**Swarm formation as backward diffusion**

Andy M. Reynolds1\* and Nicholas T. Ouellette2

1Rothamsted Research, Harpenden, AL5 2JQ, United Kingdom.

2Department of Civil and Environmental Engineering, Stanford University, Stanford, CA 94305, USA.

\*Corresponding author: Andy Reynolds

E-mail: andy.reynolds@rothamsted.ac.uk. Tel: +44 (0)1582 763133

**Considerable progress has been made in understanding insect swarms – forms of collective animal behaviour that unlike bird flocks, fish schools and animal herds do not possess global order. Nonetheless, little is known about swarm formation.** **Here we posit a mechanism for the formation of insect swarms that is consistent with recent empirical observations reported by [Patel and Ouellette 2022]. It correctly predicts new features of swarm formation that have not been reported on previously. Our simple analytically tractable model shows how harmonic potential wells, a characteristic feature of swarming, and so swarm cohesion, arise from diffusion and local fission-fusion dynamics and how, in accord with observations, these wells deepen over time. The overall form of these potential wells is predicted to depend on the number and spatial distribution of all individuals, making them manifestly a collective phenomenon. Finally, swarms are predicted to ‘cool’ (that is, condense) as they form.**

Physics-based approaches to collective animal behaviour, both experimental and theoretical, have been focused almost exclusively on animal groups that are known to be or are assumed to be in steady state [Ouellette 2022]. Little is known quantitively about how animal groups form. Studying group formation may help elucidate how the collective properties emerge from interactions among individuals. And by clarifying the transition between aggregations of nearby but independent individuals and interacting collective systems, such studies may help answer fundamental questions about what constitutes collective behaviour [Ouellette 2022]. Patel and Ouellette [2022] were among the first to make progress in this direction. They studied laboratory swarms of the non-biting midge *Chironomus riparius* during swarm formation and dissolution. Here we posit a mechanism for the formation of cohesive insect swarms that is consistent with these observations. We show how emergence of confining potential wells [Okubo 1986, Kelley and Ouellette 2013], a hallmark of insect swarms, can be attributed to individuals undergoing fission-fusion processes (described below), mirroring the case of stable swarms [Okubo 1986, Kelley and Ouellette 2013]. The new mechanism is distinctly different from aggregation due to either attractive pheromones, visual cues or acoustic cues, contentious processes in the context of insect swarms [Feugére et al. 2021, Poda et al. 2022] which in themselves do not result in the formation of potential wells and in the emergence of collective behaviour.

Here the process of swarm formation is studied in the long-time limit because although not wholly realistic it is analytically tractable and informative. Moreover, following Okubo [1986] we consider just one component of position; such models are capable of encapsulating emergent properties of insect swarms such as their tensile strength and enriching the long-standing analogy between insect swarms and self-gravitating systems [Okubo 1986, Reynolds 2019a, 2021]. We regard swarm formation as a system of immobile (swarming) and mobile (non-swarming) individuals whose spatial-temporal distributions, *I(x,t)* and *M(x,t)*, are governed by the pair of one-dimensional reaction-diffusion equations

(1)

where *α* is the rate at which individuals switch spontaneously from being immobile to being mobile (with diffusivity *DM*) and vice versa, and where *β* sets the rate at which mobile individuals switch to becoming immobile individuals after encountering a group (of size *k*) of immobile individuals (n.b. that a group of k immobile individuals occurs with probability *Ik*). When the interactions between individuals are very much faster than diffusive transport, local equilibrium is established, i.e., . When *k>1* this local equilibrium condition leads to the establishment of threshold (minimum) number densities, , below which the total population cannot fall without loss of reactive capability (Fig. 1). When and hence when (Fig. 1), Eqn. (1) reduces to the non-linear diffusion equation

(2)

where. The corresponding Ito- and Stratonovich-Langevin equations for the simulation of individual trajectories are given by

 (3a)

and

 (3b)

where *N(x,t)* is a solution of Eqn. 2 and where is a white noise such that and . It is apparent that when reactions are occurring (i.e., when) there is a feedback from the macroscopic level of description of the swarm in terms of the probability distributions, *N(x,t),* to an individual’s kinetics—that is, the system is behaving collectively.

