

Rothamsted Repository Download

A - Papers appearing in refereed journals

Reynolds, A. M. 2019. On the emergence of gravitational-like forces in insect swarms. *Journal of the Royal Society Interface*. 16 (160), p. 20190404.

The publisher's version can be accessed at:

- <https://dx.doi.org/10.1098/rsif.2019.0404>

The output can be accessed at: <https://repository.rothamsted.ac.uk/item/96xq0/on-the-emergence-of-gravitational-like-forces-in-insect-swarms>.

© 13 November 2019, Please contact library@rothamsted.ac.uk for copyright queries.

On the emergence of gravitational-like forces in insect swarms

Andy M. Reynolds

5 *Rothamsted Research, Harpenden, Hertfordshire, AL5 2JQ, UK*

Abstract Okubo [1986] was the first to propose that insect swarms are analogous to self-gravitating systems. In the intervening years striking similarities between insect swarms and self-gravitating systems have been uncovered. Nonetheless, experimental observations of
10 laboratory swarms provide no conclusive evidence of long-range forces acting between swarming insects. The insects appear somewhat paradoxically to be tightly bound to the swarm while at the same time weakly coupled inside it. Here I show how resultant centrally-attractive gravitational-like forces can emerge from the observed tendency of insects to continually switch between two distinct flight modes: one that consists of low-frequency
15 maneuvers and one that consists of higher-frequency nearly harmonic oscillations conducted in synchrony with another insect. The emergent dynamics are consistent with ‘adaptive’ gravity models of swarming and with variants of the stochastic models of Okubo and Reynolds for the trajectories of swarming insects: models that are in close accord with a plethora of observations of unperturbed and perturbed laboratory swarms. The results bring about a
20 radical change of perspective as swarm properties can now be attributed to known biological behaviours rather than to elusive physical influences.

Tel: +44 (0)1582 763133

Fax: +44 (0)1582 760981

25 Email: andy.reynolds@rothamsted.ac.uk

PACS 87.23.Ge - Dynamics of social systems

PACS 05.10.Gg – Stochastic analysis methods (Fokker-Planck, Langevin etc.)

30

Introduction

Insect swarms do not display the choreographed movements seen in fish schools and bird flocks, but their members do remain in just a small portion of the space available to them [Kelley and Ouellette 2013]. Nonetheless, individuals are behaving collectively rather than interacting independently with visual features on the ground over which swarms tend to form [Puckett and Ouellette 2014]. By drawing an analogy with Newtonian gravitational attraction, Okubo [1986] speculated that the interactions between swarming insects produces, on the average, a centrally-attractive force that acts on every individual. There is now strong experimental support for such a resultant restoring force in laboratory swarms of *Chironomus riparius* midges [Kelley and Ouellette 2013]. The emergence of this resultant restoring force has been attributed to the insects interacting via long-range gravitational-like forces [Gorbonos et al. 2016]. This is a tempting possibility because insects are thought to interact acoustically, responding to wing-beat noise whose far-field intensity is expected to decay according to an inverse square law [Sueur et al. 2005]. Gravitational-like interactions would therefore arise if one insect reacts to another by accelerating towards the source of the sound with a strength that is proportional to the received sound intensity. Experimental observations of laboratory swarms do, however, provide no conclusive evidence for such long-range forces acting between swarming insects [Puckett et al. 2014]. Instead, insects on average display an approximately equivalent acceleration towards almost any feature of the swarm (nearest neighbour, Voronoi centroid, i.e., towards the emptiest region of space in the insect's vicinity, swarm centre). This suggests that individuals are on average weakly coupled, but also tightly bound to the swarm itself [Puckett et al. 2014].

Here I show how the resultant forces can emerge from the observed tendency of insects to continually switch between two distinct flight modes: one that is composed of relatively straight to and fro movements and one that consists of higher-frequency oscillations [Okubo 1986, Puckett et al. 2015]. Model formulation is presented in next section. The new model is shown to be closely related to two successful but seemingly distinct models of insect swarms: the stochastic models of Okubo [1986] and Reynolds et al. [2017] and the 'adaptive' gravity models of Gorbonos et al. [2016]. It is also shown how the new model can account for observations that are beyond the scope of the previous models. This is followed by a Discussion.

65

Emergence of gravitational-like interactions at the macroscopic level

Model formulation and properties

Multi-camera stereo-imaging and particle-tracking techniques have provided detailed recordings of the three-dimensional trajectories of *Chironomus riparius* midges within laboratory swarms [Kelley and Ouellette 2012, Puckett et al. 2015]. By performing a time-frequency analysis of these trajectories, Puckett et al. [2015] showed that the midge flight behaviors can be segmented into two distinct modes: one that is independent and composed of low-frequency maneuvers and one that consists of higher-frequency nearly harmonic oscillations conducted in synchrony with another midge (velocities tend to be antiparallel). These observations have similitude with the observations of Okubo [1986] who remarked that the trajectories of individual midges may be classified into two distinct patterns, one being a “loose” pattern and the other a “tight” pattern. In the loose pattern, an insect exhibits relatively straight to- and fro- moments that might resemble a pendulum motion. In the tight pattern, an insect exhibits a relatively short, zigzag motion that might resemble a random flight. In practise most individuals display a pattern which combines these two extremes.

