Supplementary Material

Section 1

Reynolds number effects

In this section I show that insect swarms are predicted to undergo a transition from a turbulent-like to a laminar-like phase as the Reynolds number decreases. Reynolds number effects have not featured in the literature on collective motion despite the occasional congruence of collective animal and fluid motions [1] – as is strikingly the case for swarms of midges [2].

Okubo's [3] one-dimensional model for the simulation of trajectories of swarming insects, and its extension to 3-dimensions [4], are in close agreement with numerous observations of swarming insects and have successfully predicted new properties of insect swarms [4-7]. In these models the positions and velocities of a swarming insect are modelled jointly as a Markovian process, i.e., as a first-order autoregressive process. Here attention is focused on a higher-order variant of these models in which the positions, velocities and accelerations of a swarming insect are collectively Markovian, i.e., are modelled as second-order autoregressive processes. Physically, such modelling corresponds to the inclusion of a time scale, *T*, representative of the largest scales of motion, at first order, and the addition of a time scale, t_s, representative of the smallest scale of motion, at second order. An effective Reynolds number, defined by the ratio of these time scales, $R = (T/t_s)^2$, therefore appears as a parameter at second order. In these models, fluctuations in the strength of the central attraction that binds individuals to the centre of the swarm increases as *R* increases since the acceleration and velocity variances are related by $\sigma_A^2 = \sigma_u^2/(Tt_s)$. Such fluctuations in acceleration arise partly because of the limited number of individuals in the grouping and partly because of the nonuniformity of their spatial distribution [3]. The low Reynolds number limit may therefore pertain to large swarms where such fluctuations are expected to be suppressed (because of self-averaging). The limit *R=0*, in which such fluctuations are suppressed entirely is, however, an idealization because swarming insects can and do expend their internal energy reserves to accelerate thereby providing a further contribution to the fluctuations that are not captured by the modelling.

I now show that second-order models predict that swarms undergo a phase transition at low Reynolds number. In the extreme limit (*R=0*) and in contrast with the high Reynolds number limit [4-7]: trajectories are deterministic rather than stochastic; kinetic plus potential energies are conserved rather than fluctuating quantities; individuals preferentially reside in either the

interior or exterior of the swarm rather than tending to roam freely throughout the swarm, i.e., swarms possess nontrivial internal structure rather than being random configurations of individuals. Moreover, external perturbations are predicted to result in the synchronization of individual oscillations and consequently result in coherent motion and scale-free correlations.

When *R=0*, a second-order model for the simulation of trajectories of insects in swarms where the positions and velocities are both Gaussian distributed (with means zero and variances σ_r^2 and σ_u^2at the population level) is given by

$$\frac{d^2x_i}{dt^2} = A_i$$

where the subscripts refer to Cartesian components,

$$A = -3r\frac{\sigma_u^2}{\sigma_r^2}\left[sin\hat{\phi}\, sin\,\phi\, cos\left(\hat{\theta} - \theta\right) + cos\hat{\phi}\, cos\,\phi\right] \quad \text{(S1)}$$

$$A_1 = A_s cos\hat{\theta} sin\hat{\phi}$$

$$A_2 = A_s sin\hat{\theta} sin\hat{\phi}$$

$$A_3 = A_s cos\hat{\phi}$$

and

$x_1 = r\cos\theta\sin\varphi$, $x_2 = r\sin\theta\sin\varphi$, $x_3 = r\cos\varphi$, $u_1 = s\cos\hat{\theta}\sin\hat{\phi}$, $u_2 = s\sin\hat{\theta}\sin\hat{\varphi}$, $u_3 = s\cos\hat{\varphi}$, *r* is the radial distance from the swarm centre and *s* is the insect flight speed [4,8]. The formulation 3-dimensional second-order models for small but none-zero Reynolds numbers (R>0) remains an outstanding problem [9].

The model, Eqn. S1, predicts that insects oscillate, periodically, back-and-forth along a straight-line (Fig. S1a) quite unlike the freely roaming trajectories predicted for $R \to \infty$ by the model of Reynolds et al. [3] (FigS1b) but reminiscent of the vertical 'pendular' flights that can occur in swarms of mayflies [10] and reminiscent of mosquitoes *(Aedes provocans)* that fly continuously in alternating directions along the longitudinal axis of the swarm [11]. The result suggests that this Reynolds number effect may account, at least in part, for individual midges preferentially residing in either the interior or exterior of a swarm but nonetheless displaying similar flight behaviours [12]. That is, Reynolds number effects may enhance the preferential concentration effect above that predicted by first-order model for swarms at infinite Reynolds

number. All insects irrespective of their position and initial velocities are predicted to have the same frequency of oscillation. Consequently, insects will oscillate in phase, indefinitely, if the swarm is perturbed, by for example a gust of wind, so that all individuals acquire a common velocity. This will result in coherent motion and scale-free correlations. Moreover, along each trajectory, kinetic plus potential energy, $\frac{1}{2}\boldsymbol{u}.\boldsymbol{u}+\frac{1}{2}k\boldsymbol{x}.\boldsymbol{x}$ (where k is the effective spring constant), is a conserved quantity contrary to the case when $R \to \infty$ [13,14]. Reynolds number effects may also account for the oscillatory velocity autocorrelation functions reported by Butail et al. [15] which run counter to the theoretical expectation that swarms are critically damped when $R \to \infty$ [3]. A precursor of this possibility can be found in Reynolds [2] who predicted that swarms could transition from being overdamped to being underdamped as the Reynolds number decreases.

