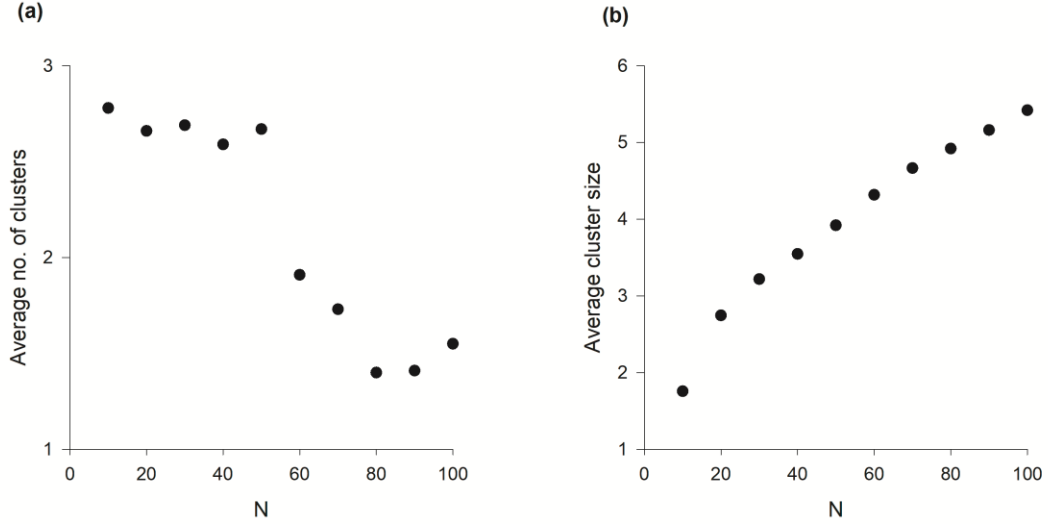


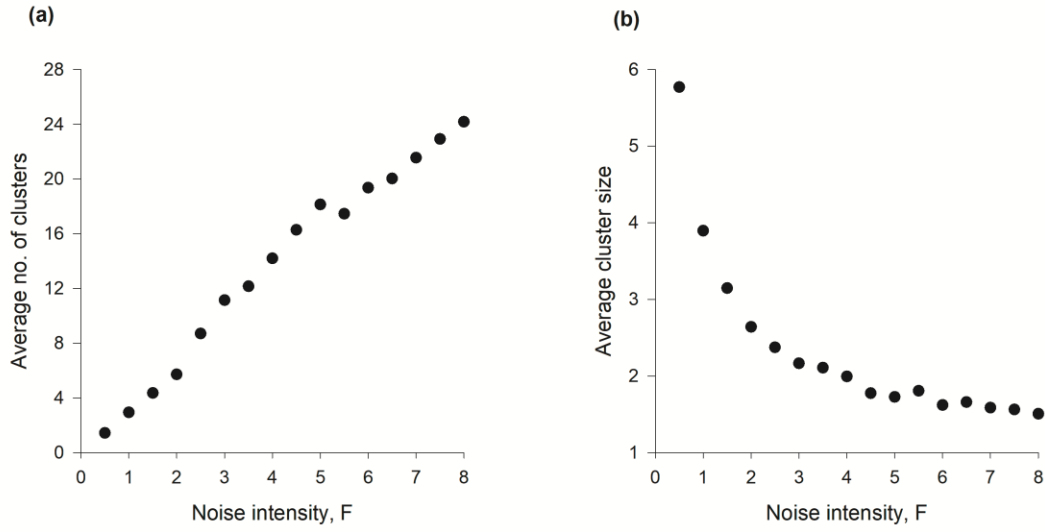
## Supplementary Material

### Algebraic Connectivity

The numbers and sizes of the predicted clusters was determined by their algebraic connectivity. To do this, entries,  $A_{ij}$ , in the adjacency matrix,  $\mathbf{A}$ , were set to unity if the multiplicative noise contribution  $F \exp\left(-\frac{(r_i - r_j)^2}{\sigma^2}\right)$  in the stochastic model, Eqn. 1, associated with the pair of individuals ' $i$ ' and ' $j$ ' exceeded the additive noise  $D$ , i.e., if individuals ' $i$ ' and ' $j$ ' are 'connected'. The eigenvalues of the associated Laplacian matrix  $\mathbf{L} = \mathbf{D} - \mathbf{A}$  were then calculated, where  $\mathbf{D}$  is the degree matrix of the adjacency matrix. The number of times 0 appears as an eigenvalue in the Laplacian is the number of clusters. Clusters are predicted to become less numerous but larger on average as the swarms grow more populous (Fig. S1). Conversely, clusters are predicted to become more numerous but smaller on average as the intensity of the multiplicative noise,  $F$ , increases (Fig. S2). The average Fielder value (the second smallest eigenvalue of the Laplacian matrix) increases as the intensity of the multiplicative noise,  $F$ , increases, indicating that the swarms are becoming better connected.



**Figure S1 Predicted numbers and sizes of clusters as a function of the swarm population size.** Predictions were obtained using Eqn. 1 with  $k = 1$ ,  $D = \frac{1}{10}$ ,  $F = 1$  and  $\sigma = 1$  a.u. Here the 'size' of a cluster is taken to be the average number of connections that connected individuals have. The standard errors for the average numbers and sizes of the clusters are about 0.1 and 0.04 respectively.