The observations of Puckett et al. [2015] and Okubo [1986] suggest that at long-times (times longer than the velocity autocorrelation timescale), individual flight patterns can effectively be partitioned into episodes of “hovering” and “flying” (diffusing) and that the long-time dynamics can be approximated by a pair of reaction-diffusion equations

$$\begin{aligned}\frac{\partial H}{\partial t} &= -\alpha H + \beta HF \\ \frac{\partial F}{\partial t} &= \alpha H - \beta HF + D \frac{\partial^2 F}{\partial x^2}\end{aligned}\tag{1}$$

Here $H(x,t)$ and $F(x,t)$ are the densities of hoverers and fliers located at position x at time t , α is the rate at which individuals switch from being hoverers to being fliers (with diffusivity D) and β sets the rate at which fliers switch to becoming hoverers after interacting with hoverers [An alternative, seemingly very credible model is examined then discounted in the Supplementary Material S1]. These pairwise interactions (biological behavioural traits) could be mediated either acoustically or visually. When the reaction dynamics are very much faster than the diffusive transport, local equilibrium is established, i.e., $\alpha H - \beta HF = 0$. The stable equilibria are $F=\alpha/\beta$, $H=C-F$ if the density of individuals (fliers and hoverers) $C>\alpha/\beta$ and $H=0$, $F=C$ if $C<\alpha/\beta$.

100 Adding together the two parts of Eqn. 1 under the assumption of local equilibrium gives

$$\begin{aligned}\frac{\partial C}{\partial t} &= D \frac{\partial^2 F}{\partial x^2} \\ &= D \frac{\partial^2}{\partial x^2} \left(\frac{\alpha}{\beta} \right)\end{aligned}\quad (2)$$

when $C > \alpha/\beta$. This shows that the spatial distribution of all individuals within the swarm is 'frozen' in time, since the right-hand side of the diffusion equation, Eqn. 2, vanishes. That is, the reaction dynamics exactly cancel out the effects of diffusion, thereby creating a stable swarm. Individual fliers are, nonetheless, diffusing within the confines of the swarm. This is made manifest when Eqn. 2 is rewritten as

$$\begin{aligned}\frac{\partial C}{\partial t} &= D' \frac{\partial}{\partial x} \left[\frac{\partial}{\partial x} \left(\frac{C}{P} \right) \right] \\ &\equiv D' \frac{\partial}{\partial x} \left[\frac{1}{\sqrt{P}} \frac{\partial}{\partial x} \left(\frac{C}{\sqrt{P}} \right) - \frac{C}{2P} \frac{\partial \ln P}{\partial x} \right] \\ &\equiv D' \frac{\partial}{\partial x} \left[\frac{1}{P} \frac{\partial C}{\partial x} - \frac{C}{P} \frac{\partial \ln P}{\partial x} \right]\end{aligned}\quad (3)$$

where $P \equiv C$ (is a place holder) and $D' = \frac{\alpha}{\beta} D$.

110 The first, second and third forms of Eqn. 3 correspond to random walk models

$$dx = \sqrt{\frac{2D'}{P}} d\xi \quad (4)$$

$$dx = \frac{1}{2} \frac{D'}{P} \frac{\partial \ln P}{\partial x} dt + \sqrt{\frac{2D'}{P}} d\xi \quad (5)$$

$$dx = \frac{D'}{P} \frac{\partial \ln P}{\partial x} dt + \sqrt{\frac{2D'}{P}} d\xi \quad (6)$$

115 where x is the position of an individual at time t , $d\xi$ are increments of a white noise process with autocorrelation $\langle d\xi(t) d\xi(t') \rangle = \delta(t-t') dt$ for noises at time t and t' and where the amplitudes of the noise terms, $\sqrt{2D'/P}$, are evaluated: at the start of each step (the 'Ito'

120 interpretation) in Eqn. 4; at the mid-point of each step (the ‘Stratonovich’ interpretation) in Eqn. 5; and at the end of each step (the ‘Hänggi-Klimontovich’ interpretation) in Eqn. 6. This non-uniqueness of the corresponding random walk model arises because the interpretation of the intensity of the coloured driving noise is ambiguous in the long-time limit. The colouring of the driving noise is indicative of there being a feedback from the macroscopic level of description of the swarms in terms of the probability density, P , to the microscopic kinematics. An individual’s movement is therefore dependent on global properties of the swarm.

125

Directly analogous results can be obtained albeit non-analytically using a stochastic model that captures both short- and long-time dynamics [Supplementary Material S2].

130 Equation (6) is the long-time limit of a close relative of the stochastic models of Okubo [1986] and Reynolds et al. [2017] for the joint evolution of an insect’s position, x , and velocity, u ,

$$\begin{aligned}
 du &= -\frac{u\sqrt{P'}}{T}dt + \frac{\sigma_u^2}{\sqrt{P'}}\frac{\partial \ln P}{\partial x}dt + \sqrt{\frac{2\sigma_u^2}{T}}d\xi \\
 dx &= udt
 \end{aligned}
 \tag{7}$$

where $P' = \frac{\beta}{\alpha}P$ and where σ_u^2 is a velocity scale rather than a mean-square velocity *per se*.

Equation 6 is obtained from Eqn. 7 as the velocity autocorrelation timescale $T \rightarrow 0$ with $T\sigma_u^2 \rightarrow D$, i.e., $t/T \rightarrow \infty$.