Note that other stochastic models [4] are compatible with Gaussian distributions of positions and velocities which in the limit *R=0* predict that individuals orbit around the centre of the swarm whilst precessing. Along each such trajectory, kinetic energy is conserved. Horizontal looping flights have been observed and may allow males to systematically scan the swarm periphery for approaching females [10].

Extracting reliable estimates for Reynolds numbers for insect swarms from current observations [16] is problematic because estimates for t_s are comparable with the data sampling time (100 Hz), i.e., the shortest scales of motion are not resolved in sufficient detail. Nonetheless, Reynolds number effects may account for the tendency for observable energy to be conserved (i.e., the tendency for minimal consumption of internal energy) and for the tendency of trajectories to become less convoluted as the population size of the swarm increases (Figs. S2-S3). These effects can cause loss of seemingly advantageous properties, such as critical damping [17] and stabilization against environmental perturbations [18], that arise accidentally as $R_e \to \infty$. This may provide a selection pressure for relatively small swarms (high Reynolds numbers) [a counter argument is presented in Section 3]. There could also be a trade-off between the advantageous properties which require consumption of internal energy in addition to that required for lift generation, and minimal consumption of internal energy reserves. Moreover, the tendency for trajectories to become less convoluted as the Reynolds number decreases (i.e., as the swarm increases) may make larger swarms accessible to larger, less agile individuals and conversely may make smaller swarms the preserve of smaller, agile individuals. Neems et al. [19] reported on such body-size segregation in swarms of male *chironomid* midges. Note also that when *R=0* jerks are

predicted to be anti-aligned with velocities, i.e., jerks are predicted to be aligned with the long axis of an individual. The disruptive impact of jerks on flight control is thereby minimized when *R=0*.

An open question for future research is the impact of the speed-dependency of the average restoring forces [4] on energy conservation; a factor that was set aside in the above analysis. This could be problematic because potential energies may not strictly exist for such forces. Nonetheless, the results of numerical simulations (not shown) using a 1-dimensional model reveal that when *R=0* such forces generally give rise nearly elliptical trajectories in phase space, suggesting that some quantity, closely akin to conventional observable energy, is, to good approximation, conserved. Indeed, fluctuations in the conventional observable energies, $\frac{\sigma_E}{\langle E \rangle} \sim 0.01$ where $E = \frac{1}{2}u.u + \frac{1}{2}kx^2$ and where *k* are effective spring constants, determined by the best fit ellipses to the phase space trajectories (the exact form of the observable energy includes an additional contribution from a phase-space path-dependent term). Consequently, speed-dependent forces complicate rather than invalidate the above analysis.

In the next section I show that Reynolds number effects play a pivotal role in determining a key macroscopic state variable analogous to temperature.

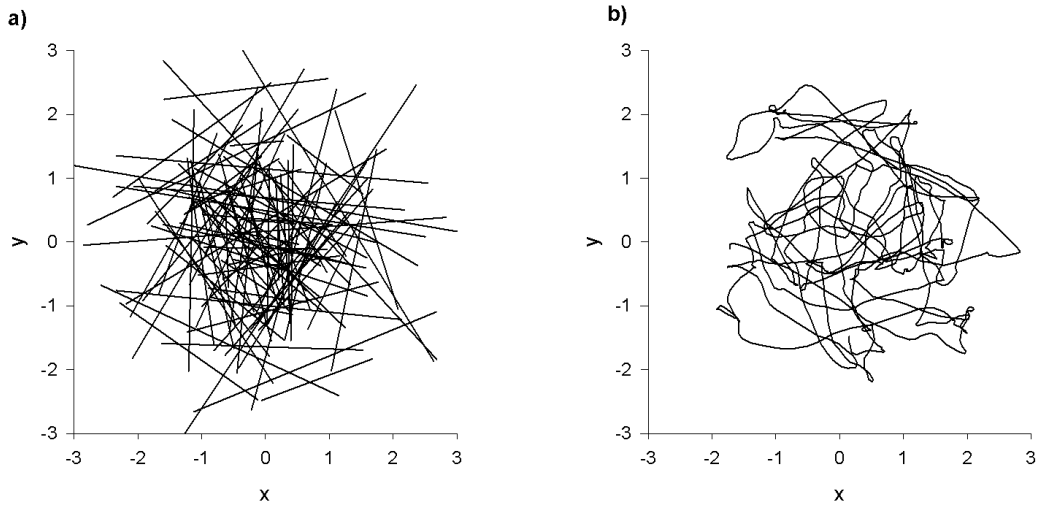

Figure S1 Examples of predicted trajectories for *R=0* (a) and $R \to \infty$ (b). One hundred predictions for *R=0* were obtained using Eqn. S1 with all parameters set to unity. A single prediction for $R \to \infty$ was obtained using the model of Reynolds et al. [2] with all parameters set to unity.