Note that when *k=1*, diffusion is “frozen”, i.e., any distribution is predicted to be stable even though individuals within the population are moving. Frozen diffusion accounts for many characteristics of stable swarms [Reynolds 2019b]. Reaction-diffusion dynamics analogous to Eqn. 1 may also account for the formation of transient local order (synchronized subgroups in natural swarms [Reynolds 2018].

Eqn. 2 has the solution

 (4)

where . [The three-dimensional form of Eqn. 4 is given by

with .] Normal diffusion with diffusivity  arises when . The existence of a minimum concentration for the initiation of swarm formation may explain why swarms form preferentially over prominent visual features, known as swarm markers [Puckett and Ouellette 2014].Note also that when *k=3*, . Increasing *α/β* (by, for example, increasing the level of illumination in the experiments of [Patel and Ouellette 2022]), increases *Nc* and so could prevent or destabilize swarm formation because it could result in a loss of reactive capability. Similarly increasing *α/*β when diffusion is frozen results in ‘melting’, i.e., it results in less cohesive swarms whereas decreasing *α/*β (i.e., decreasing the light level) has no effect on an already stable (frozen) swarm. This maybe the most parsimonious explanation for the observations of swarm dissolution made by Patel and Ouellette [2022]

The half-width of the density profiles, Eqn. 4, evolve in time according to which corresponds to a ‘backward’ diffusion process when , i.e., to the formation of a swarm (Fig. 2a). Backward diffusion will eventually be arrested if the immobile individuals are weakly diffusive with diffusivity much less than the diffusivity of mobile individuals. Backward diffusion will be counter-balanced by diffusion of immobile (i.e., weakly diffusive) individuals when the width of the density profile, . This occurs at a time , after which density profiles will lose their power-law tails and will effectively become frozen. Swarm sizes may also be determined by the balancing of two opposing biological factors: an individual’s probability of mating success, which is greatest in small swarms, and an individual’s predation risk, which is also greatest in small swarms [Neems et al. 1992].

The predicted number of individuals in the swarm increases over time (Fig. 2b) as the swarm size decreases (Fig. 2c) in accordance with observations [Patel and Ouellette 2021]. More strikingly, radial accelerations are predicted to appear with the onset of swarm formation. The mean radial acceleration is predicted to be initially close to zero, but rapidly saturates to a negative value (that is, pointing toward the centre of the swarm) (Fig. 2d); so mirroring observations [Patel and Ouellette 2021]. Accelerations do not feature explicitly in the long-time (diffusive) limit but will feature in higher-order formations in which the diffusion equation in Eqn. 1 is replaced by a Fokker-Planck equation for the joint evolution of position and velocity (rather than just position). It follows from such Fokker-Planck equations that mean accelerations, are determined by

=0 (5)

where is the joint distribution of velocities and positions. Integrating Eqn. 5 over velocities gives a general expression for the mean velocity, ,

 (6)

in terms of the distribution for positions, . Equations 5 and 6 guarantee that an individual’s mean velocity and mean acceleration are consistent both with the density profiles, Eqn. 4, and with prescribed velocity statistics. Here, we assume that velocity statistics are Gaussian with constant variance so that

 (7)

It follows from Eqns. 5-7 that

 (8)