135

In the models of Okubo [1986] and Reynolds et al. [2017] interactions between the individuals are not explicitly modeled [but they can be as shown in Reynolds [2018a] and in the Supplementary Material S3]; rather, their net effect is subsumed into a restoring force term. In

the model of Reynolds et al. [2017] this term is given by $\sigma_u^2 \frac{\partial \ln P}{\partial x}$, (i.e., by $-\frac{\sigma_u^2}{\sigma_x^2}x$ for swarms

140 with Gaussian density profiles, as in Okubo’s [1986] classic model where individuals in the swarm behave on the average as if they are trapped in an elastic potential well). In the new model, Eqn. 7, this restoring force is renormalized according to the local density and is given

by $\frac{\sigma_u^2}{\sqrt{P'}}\frac{\partial \ln P}{\partial x}$. As a result, the central attraction is relatively low in the core of the swarm

where the density is relatively high and relatively high in the outskirts of the swarm where the

145 density is relatively low. This closely mirrors ‘adaptive’ gravity models of insect swarms
 wherein effective forces (presumed to be acoustic interactions) are renormalized according to
 the local noise amplitude [Gorbonos et al. 2016]. In Gorbonos et al. [2016] this modelling
 assumption was motivated by the fact “that for many animals, the perception of sound is not
 fixed, but rather adapts to the total sound intensity so that acoustic sensitivity drops when
 150 there is strong background noise. This is a common feature of biological sensory organs,
 preventing damage and their saturation.” It is crucial to bring model predictions in line with
 observations [Gorbonos et al. 2016]. By preventing collapse (Jeans instability) it also endows
 swarms with a natural mechanism for self-stabilization [Gorbonos and Gov 2018]. Here
 ‘adaptation’ arises freely and is not imposed on the model. Similarly, the ‘frictional term’,
 155 $-u/T$, which in the models of Okubo [1986] and Reynolds et al. [2017] causes velocity
 fluctuations to relax back to their (zero) mean value is here replaced by $-u\sqrt{P'}/T$. This
 modification can be attributed to the interactions between the hoverers and fliers. Note that a
 similar modification, $-uP'/T$, is induced when short-range repulsions are incorporated into
 numerical simulations made with the model of Reynolds et al. [2017] [Supplementary Material
 160 S4]. The noise term represents fluctuations in the resultant internal force that arise partly
 because of the limited number of individuals in the swarm and partly because of the
 nonuniformity in their spatial distribution [Okubo 1986].

For locations in and around the core of swarm, the new model, Eqn. (7), reduces (up to
 165 multiplicative constants, $\sqrt{P'(0)}$) to the model of Reynolds et al. [2017]. This in turn effectively
 reduces to Okubo’s [1986] classic model

$$du = -\frac{u\sqrt{P'(0)}}{T}dt - \frac{\sigma_u^2 x}{\sigma_x^2 \sqrt{P'(0)}}dt + \sqrt{\frac{2\sigma_u^2}{T}}d\xi$$

$$dx = udt$$

(8)

when positions are Gaussian distributed. These models agree well with numerous
 170 experimental observations of laboratory swarms [Reynolds et al. 2017, Reynolds 2018a,
 Reynolds 2019, van der Vaart 2019]. The new model does, however, account for observations
 that are beyond the reach of previous stochastic models; namely the dependency of effective
 spring constants on swarm size [Gorbonos et al. 2016]; the emergence of non-Gaussian
 velocity statistics [Kelley and Ouellette 2013]; and the near constancy of swarm densities
 175 [Kelley and Ouellette 2013, Puckett and Ouellette 2014].

Accounting for observations that are beyond the scope of previous models

Effective spring constants

180 Large laboratory swarms and wild swarms tend to be cylindrical in shape with the central axes orientated vertically (along the z-axis) [Kelley and Ouellette, 2013, Attanasi et al. 2014]. In the cores of swarms with Gaussian density profiles, the restorative force term in Eqn. 7 increases linearly with distance from the swarm centre. In these locations, the restorative force can therefore be characterized by an effective spring constant, $K = \frac{\sigma_u^2}{\sigma_x^2 \sqrt{P'(0)}}$. For highly

185 cylindrical swarms with $\sigma_x = \sigma_y = \sigma_z$, Eqn. 7 predicts that $K_x = K_y < K_z$, $K_x \propto \sigma_x^{-1}$ and $K_z \propto \sigma_z^{-3/2}$. Lower effective spring constants in the z-direction are observed in laboratory swarms [Kelley and Ouellette 2013] as are the two different scalings with swarm size [Gorbonos et al. 2016]. These predictions also closely match predictions of Gorbonos et al.'s [2016] adaptive gravity model. Nonetheless, if individuals were interacting with one another

190 via long-range gravitational-like forces then all swarms would be spherical in shape, or nearly so. If, on the other hand, swarms are bound together by the interactions between hoverers and fliers, then any shape swarm is possible (stable) in principle [Eqn. 2]. Swarm shapes may, however, be constrained by the nucleation process [Supplementary Material S5]. In contrast with the new model, Eqn. 7, Okubo's [1986] stochastic model predicts contrary to experiment

195 a single scaling with swarm size, namely $K_x = K_y \propto \sigma_x^{-2}$ and $K_z \propto \sigma_z^{-2}$.