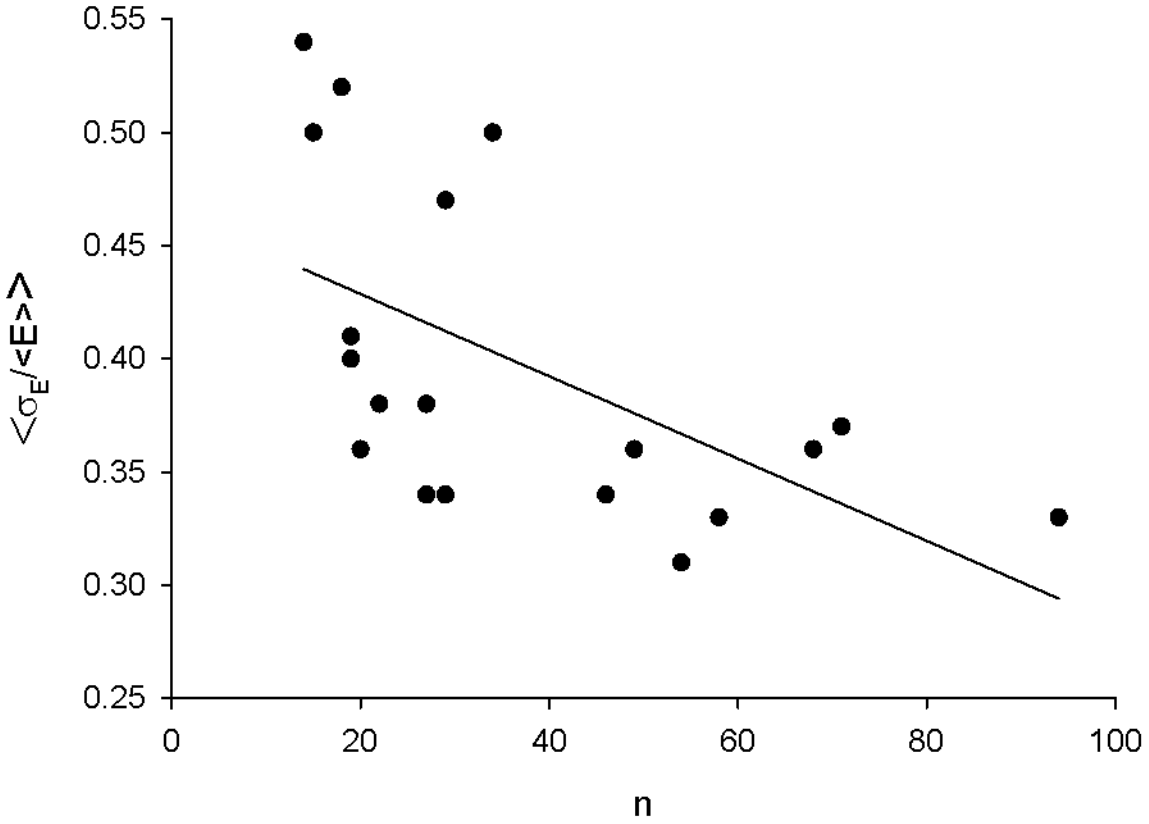

Figure S2 Fluctuations in the observable energy, *E*, tend to decrease as the number, n, of individuals in the swarm increase. Data are shown for 19 swarms reported on by Sinhuber et al. [16] (•). Also shown to guide the eye is the best fit line obtained by linear regression (R^2=0.32). The observable energy is the kinetic energy plus the potential energy, $E = \frac{1}{2}\boldsymbol{u}.\boldsymbol{u} + \frac{1}{2}k_x x^2 + \frac{1}{2}k_y y^2 + \frac{1}{2}k_z z^2$ where the k's are effective spring constants estimated from linear regression of each component of the mean acceleration onto the distance, *x*, *y* and *z*, from the centre of the swarm. The fluctuations, $\frac{\sigma_E}{\langle E \rangle}$, were calculated for each trajectory and are then averaged over all recorded trajectories in the dataset for a given swarm. For these swarms, horizontal movements give estimates for the Re~O(100) whilst vertical movements give estimates for the Re~O(10).

