qquad dx = -kxdt + \sqrt{2D}d\xi \qquad\qquad\qquad (5)$$

[1,14]. In other words, in wild swarms the attraction to the swarm centres is countered by sub-diffusion whereas in laboratory swarms the attraction is countered more strongly by diffusion. It is noteworthy that if $N(x)$ is interpreted as being the instantaneous rather than

90 the equilibrium distribution then distant fluctuations in the density of a wild swarm are predicted to be felt locally This may explain the findings of Attanasi et al. [9,10] who reported that wild swarms tune their control parameters to the swarm size. This was interpreted by Attanasi et al. [9,10] under the guise of criticality. Here it is simply a mathematical consequence of fusion-fission dynamics.

95 More generally sub-groups of size *n* correspond to q-Gaussians with *q=2-n* [17]. A population of different-sized subgroups can be expected to correspond to a series of q-Gaussians with q=0, -1, -2,…., so that the overall density profile becomes

$$N(x) = \frac{1}{\sqrt{\pi}\sigma} \sum_{n=2} f(n) \quad \begin{array}{ll} \sqrt{Q}\dfrac{\Gamma(Q+3/2)}{\Gamma(Q+1)}\left(1 - Q\dfrac{x^2}{\sigma^2}\right)^Q & for \quad |x| < \sigma/\sqrt{Q} \\[2ex] 0 & for \quad |x| \geq \sigma/\sqrt{Q} \end{array} \qquad (6)$$

where $Q = \dfrac{1}{1-q}$, $\sigma = \sigma_x$ and where here f(n) is taken directly from observations [11]. This

100 prediction provides good representations of the density profiles of wild swarms [11] (Figs. 1-3). This shows how seemingly disparate observations (distribution of subgroup sizes and overall density profiles) can be tidied together consistently by the new theory. The model distributions were fitted to the telemetry data [11] by matching the variances of the model distributions to the observations [for a Gaussian distribution this is the log maximum

105 likelihood estimate] and the best model distribution was identified using the Akaike information criterion. An Akaike weight (reported in Figs 1-3) is the weight of evidence in favour of the q-Gaussians providing the better fit to the data. They can vary from 0 (no support) to 1 (complete support).

110   Okubo [1] was the first to propose that insect swarms are analogous to self-gravitating systems. This analogy stems from the fact that individual insects are bound to the swarm centre by a force that increases linearly with distance from the swarm centre [1,2]. This is encapsulated in Eqn. 1 and is consistent with insects interacting via an inverse-square law. An inverse-square law is expected if, as is widely believed, insects are interacting

115   acoustically with one another [14]. In this regard, q-Gaussians, also known as polytropic distributions, are interesting because they constitute the simplest, physically plausible models for self-gravitating stellar systems [19]. They arise in a very natural way from the theoretical study of self-gravitating systems. The parameter q is related to the polytropic index, n, that links pressure and density, $P \propto \rho^{1+\frac{1}{n}}$, by $\frac{1}{1-q} = n - \frac{1}{2}$. This is consistent with

120   observations of laboratory swarms which have Gaussian density profiles (corresponding to $q \to 1$) [1,2] and have isothermal cores ($P \propto \rho$) [8] (corresponding to $n \to \infty$). A polytrope with index $n = \infty$ corresponds to an isothermal self-gravitating sphere of gas, whose structure is identical to the structure of a collisionless system of stars like a globular cluster. Laboratory swarms are therefore predicted to be analogous to globular clusters, as claimed

125   by Gorbonos et al. [15]. Wild swarms are different as q-Gaussians with *q=0* (i.e., n=3/2) are predicted to make the dominant contribution to the overall aerial density profile. A polytrope with index $n = 1.5$ is a good model for fully convective star cores (like those of red giants), brown dwarfs, giant gaseous planets (like Jupiter), or even for rocky planets [20].

130   The foregoing analyses suggests that the presence of a fluctuating environment drives the formation of transient, local order (synchronized subgroups), and that this local order pushes the swarm as a whole into a new state that is robust to environmental perturbations. It may therefore reconcile seemingly conflicting observations of insect swarms [1-8] made in the laboratory and in the wild [9-11] because it suggests that different kinds of group

135   morphologies and swarm dynamics are simply different phases of the same phenomenon. It may also sharpen a long-standing analogy with self-gravitating systems [1], an analogy that is gaining renewed attention [13-16].