Accounting for the emergence of non-Gaussian velocity statistics

For locations in the outskirts of the swarm the new model, Eqn. 7, departs from the models of Okubo [1986] and Reynolds et al. [2017]. It predicts that velocity statistics are heterogeneous rather than homogeneous (position-independent) (Fig. 1a-c) and it predicts that mean

200 accelerations grow non-linearly rather than linearly with distance from the swarm centre (Fig. 1c). The former prediction is supported by observations (Fig. 2a). In accordance with model expectations, the velocity-variance profile is concave. This is consistent with the velocities of solitary insects being generally higher than the velocities of insects within swarms [Puckett and Ouellette, 2014]. It is also consistent with velocity (and speed) distributions having nearly

205 exponential tails that develop with increasing swarm size [Kelley and Ouellette 2013] (Fig. 2b, Supplementary Material S6). The latter prediction is consistent with simulation data produced

by Gorbonos et al.'s [2016] adaptive gravity model and more tentatively with experimental observations [Okubo 1986]. Note that in the stochastic models of Reynolds et al. [2017], velocity statistics are a model input and not a model prediction.

210

Near constant densities

The density of insects within laboratory swarms of midges is approximately constant [Kelley and Ouellette 2013, Puckett and Ouellette 2014]. This is different from what has been observed for bird flocks where the number density can fluctuate hugely from flock to flock [Ballerini et al. 2008]. In contrast with previous models [Okubo 1986, Gorbonos et al. 2016, Reynolds et al. 2017] this constancy is predicted by the new model. The total number of fliers within a swarm of size R_s is predicted to be $N_F = (\alpha/\beta)R_s$ [See text relating to Eqn. 1].

215

Therefore, the total number of individuals within a swarm $N \propto R_s$ since $N_F \propto N_H$ [Puckett et al. 2015]. This constancy although accidental may be significant because it implies that the continual flow of individuals into and out of a swarm [Kelley and Ouellette 2012, Ni and Ouellette 2016, Sinhuber et al. 2019] drives changes in swarm morphology. Somewhat counterintuitively such fluctuations are predicted to endow swarms with stabilizing macroscopic mechanical properties similar to solids, including a finite Young's modulus and yield strength [Reynolds 2019], properties which have been observed in the laboratory [Ni and Ouellette 2016]. The fluctuations also have the potential to change fundamentally the characteristics of individual flight patterns. Reynolds and Ouellette [2016] showed that center of mass fluctuations allow for the emergence of Lévy flight patterns which have subsequently been linked to population maintenance in energetic environments [Michalec et al. 2018].

220

225

230 *Alternative models*

Equation 6 can be recovered from other variants of the models of Okubo [1986] and Reynolds et al. [2017]. It can, for example, be recovered from

$$du = -\frac{uP}{T'}dt + \sigma_u^2 \frac{\partial \ln P}{\partial x} dt + \sqrt{\frac{2\sigma_u^2 P}{T'}} d\xi \quad (9)$$

$$dx = udt$$

235

where $T' = \frac{\alpha}{\beta}T$. Despite its appeal, this and other such variants are incompatible with the observed near homogeneity of velocity statistics within the core of a swarm [Reynolds et al.

2017] and with the near constancy of the Lagrangian velocity structure function, $\langle \Delta u^2 \rangle$ [van der Vaart, Private Communication].

240 *Accounting for speed-dependent forces*

The foregoing analysis does not directly encompass one of the most intriguing observations: namely the observed speed-dependency of the resultant attractive force [Reynolds et al. 2017]. Nonetheless, such a dependency is not unexpected given that the resultant force is here attributed to the interaction between ‘hoverers’ and ‘fliers’ which is itself predicated on movement detection. It is therefore seemingly natural to suppose that the rate parameter, β ,

245 (which governs the interactions between ‘hoverers’ and ‘fliers’ and which has the dimensions of velocity) is, in fact, speed dependent. The simple parameterization $\beta = \frac{\sigma_u^2}{\sigma_u + |u|}$ results in

stable swarms which in accordance with observations [Kelley and Ouellette 2014, Reynolds et al. 2017]: have Gaussian density profiles (Fig. 3a); velocity distributions with Gaussian cores and exponential tails (Fig. 3b); nearly homogeneous velocity statistics (Fig. 3c); and speed-dependent resultant forces which increase monotonically with an individual’s speed (Fig. 3d). Comparable predictions are obtained with other simple, biologically plausible, parameterizations of β that decrease monotonically with increasing speed.

255 **Discussion**

Stochastic and mechanistic models of insect swarms that draw inspiration from self-gravitating systems are gaining traction because they agree well with experimental observations [Okubo 1986, Reynolds et al. 2017, Reynolds 2018a,b, Gorbonos et al. 2016, van der Vaart et al. 2019]. The stochastic model of Reynolds et al. [2017] is, for example, in close quantitative agreement with data from high-precision, carefully-controlled laboratory experiments [Kelley and Ouellette 2013, Ni and Ouellette 2016, Sinhuber and Ouellette 2017, Sinhuber et al. 2019, Vaart et al. 2019]. It predicts correctly that swarms consist of a core “condensed” phase surrounded by a dilute “vapor” phase [Reynolds 2018a] and it predicts correctly that swarms possess emergent continuum mechanical properties, displaying a collective viscoelastic response to applied oscillatory visual stimuli [van der Vaart et al. et al. 2019]. Moreover, mathematical analysis of the model explains why swarms of flying insects have macroscopic mechanical properties similar to solids, including a finite Young’s modulus and yield strength [Reynolds 2019]. Mathematical analysis also revealed why in contrast with laboratory insect