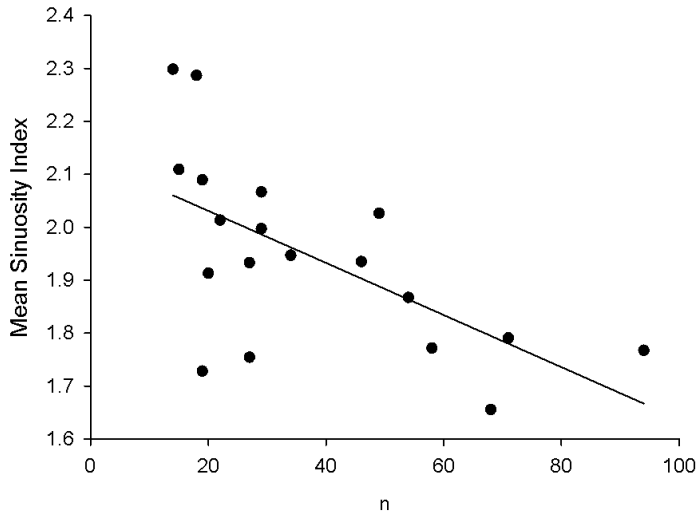

Figure S3 Trajectories tend to become less convoluted as the number, *n*, of individuals in the swarm increases. Data are shown for 19 swarms reported on by Sinhuber et al. [16] (•). Also shown to guide the eye is the best fit line obtained by linear regression (R^2=0.39). The sinuousity index is the actual length of the trajectory in 10 s windows divided by the shortest possible length. The value of the index ranges between 1 (as the case of a straight line) and infinity (as in the case of a closed loop). Averaging is over all consecutive 10 s windows of all trajectories in the dataset for each swarm. Similar trends are found for 5 s windows.

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Section 2

Individual differences together with Reynolds number effects play a pivotal role in determining a key macroscopic state variable analogous to temperature

In recent years it has become apparent that collective animal behaviour cannot be understood by passive observations alone [Ouellette 2019]. Instead, one must interact with the collective. One of the first such experiments was undertaken by Ni et al. [2015] who reported on the group-level response of mating swarms of the midge *C. riparius* to an external stimulus, namely the playing back of the recorded sound of flying midges. When exposed to the sound of a female midge, the swarm immediately dissolved as all the males flew towards the speaker and landed on it. When exposed to the sound of a male midge at constant intensity, no change in the swarm behaviour was observed after a brief, transient dilation at the start of the playback. But when the intensity of the male sound was modulated by multiplying it by a sinusoidally varying signal with frequency ω, a clear and repeatable response as observed. Although, the power spectra of individuals did not significantly change, a net response was manifest as a strong peak in the power spectrum of the swarm's centre of mass at the modulation frequency of the external sound. In space, the centre of mass traced out elliptical, oscillatory trajectories. The perturbation, like other forms of perturbation [Sinhuber et al. 2018,2021, Reynolds 2018, 2021, van der Vaart et al. 2019, 2020] has therefore driven the swarm into a new state with properties distinctly different from those of quiescent swarms.

These observations are predicted by the (infinite Reynolds number) model of Reynolds et al. [2017] (a first order autoregressive process in which the position and velocity of an individual evolve jointly as a Markovian process) under the assumption that: the external sound pulls the swarm off the 'swarm maker', a visually prominent feature over which the unperturbed swarm is centred, so that the centre of attraction (centre of the confining harmonic potential [Obuko 1986, Kelley et al. 2013]) is taken to oscillate sinusoidally at the modulation frequency of the external sound (Fig. S1). This is biologically plausible because the sinusoidal modulation of the sound could simulate the distance to nearby swarming males, with an attraction when the distance to the nearby males is increasing and a repulsion when they get too close to each other. Simulated individuals will respond to this form of perturbation in the same way, and consequently a new coherence in the phases is induced by the driving signal, mirroring the mechanism that may give rise to the coherent motion of flocking birds [Reynolds 2023]. As observed the centre of mass velocity varies is predicted to oscillate at the driving frequency (Fig. S2a) even though, as observed [Ni et al. 2015], the perturbation does not affect the flight

behaviours of the simulated individuals. And as observed, the peak magnitude of the phase-averaged centre-of-mass velocity varies linearly with the magnitude of driving force, when this force is small. Such a response is typical of passive material in an external field. Nonetheless, in contrast with passive material near thermodynamic equilibrium, Ni et al. [2015] observed that the fluctuation-dissipation theorem is violated. This is expected because active processes associated with individual behaviour leads to fluctuations that are larger what they be for a purely thermal system. The fluctuation dissipation theorem dictates that $\omega C(\omega) \propto \chi''(\omega)$ where $C(\omega)$ is the Fourier transform of the velocity autocorrelation function in the absence of the driving and $\chi''(\omega)$ is the imaginary part of the susceptibility. Classically, the constant of proportionality between $\omega C(\omega)$ and $\chi''(\omega)$is related to the temperature. For active systems the ratio of these quantities can be used to define a state variable, like an effective temperature [Martin et al. 2001]. Ni et al. [2015] reported that $\omega C(\omega)/\chi''(\omega)$ falls off with frequency roughly as $\omega^{-3/2}$.