where . The predicted presence of such a velocity during swarm formation is supported by our analysis of the data of Patel and Ouellette [2022] (Fig. 3). From a biological or behavioural perspective this prediction is striking because the response (that is, the magnitude of the average mean velocity) increases rather than decreases with increasing distance from the centre of attraction. Up to a multiplicative constant, Eqn. 8, equals the first term on the righthand side of Eqn. 3b (higher order analogues of Eqn. 3a are non-physical because kinetic energies are unbounded). The first two terms on the righthand side of Eqn. 8 are just the change in the mean velocity, which becomes negligible at long times. The third term indicates that individuals are predicted to be attracted to the swarm (by an effective force that decreases with increasing distance from the edge of the swarm) and that within the core of a swarm they are predicted to behave as if they are trapped in a harmonic potential well that during swarm formation deepens over time (whilst the spatial extent of the swarms - as marked by the maximum in the potential well - remains nearly constant) (Fig. 4). Such trapping is a defining characteristic of midge swarms [Okubo 1986, Kelley and Ouellette 2013], and one that can distinguish between aggregates of non-interacting individuals and ‘real’ swarms that are behaving collectively [Patel and Ouellette 2021]. This collective behaviour is made explicit in the second form of Eqn. 8 where an *individual’s* mean acceleration is seen to depend on the number and spatial distribution of *all* individuals. The depth of the potential well (and so the stability of the swarm) decreases as *k* increases. Note also that if the velocity statistics are taken to be non-Gaussian (as must be the case when accounting, for example, for insects having a maximum attainable flight speed) then the mean attraction (third term on right-hand side of Eqn. 8) become velocity-dependent, as observed [Reynolds et al. 2017].

From a physical perspective, it is interesting to note that the proportion of mobile individuals within the swarm and their mean speed are predicted to decrease over time (Figs. 1 and 3), i.e., the mean kinetic energy, a proxy for temperature, is predicted to decrease over time as the swarm condenses. From a mathematical perspective, it is interesting to not thatthe solutions, Eqn. 4, corresponding to backward diffusion are truncated q-Gaussians with . The truncation allows for normalization (regularization) of the solutions pertaining to backward diffusion which would be otherwise problematic*.* In this way we can give meaning to q-Gaussians with *q*>3 and attribute their occurrence to physical processes, whereas previously they were discounted. Outside of the swarm (where concentrations fall below the truncation value), individuals are predicted to be diffusive, i.e., during formation swarms, like their stable counterparts [Kelley and Ouellette 2013], are predicted to be surrounded by ‘halos’ of mobile individuals. This effect may be related to observations of distinct properties in the interior and exterior layers of swarms [Sinhuber and Ouellette 2017].

The putative occurrence of *q*>3 Gaussians is consistent with a variety of theories, supported by observations, which indicate that the density profiles of laboratory swarms are q-Gaussians with *q* ranging between 1 and 2, whilst wild swarms which must contend with environmental disturbances have *q*<1 [Reynolds 2021]. Nonetheless, the *1/r* long-range behaviour of the attractive force, Eqn. 8, appears not be consistent with the long-standing analogy between insect swarms and self-gravitating systems: far from a self-gravitating system the force of attraction obeys an inverse square law. The *r*-dependency may, however, be different in higher-dimensional models.

Our results provide further support for using the emergent central potential as an order parameter to describe swarming [Patel and Ouellette 2022, Reynolds et al. 2022]. As observed [Patel and Ouellette 2022], its rapid emergence and stabilization suggest that during swarm formation aggregations of individuals very rapidly become real swarms with collective properties.

**Acknowledgements**

AMR is indebted to Stefan Geritz who bringing to his attention the possibility of attaining backward diffusion from fission-fusion dynamics, and for hosting a visit to the University of Helsinki during which time solutions to the model, Eqn.1, were established. The work at Rothamsted forms part of the Smart Crop Protection (SCP) strategic programme (BBS/OS/CP/000001) funded through the Biotechnology and Biological Sciences Research Council’s Industrial Strategy Challenge Fund. The work at the University of Helsinki was funded by the Centre of excellence in Analysis and Dynamics Research of the Academy of Finland.

**References**

Feugére, L. et al. Mosquito sound communication: are male swarms loud enough to attract females? *J. Roy. Soc. Int.* **18**, 20210121 (2021).

Kelley, D.H. & Ouellette, N.T. Emergent dynamics of laboratory insect swarms. *Sci. Rep.* **3**, 1073, 1-7 (2013).

Neems, R.M., Lazarus, J., & Mclachlan, A.J. Swarming behavior in male chironomid midges: a cost-benefit analysis*. Behav. Ecol.* **3**, 285-290 (1992).

Patel, M.L. &Ouellette, N.T. Formation and dissolution of midge swarms. *Phys. Rev. E* **105**, 034601 (2022).