swarms, wild insect swarms display significant coordinated behaviour [Reynolds 2018b]. This
270 showed how 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. At same the time, striking similarities
between insect swarms and self-gravitating systems are being uncovered [Reynolds 2018b,
Gorbonos et al. 2016, Gorbonos and Gov 2018, Supplementary Material S7-S11].
275 Nonetheless, this success need not be attributed to insects interacting with one another via
gravitational-like forces which would be an over interpretation of experimental observations
[Puckett et al. 2014]. Here I showed how resultant gravitational-like forces can emerge from
the observed tendency of insects to continually switch between non-diffusive and diffusive
flight modes. In other words, the sporadic formulation of bound pairs was shown to be
280 sufficient to bind the swarm together. The emergent resultant gravitational-like forces were
found to be consistent with Gorbonos et al.'s [2016] adaptive gravity model rather than with
Newtonian gravity. That is, the resultant central attraction was predicted to be relatively low in
the core of the swarm where the density is relatively high and relatively high in the outskirts of
the swarm where the density is relatively low. The emergent dynamics were also found to be
285 consistent with variants of the stochastic models of Okubo [1986] and Reynolds et al. [2017];
models that faithfully reproduce many observations made in the laboratory [Okubo 1986,
Reynolds et al. 2017, Reynolds 2018a, Reynolds 2019, van der Vaart et al. 2019]. These
models can therefore be reinterpreted in a radically new way that is biological rather than
physical and in a way that this is rooted firmly in observations [Okubo 1986, Puckett et al.
290 2015] rather than challenged by them [Puckett et al. 2014]. The new analysis suggests that
despite their success the models of Okubo [1986] and Reynolds et al. [2017] are effective
(phenomenology) models. It also suggests that the success of Gorbonos et al.'s [2016]
adaptive gravity model can be attributed to the fact that it will necessarily predict the
emergence of resultant gravitational-like forces and not because it is founded on a realistic
295 representation of the way in which insects interact with one another. The new analysis thereby
provides a bridge between the stochastic models of Okubo [1986] and Reynolds et al. [2017],
and the manifestly gravitational model of Gorbonos et al. [2016] by showing how both kinds of
model encapsulate similar dynamics and how both can be freed from their original
formulations. Moreover, the new stochastic models were shown to predict correctly features
300 of insect swarms (e.g., anisotropic scaling of effective spring constants, constancy of density)
that are beyond the scope of the models of Okubo [1986] and Reynolds et al. [2017] but within
reach of adaptive gravity models [Gorbonos et al. 2016]. Conversely, it reconciles the notion
of adaptive gravity with the existence of highly cylindrical wild swarms [Attanasi et al. 2014]
and with speed-dependent accelerations [Reynolds et al. 2017]. The new analysis also shows
305 how the behaviour of swarms studied in quiescent laboratories can be reconciled with the

behaviours of wild swarms which must contend with environmental disturbances. In contrast with laboratory swarms, wild swarms form transient synchronized subgroups that push the swarms into the new state that is robust to environmental perturbations [Reynolds 2018b]. This behaviour (i.e., this strengthening of the effective gravity) may now be seen as an extension of the behaviour (formulation of transient bound pairs) that underlies the emergence of effective gravity itself.

Acknowledgements

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. I thank Nick Ouellette, Michael Sinhuber and Kasper van der Vaart for encouraging discussions and for providing data crucial for model development. I am indebted to Stefan Gertiz for showing me how fission-fusion processes can arrest diffusion.

Competing Interests

I have no competing interests.

Data accessibility

Computer codes can be obtained from the author.

References

- Attanasi, A. et al. Collective behaviour without collective order in wild swarms of midges. *PLoS Comp. Biol.* **10**, e1003697 (2014).
- 330
- Ballerini, M., Cabibbo, N., Candelier, R., Cavagna, A., Cisbani, E., Giardina, I., Orlandi, A., Parisi, G., Procaccini, A., Viale, M. & Zdravkovic, V. Empirical investigation of starling flocks: a benchmark study in collective animal behaviour. *Anim. Behav.* **76**, 201-215 (2008).
- 335
- Borgas, M. Flesch, T.K., Sawford, B.L. Turbulent dispersion with broken reflectional symmetry. *Bound-Layer Meteor.* **332**, 141-156 (1997).
- Eddington, A.S. The internal constitution of the stars. *The Observatory* **43**, 341-358 (1920).
- 340
- Gorbonos, D., Ianconescu, R., Puckett, J. G., Ni, R., Ouellette, N. T. & Gov, N. S. Long-range acoustic interactions in insect swarms: an adaptive gravity model. *New J. Phys.* **18**, 073042 (2016).
- Gorbonos, D. & Gov, N.S. Stable Swarming Using Adaptive Long-range Interactions. *Phys. Rev. E* **95**, 042405 (2017).
- 345
- Hawking, S. W. Particle creation by black holes. *Comm. Math. Phys.* **43**, 199–220 (1975).
- Kelley, D.H. & Ouellette, N.T. Emergent dynamics of laboratory insect swarms. *Sci. Rep.* **3**, 1073, 1-7 (2013).
- 350
- Michalec, F-G., Fouxon, I., Souissi, S. & Holzner, M. Zooplankton can actively adjust their motility to turbulent flow. *Proc. Natl. Acad. Sci. USA.* **114**, E 11199-11207 (2018).
- 355
- Neems, R.M., Lazarus, J. & Mclachlan, A.J. Swarming behaviour in male chironomid midges: a cost-benefit analysis. *Behav. Ecol.* **3**, 285-290 (1992).