The model of Reynolds et al. [2017] suggest that such a violation of the fluctuation dissipation theorem can be attributed to individuals responding differently to the external perturbation because without such individual differences the model satisfies the fluctuation dissipation theorem. It is also necessary to account for Reynolds number effects. This is because the observed form of $\omega C(\omega)$ which falls off with frequency roughly as ω^{-2} is incompatible with the infinite Reynolds number models which predict that the falling off with frequency cannot be faster than as ω^{-1} [Sawford 1991]. Finite Reynolds number models, on the other hand, predict that the falling with frequency cannot be faster than as ω^{-3} [Sawford 1991]. These models, like their infinite number Reynolds counterparts, satisfy the fluctuation dissipation theorem. Nonetheless, preliminary simulations with the 1-dimensional finite Reynolds number model proposed by Reynolds and Ouellette [2016] (a second order autoregressive process in which the position, velocity and acceleration evolve jointly as a Markovian process) predicts that $\omega C(\omega)/\chi''(\omega)$ decreases with frequency roughly as $\omega^{-3/2}$ when, consistent with the observed unresponsiveness when $\omega = 0$ [Ni et al. 2015], an individual's propensity to respond to the acoustic perturbation increases linearly with increasing frequency, ω (Fig. S3). Individual differences along with Reynolds number effects may therefore play a pivotal role in the macroscopic state variable.

The above putative behavioural response maybe biologically plausible because in mosquito swarms, frequency modulations (known as RFM 'rapid frequency modulations') occur just before mating in males and females, i.e., just after a male seizes a female during the final

stages of copulation when pairs make connection. The role of RFM is unclear [Feugère et al. 2022]. Feugère [Private Communication] speculated that these RFM's may be used by nearby males to detect mating pairs and assess their chance with the female. If so, then Feugère [Private Communication] reasoned that as the modulation frequency of the external perturbation gets close to the RFM *more* males may be attracted or repulsed by the external perturbation. In this way the 'late' male can stay close enough to a chasing pair to grab the female is she rejects the chasing male.

A more complete analysis requires the formulation of 3-dimensional finite Reynolds number models. The formation of 3-dimensional finite Reynolds number models does, however, remain a formidable challenge [Reynolds 2020].

Acknowledgements

I thank Lionel Feugère for insightful comments about the potential role of rapid frequency modulations.

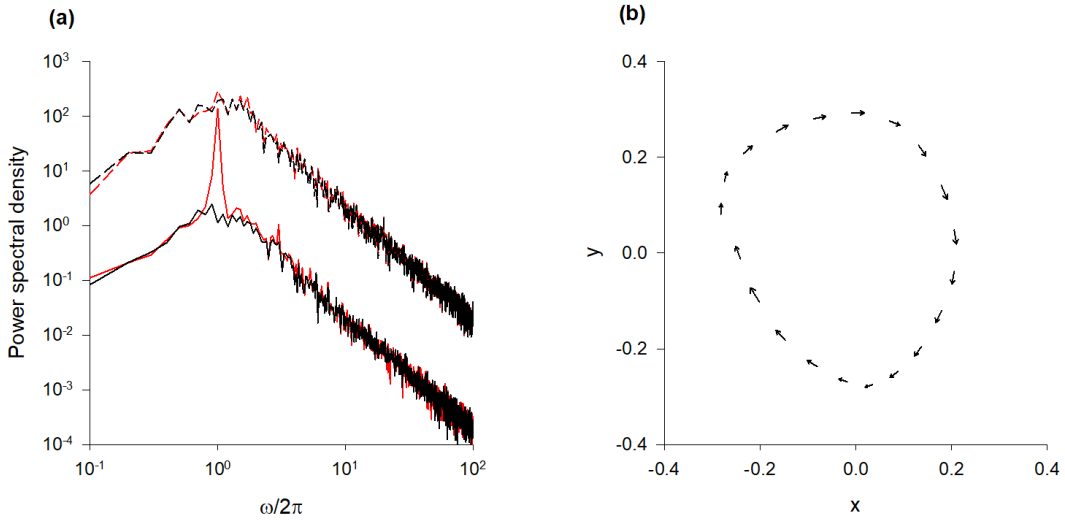
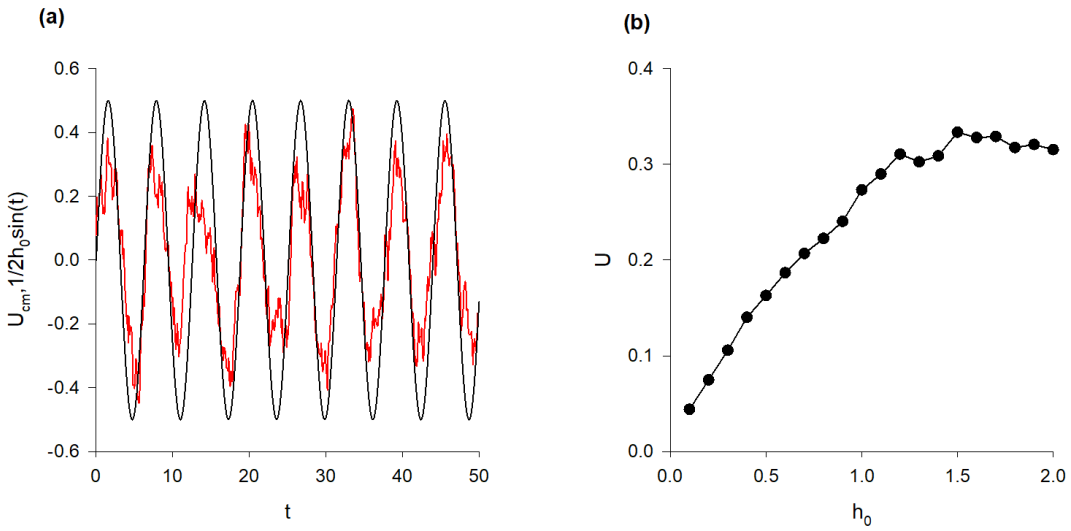