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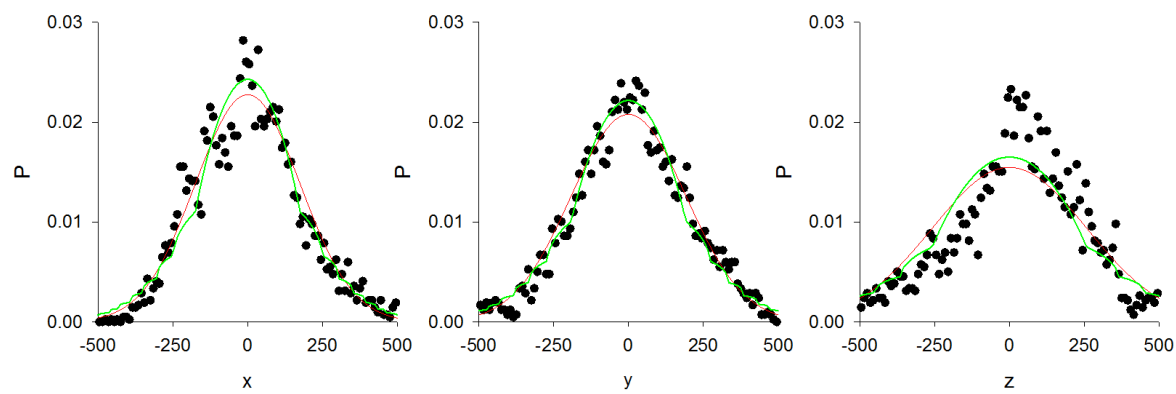[20] Chandrasekhar, S. *An Introduction to the Study of Stellar Structure*, New York: Dover (1939).

Figure 1. Analysis of a male-only swarm with 22 individuals (ref. Males08292120). Distribution, P, of distances of each individual from the swarm centre. Telemetry data (●). q-Gaussian ansatz (green line). Shown for comparison is the best fit Gaussian (red-line). The Akaike weights for the q-Gaussians are 1.00, 1.00 and 1.00.
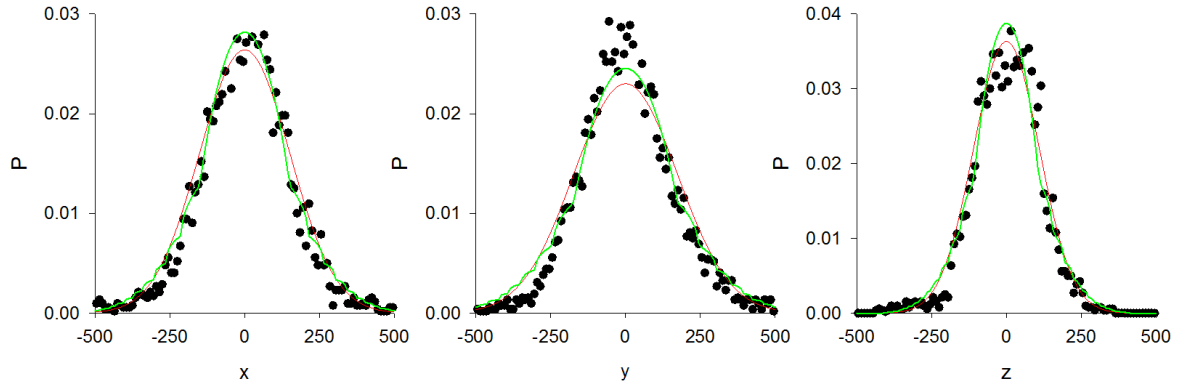
Figure 2. Analysis of a male-only swarm with 22 individuals (ref. Males08292120). Distribution, *P*, of distances of each individual from the swarm centre. Telemetry data (●). Best fit q-Gaussian (green line). Shown for comparison is the best fit Gaussian (red-line). The Akaike weights for the q-Gaussians, are 1.00, 1.00 and 0.00.
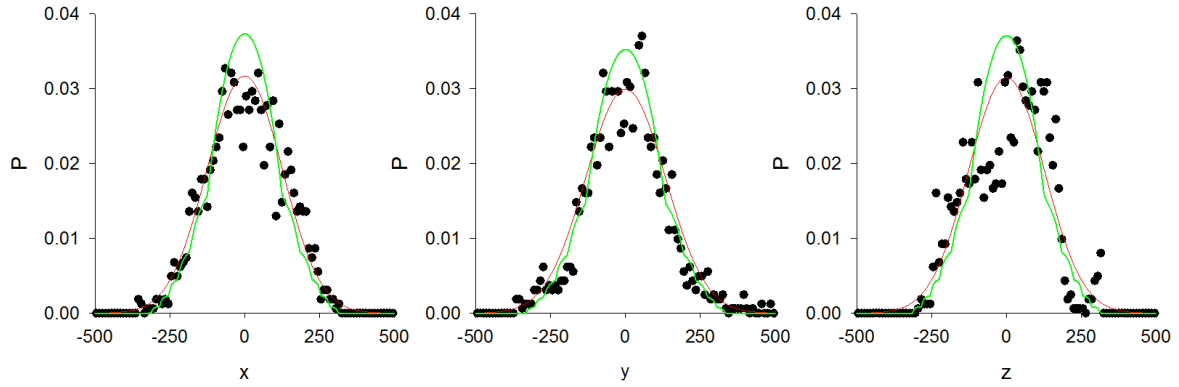
Figure 3. Analysis of a male-only swarm with 7 individuals (ref. Males08252010a).
Distribution, *P*, of distances of each individual from the swarm centre. Telemetry data (●).
210   Best fit q-Gaussian (green line). Shown for comparison is the best fit Gaussian (red-line).
The Akaike weights for the q-Gaussians are 1.00, 1.00 and 0.00.