- Ni, R. & Ouellette, N.T. Velocity correlations in laboratory insect swarms. *Eur. Phys. J. Spec. Top.* **224**, 3271-3277 (2015).
- 360 Ni, R. & Ouellette, N.T. On the tensile strength of insect swarms. *Phys. Biol.* **13**, 045002 (2016).
- Ni, R., Puckett, J.G., Dufresne, E.R. & Ouellette, N.T. Intrinsic fluctuations and driven response of insect swarms. *Phys. Rev. Lett.*, **115**, 118104 (2015).
- 365 Okubo, A. Dynamical aspects of animal grouping: swarms, schools, flocks and herds. *Adv. Biophys.* **22**, 1-94 (1986).
- 370 Ouellette, N.T. Toward a “thermodynamics” of collective behaviour. *SIAM News* (2017).
- Puckett, J.G. & Ouellette, N.T. Determining asymptotically large population sizes in insect swarms. *J. Roy. Soc. Inter.* **11**, 20140710 (2014).
- 375 Puckett, J.G., Kelley, D.H. & Ouellette, N.T. Searching for effective forces in laboratory insect swarms. *Sci. Rep.* **4**, 4766 (2014).
- Puckett, J.G., Ni, R. & Ouellette, N.T. Time-frequency analysis reveals pairwise interactions in insect swarms. *Phys. Rev. Lett.* **114**, 258103 (2015).
- 380 Reynolds, A.M. On Lagrangian stochastic modelling of material transport in oceanic gyres. *Physica D* **172**, 124-138 (2002).
- Reynolds A.M. & Geritz S.A.H. Tsallis distributions, Lévy walks and correlated-type anomalous diffusion result from state-dependent diffusion. *Physica A* **424**, 317-321 (2015).
- 385

Reynolds A.M. & Ouellette N.T. Swarm dynamics may give rise to Lévy flights. *Sci. Rep.* **6**, 30515 (2016).

390 Reynolds, A.M., Sinhuber M. & Ouellette N.T. Are midge swarms bound together by an effective velocity-dependent gravity? *Euro. Phys. J. E* **40**,46 (2017).

Reynolds, A.M. Langevin dynamics encapsulate the microscopic and emergent macroscopic properties of midge swarms. *J. Roy. Soc. Inter.* **15**, 20170806 (2018a).

395 Reynolds, A.M. Fluctuating environments drive insect swarms into a new state that is robust to perturbations. *Europhys. Lett.* **124**, 38001 (2018b).

Reynolds, A.M. On the origin of the tensile strength of insect swarms. *Phys. Biol.* **16** 046002 (2019).

400

Sawford, B.L. Rotation of trajectories in Lagrangian stochastic models of turbulent dispersion. *Bound-Layer Meteor.* **93**, 411–424 (1999).

Sciama, D.W. On the Origin of Inertia. *Roy. Astro. Soc.* **113** 34–42 (1953).

405

Shishika, D., Manoukis, N.C., Butail, S. & Paley, D.A. Male motion coordination in anopheline mating swarms. *Sci. Rep.* **4**, 6318 (2014).

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

410

Sinhuber, M., van der Vaart, K. & Ouellette, N.T. Response of insect swarms to dynamic illumination perturbations. *J. R. Soc. Interface* **16**, 20180739 (2019).

415 Sinhuber, M., van der Vaart, K., Ni, R., Puckett, J.G., Kelley, D.H. & Ouellette, N.T. Three-dimensional time-resolved trajectories from laboratory insect swarms. *Sci. Data* **6**, 190036 (2019).

Sinhuber, M., van der Vaart K., Feng, Y., Reynolds, A.M. & Ouellette, N.T. An equation of state for insect swarms. (Submitted).

420

Sueur, J., Tuck, E.J. & Robert, D. J. Sound radiation around a flying fly. *Acoust. Soc. Am.* **118** 530 (2005).

425 Vaart, van der K, Sinhuber, M. Reynolds, A.M. & Ouellette, N.T. Mechanical spectroscopy of insect swarms. *Sci. Adv.* **5**, eaaw9305 (2019).