Figure S1 a) Predicted power spectra of one component of the velocity for a single midge in a swarm (dashed lines) and the centre of mass of the swarm (solid line). Data are shown for an undriven swarm (black lines) and for a swarm whose centre of attraction is sinusoidally modulated at frequency of ω=1 with amplitude h_0=1 a.u. **b)** Predicted phase-averaged velocities and trajectories for the centre of mass of the driven swarm. Predictions are shown for a swarm containing 100 individuals and were obtained using the model of Reynolds et al. [2017] with all parameters set to unity.



285 **Figure S2 a)** One component of the predicted centre of mass velocity (red line), U_{cm}, together with the position of centre of attraction (black line) that is sinusoidally modulated at frequency of ω=1 with amplitude 1 a.u (rescaled to each of comparison). **b)** The amplitude, U, of the predicted centre of mass velocity as a function of the amplitude, h_0, of the sinusoidally modulation of the centre of attraction. Predictions are shown for a swarm containing 100
290 individuals and were obtained using the model of Reynolds et al. [2017] with all parameters set to unity.

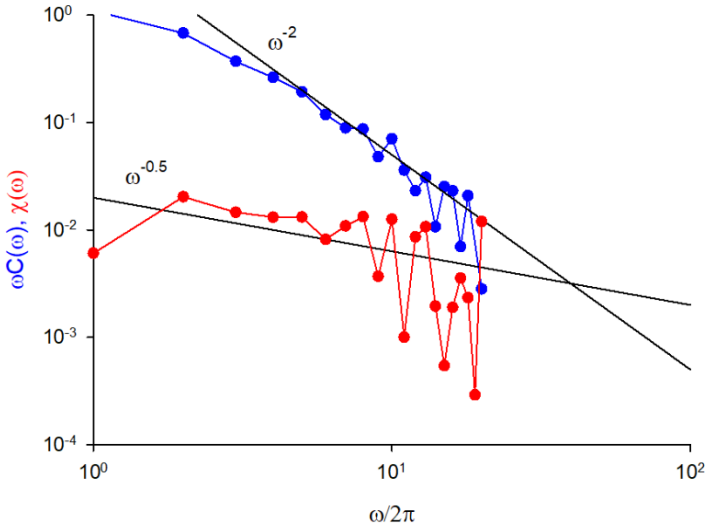


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Figure S3 The power spectral density $\omega C(\omega)$ of the predicted velocity fluctuations for an undriven swarm (blue line) and $\chi''(\omega)$, the imaginary part of the susceptibility (red line). Approximate power-law scaling of $\omega C(\omega)$ and $\chi''(\omega)$, roughly indicative of $\omega C(\omega)/\chi''(\omega) \propto \omega^{-3/2}$ is shown (black lines) Predictions were obtained using the model of Reynolds and
300 Ouellette [2016] with all parameters, apart from the acceleration timescale, set to unity. The acceleration timescale was set to 0.1 a.u., corresponding to an effective Reynolds number of 100. The proportion of responsive individuals is ω/80.

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Section 3

Selection pressures

In this section I argue that advantageous properties of swarming need not be the result of selection pressures.

Midge swarms have properties, like robustness to environmental perturbations, critical damping, stabilizing inward effective pressures) which might be the result of selection pressures for advantageous behaviours, or they could be accidental, in which case there could be selection pressures against losing such properties [1-5]. A recent study of bee 'clouds' might help to be resolve this issue [6]. This is because some of these advantageous properties of midge swarms (near critical damping, negative surface confining pressures) (Figs. S1 and S2) together with the act of swarming itself are also evident in bees (that like midges form a swarm confined by a potential well, Fig. S2) but in the bees these properties cannot be result of selection pressures for advantageous behaviours because the experimental scenario is without a natural analogue. In the bee study, the hive was artificially and temporally blocked resulting in a dense cloud of bees loitering outside of the hive; a behaviour quite unlike other forms of aerial aggregations associated with cooling off, the following of scouts to establish a new hive, following overcrowding of the established hive.

Midge swarms have other seemingly advantageous properties, emergent mechanical-like properties, including tensile strength and viscoelastic behaviours, that only become evident when swarms are perturbed [3,4]. These properties are predicted by minimal (maximum entropy) dynamical models that, by construction, are consistent with observed distributions of individual positions and velocities of swarming midges [7]. Such distributions also characterize the bee clouds (Fig S2). This suggests the bee clouds will have emergent mechanical-like properties in common with the midge swarms. But as with critical damping and confining surface pressures, these putative properties of bee clouds cannot be the result of selection pressures for advantageous behaviours.