Puckett, J.G. and Ouellette, N.T. Determining asymptotically large population sizes in insect swarms. *J. Roy. Soc. Int.* **11**, 20140710 (2014).

Poda, S.B. et al. No evidence for long-range male sex pheromones in two malaria mosquitoes. *Nat. Ecol. and Evol.* **6**, 1676-1686 (2022).

Okubo, A. Dynamical aspects of animal grouping: swarms, schools, flocks, and herds. *Adv. Biophys*. **22**, 1-94 (1986).

Ouellette, N.T. A physics perspective on collective animal behavior. *Phys. Biol.* **19**, 021004 (2022).

Reynolds, A.M. Fluctuating environments drive insect swarms into a new state that is robust to perturbations. *Eur. Phy. J. E.* **124**, 38001 (2014).

Reynolds, A.M. On the origin of the tensile strength of insect swarms. *Phys. Biol.* **16**, 46002 (2019a).

Reynolds, A.M. On the emergence of gravitational-like forces in insect swarms. *J. Roy. Soc. Int.* **16**, 20190404 (2019b).

Reynolds, A.M. Intrinsic stochasticity and the emergence of collective behaviours in insect swarms. *Eur. Phys. J. E.* **44** 22 (2021).

Reynolds, A.M. et al. Stochastic modelling of bird flocks: accounting for the cohesiveness of collective motion. *J. R. Soc. Int.* **19**, 20210745 (2022).

Sinhuber, M. & Ouellette, N. T. Phase coexistence in insect swarms. *Phys. Rev. Lett.* **119**, 178003 (2017).



**Figure 1.** Local equilibrium, , results in a minimum concentration, *Nc*, (here just less than 2 indicating that the swarm must contain at least 2 individuals because swarm cardinality is integer) of reactants, when k>1 (solid line). Results are shown for *k=3*,  The maximum possible concentrations of mobile *M* individuals are indicated (dashed line). If *N<Nc* then *M=N* and *I=0*, i.e., every individual is mobile and diffusing. If *N>Nc* then the reaction dynamics have two stable equilibria, respectively: one on the line *M=N* and one on the lower branch of the hyperbola, separated by an unstable equilibrium on the upper branch of the hyperbola. Perturbations drive unstable equilibrium states to *M=N* when they increase *M* and to the lower branch of the hyperbola when they decrease *M*.



**Figure 2**. **Predicted characteristic features of swarm formation.** **a)** Time-reversed diffusion leading to the formation of a cohesive swarm. **b)** Total number of individuals in the swarm as a function of time. **c)** The physical size of the swarm as quantified by the root-mean-square swarm size. **d)** Mean radial accelerations, Eqn. 8, as a function of time. Predictions are shown for *k=3* with all other model parameters set to unity. The initial time *t*o=2 accounts for an initial accumulation of individuals above the swarm marker – a visually prominent feature above which swarms form. And it circumvents the predicted occurrence of arbitrarily large mean velocities at short times; . These are an artefact of the having derived the number densities, *N(x,t),* in the long-time diffusion limit.

**a)**

******

**b)**



**Figure 3. Mean radial velocities during swarm formation. a) Spatial averaging.** The mean is takenover all positionsin a single swarm (black line). The model prediction (red line) is also shown. **b) Time averaging.** Averaging over times 1 to 10 s after the initiation of swarm formation. Results are shown for several different swarms, each in a different colour, as a function of the radial distance from the swarm centre, *r*. As predicted (see text) the magnitude of this quantity increases with increasing distance from the swarm centre. Data are taken from [Patel and Ouellette 2022]. Note that the data are not sufficient to test model predictions without either spatial or temporal averaging.



**Figure 4. Predicted spontaneous attraction to the swarm and spontaneous emergence of a potential well with a harmonic core.** The deepening of the potential well saturates at long times. The root-mean-square sizes of the swarms range between 0.56 and 0.52 a.u. Predictions were obtained from the third term on the right-hand side of Eqn. 8 with *k=3* and all other parameters set to unity.