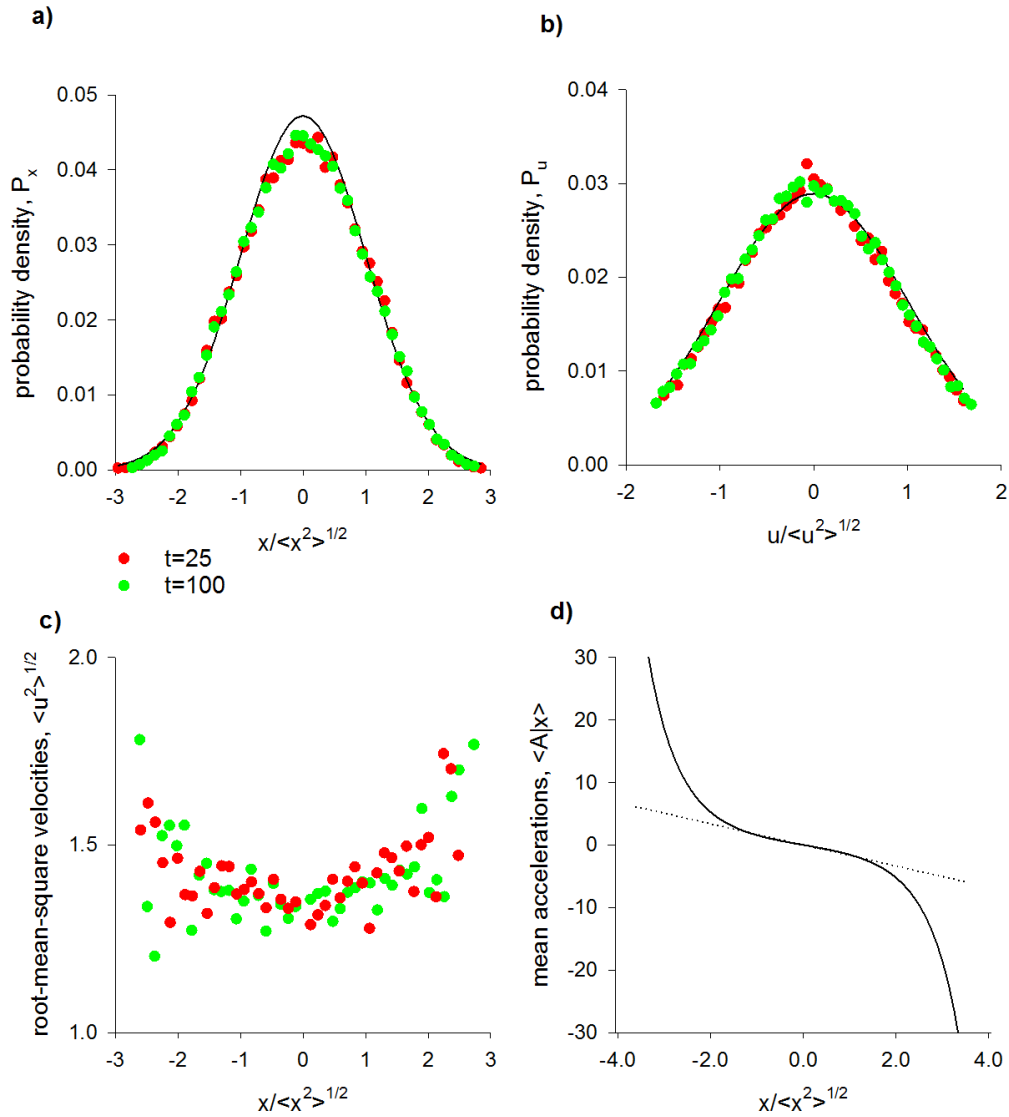


Figure 1 a, b) Swarms are predicted to have stationary position and velocity statistics. c) Root-mean-square velocities are predicted to be approximately homogeneous within the swarm's core. d) Individuals are predicted to be effectively bound to the centre of the swarm by a force (mean acceleration $\langle A|x \rangle$) which in the core of the swarm grows linearly with distance from the swarm centre. Predictions are shown at times $t=25$ (●) and $t=100$ (●) together with the best-fit Gaussian distributions (solid-lines). Predictions are shown

430

435

for Eqn.7 with $P(x) = \frac{1}{\sqrt{2\pi}\sigma_x} \exp\left(-\frac{x^2}{2\sigma_x^2}\right)$, $\sigma_x = 1$, $\sigma_u = 1$, $\alpha = 1$ and $\beta = 1$.

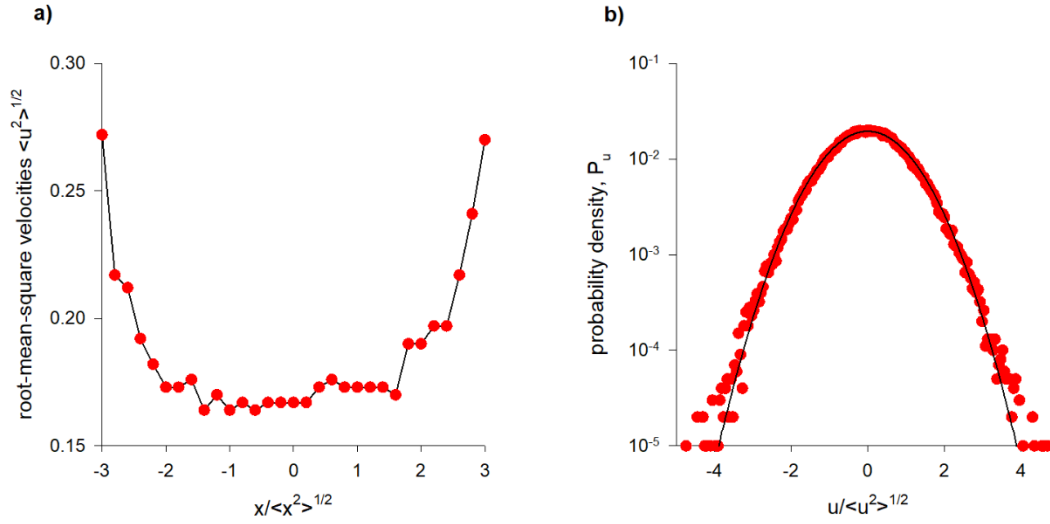


Figure 2) Hallmarks of model predictions in laboratory swarms. a) Root-mean-square velocities profiles are consistent with theoretical expectations (Fig. 1c). b) In accordance with observations [Kelley and Ouellette 2013] velocity distributions of large swarms are predicted to have Gaussian cores and exponential tails. Data (●) are taken from Sinhuber et al. [2019]. All 17 dusk-time swarms. The line is added to guide the eye.