This may also be true of individual flight behaviours that underpin the stability of the cloud. Mahadeeswara and Srinivasan [9] reported that the flight speed of a loitering bee is matched to the curvature, moment to moment, in such a way as to maintain the centripetal force at an approximately constant, irrespective of the instantaneous speed or curvature of the turn. This ensures that turns are well coordinated, with few or no sideslips, i.e., it ensures that the bees are not overcome by centrifugal forces during the turn, and always maintain the intended trajectory. Nonetheless, this advantageous flight characteristic might not represent an evolved trait as it also arises freely (accidentally) in minimally structured (maximum entropy) stochastic models for the trajectories of swarming insects (Fig. S3). Associated observed flight characteristics such as the flight speed tending to decrease whilst entering a turn and increase whilst exiting it [9] are also predicted by the model (results not shown).

Finally, swarms of mosquitoes display occasional changes of level which may serve to test the rate of female arrival at various heights [11]. This apparent coordinated behaviour appears to be distinct from swarming (maintenance of cohesion). It is tempting to attribute its occurrence to selection pressures for advantageous behaviours. The results of numerical simulations do however suggest like other advantageous properties [1-5] that it is an accidental by-product of swarming behaviour and arises because the height of the centre of the swarm (i.e., the centre of attraction) is a dynamical quantity determined by the instantaneous locations of the individuals in the swarm (Fig. S4). Fluctuations in the horizontal positions of the swarms are expected to be less apparent because swarms tend to be centred over prominent ground-based features (known as swarm markers).

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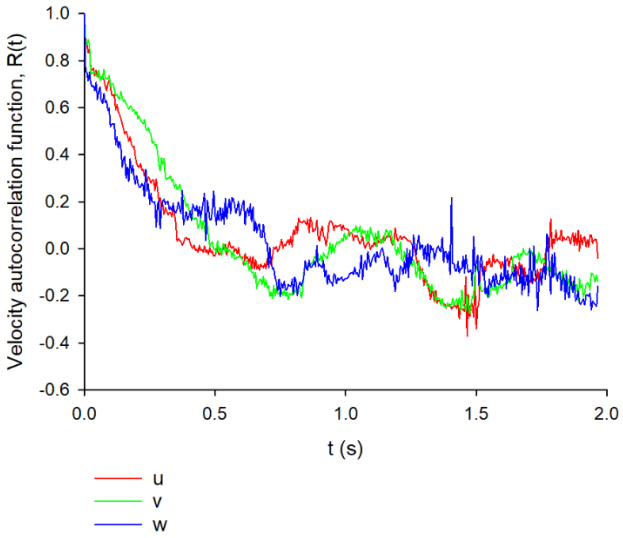

Figure S1 Bee clouds appear to be critically damped, poised between being over- and underdamped. An overdamped cloud is characterized by velocity autocorrelation functions each with a single negative lobe. An underdamped cloud is characterized by oscillatory velocity autocorrelations. Single negative lobes and oscillatory behaviour are barely evident here. Data are taken from Mahadeeswara & Srinvasan Event 1. Bees 5 to 92.

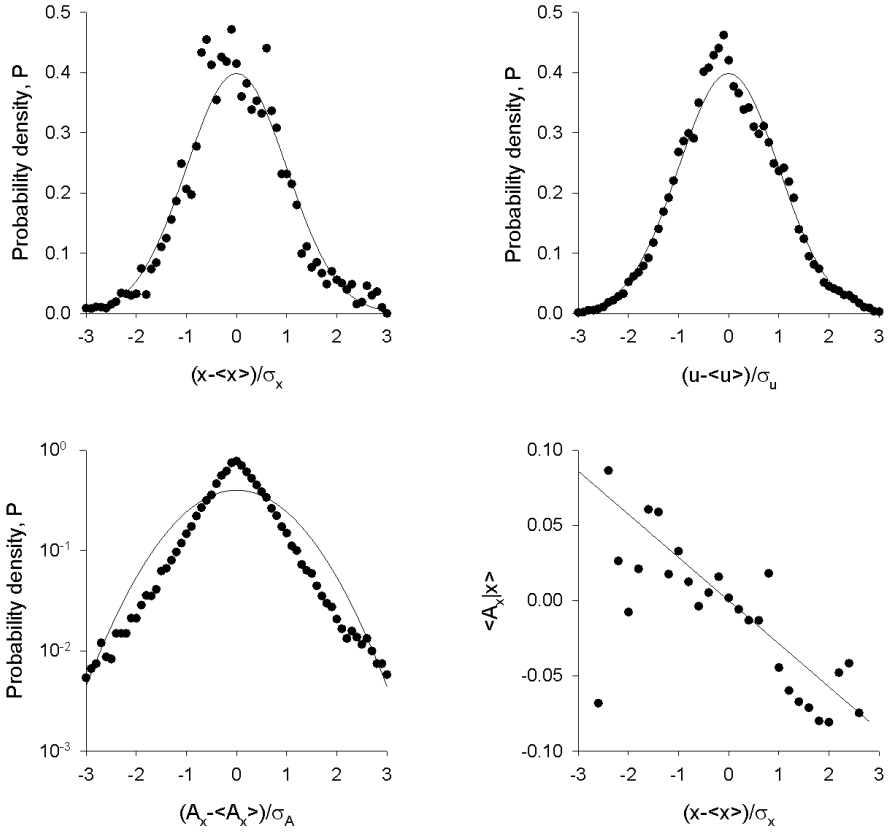

Figure S2 The emergent properties of bee clouds closely resemble the emergent properties of laboratory swarms of midges. Distributions of position, velocity, and acceleration (•) together with Gaussian distributions with mean zero and unit variance (line soilds). Speed distributions (not shown) have Maxwellian cores and long exponential tails. In common with laboratory swarms of midges [7], positions and velocities are nearly Gaussian whilst distributions of accelerations have nearly exponential tails. Conditional mean accelerations (•) increase nearly linearly as a distance from the cloud centre increases. Individual bees in the cloud, like individual midges in laboratory swarms [7], therefore behave on the average as if they are trapped in an elastic potential well (since the effective force is linear in position). The difference between the average kinetic energy and average potential energy, $\frac{1}{2}\langle u^2\rangle - \frac{1}{2}k\langle(x-\langle x\rangle)^2\rangle$, is positive, where *k* is an effective spring constant obtained by linear regression of the conditional mean accelerations on position (solid line). This indicates that the cloud is experiencing a stabilizing inwards effective pressure on its surface [2]. Data are taken from Mahadeeswara & Srinivasan, Event 1. Bees 5 to 92.

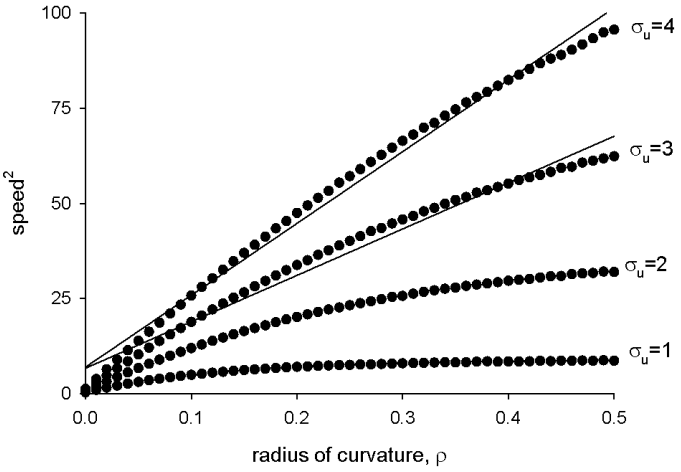

Figure S3 Predicted variation of speed squared with the radius of curvature. The instantaneous curvature of a trajectory $\kappa = |\dot{\boldsymbol{r}} \wedge \ddot{\boldsymbol{r}}|/|\dot{\boldsymbol{r}}^{\boldsymbol{3}}|$ where *r(t)* is the position of the individual at time t. The radius of curvature $\rho = \frac{1}{\kappa}$. The centripetal acceleration $a = \frac{\dot{\boldsymbol{r}}.\ddot{\boldsymbol{r}}}{\rho}$. When centripetal acceleration is constant $\dot{\boldsymbol{r}}.\ddot{\boldsymbol{r}} \propto \rho$. Simulated individuals fly with near constant centripetal accelerations (solid circles) when the required speeds are accessible (less than about 3 times the variance). Note, however, that the tightest turns, which are potentially the most destabilizing, are always executed with near constant centripetal acceleration. The solid lines are least square regressions ($R^2 \approx 0.98$). Predictions were obtained using the stochastic model of Reynolds et al. [7] for the root-mean-square velocities indicated and with all other model parameters set to unity (a.u.).

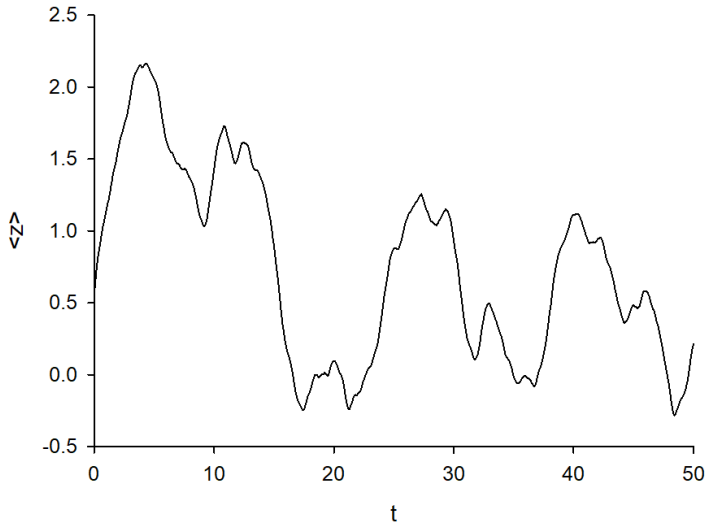

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Figure S4. Shifts in the height of the swarm centroid that may be biological significant are predicted to arise spontaneously when the centre of attraction is not fixed but is instead taken to the instantaneous centre of the swarm. Predictions are shown for a swarm containing 50 individuals and were obtained using the stochastic model of Reynolds et
460 al. [7] with all parameters set to unity.