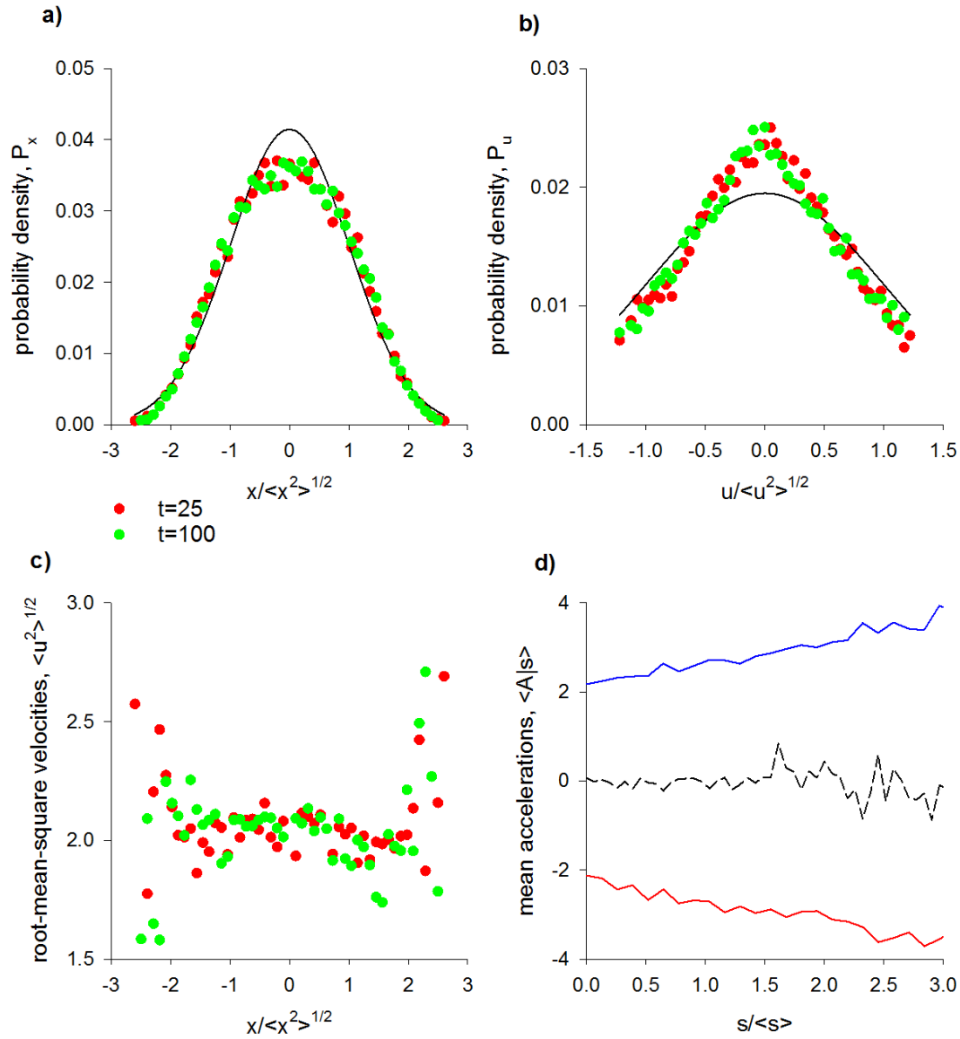
440

Predictions (●) were obtained using the new stochastic model, Eqn. 7, with

$$P(x) = \frac{1}{\sqrt{2\pi}\sigma_x} \exp\left(-\frac{x^2}{2\sigma_x^2}\right), \sigma_x = 5, \sigma_u = 1, \alpha = 1 \text{ and } \beta = 1 \text{ a.u.}$$

Shown for comparison is a Gaussian distribution with equivalent mean and variance (solid-line).

445



450 **Figure 3 a, b) Swarms are predicted to have stationary position and velocity statistics when interactions are speed dependent. c) Root-mean-square velocities are predicted to be approximately homogeneous within the swarm's core. d) Individuals are predicted to be effectively bound to the centre of the swarm by a force (mean acceleration $\langle A|s \rangle$) that increases with an individual's flight speed in accordance with observations [Reynolds et al. 2017] (red line shows data for right side only, blue line show data for left side only; and dashed line shows data for both sides which is close to zero, as required by symmetry). Predictions are shown at times $t=25$ (●) and $t=100$ (●) together with best fit Gaussian distributions (solid-lines). Predictions are shown for Eqn.7 with**

455

$$P(x) = \frac{1}{\sqrt{2\pi}\sigma_x} \exp\left(-\frac{x^2}{2\sigma_x^2}\right), \sigma_x = 1, \sigma_u = 1, \alpha = 1 \text{ and } \beta = \frac{\sigma_u^2}{\sigma_u + |u|} \text{ a.u.}$$