25 **Figure S2 Predicted numbers and sizes of clusters as a function of the multiplicative noise intensity,  $F$ .** Predictions were obtained for a swarm containing  $N=50$  individuals using Eqn. 1 with  $k = 1, D = \frac{1}{10}$  and  $\sigma = 1$  a.u. Here the 'size' of a cluster is taken to be the average number of connections that connected individuals have. The standard errors for the average numbers and sizes of the clusters are about 0.1 and 0.04 respectively.

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## **Midge swarms are predicted to undergo a phase transition to states characterized by stellar polytropic sphere (q-Gaussian) distributions**

Here I show that stellar polytropic sphere distributions (q-Gaussians) which constitute the simplest, physically plausible models for self-gravitating stellar systems [Binney and Tremaine 1987], are predicted by minimally structured, stochastic models to characterize the trajectories of swarming midges once the swarms have become sufficiently large. The new result extends the long-standing similitude that insect swarms have with self-gravitating systems [Gorbonos et al. 2016, 2020, Gorbonos and Gov 2017, Okubo 1986, Reynolds 2018a, 2019, 2021, 2023a]. And somewhat paradoxically show how the presence of intrinsic noise can enhance the stability of swarms and sharpen their borders; thereby adding to the growing understanding as to how noise can facilitate order and structure in collective behaviour [Yates et al. 2009, Jhawar & Guttal 2020, Reynolds 2023b]. The new results arise from a simple modification to Okubo's [1986] classic model for the trajectories of swarming midges.

Okubo's [1] 1-dimensional stochastic model for one component of the midge's position relative to the center of the swarm,  $x$ , and for one component of the insect's velocity,  $u$ , is given by

$$du = -kudt - \omega^2 xdt + \sqrt{2B}d\xi(t) \quad (S1)$$

$$dx = udt$$

The first term on the right-hand side of Eqn. (S1) tends to drive velocities back to their mean zero value.  $k$  is the 'frictional coefficient'. Interactions between the individuals are not explicitly modeled; rather, their net effect is subsumed in a restoring force term (the second term on the right-hand side of Eqn.1). This is consistent with subsequent observations which have shown that to leading order insects appear to be tightly bound to the swarm itself but weakly coupled to each other inside it [Puckett et al. 2014]. In accordance with observations [Okubo 1986, Kelley and Ouellette 2013] the strength of the restorative force increases linearly with distance from the swarm centre.  $\omega$  is the frequency of this average restorative force (a harmonic attractive force). The third term, the noise term, represents fluctuations in the resultant internal force.  $B$  is the magnitude of the stochastic noise and  $d\xi$  is an incremental Wiener process with correlation property  $\langle d\xi(t)d\xi(t + \tau) \rangle = \delta(\tau)dt$  where the angular brackets denote an ensemble average. Simulated velocities are position-independent, and Gaussian distributed with mean zero and variance  $\sigma_u^2 = \frac{B}{k}$ . Simulated positions are Gaussian distributed with mean zero and variance  $\sigma_x^2 = \frac{\sigma_u^2}{\omega^2}$ . These predictions are broadly consistent with observations of

laboratory swarms of the the non-biting midge *Chironomus riparius* [Kelley and Ouellette 2013].

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Okubo [1986] attributed the fluctuations in the resultant internal force to the combined effects of the limited number of individuals in the swarm, the non-uniformity in their spatial distribution, and to chance close encounters of the modelled individual with other individuals. Okubo [1986] tactfully assumed that the stochastic noise term encapsulating these fluctuations was position independent. This seems appropriate because Okubo's model [1986] and its subsequent extension to 3-dimensions are in close agreement with numerous observations of midge swarms studied under controlled laboratory conditions [Reynolds 2017, 2018b, van der Vaart et al. 2019, 2020]. These laboratory swarms contain less than 100 individuals but appear nonetheless to be asymptotically large, as their statistical properties saturate when the swarm contain of order 10 individuals [Puckett and Ouellette 2014]. Here, however, attention is focused on much larger swarms containing 1000's or more individuals, as can occur in the wild [Attanasi et al. 2014]. In these cases, the chance close encounters can be expected to make the dominant contribution to the noise term, and such encounters can be expected to be more likely at the core of the swarm where the number of fast fliers is highest and more likely for slower fliers that are less able to head-off collisions with the fast fliers. The simplest form of the noise intensity that encapsulates these expectations, and the one adopted here, is  $B = 1 - a\frac{x^2}{2} - b\frac{u^2}{2}$  where  $a$  and  $b$  are positive constants. Using the methodology of Reynolds [2017], it is readily shown that with this noise intensity, Eqn. 1 predicts that the positions and velocities of the modelled insects have stellar polytropic sphere distributions:

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$$P(u, x) = N(1 - (1 - q)\varepsilon)^{\frac{q}{1-q}} \quad \text{if } \varepsilon < \frac{1}{1-q} \quad (\text{S2})$$

$$= 0 \quad \text{if } \varepsilon \geq \frac{1}{1-q}$$

where  $N$  is a normalization constant,  $0 < q < 1$ , and where  $\varepsilon = \left(\omega^2 \frac{x^2}{2} + \frac{u^2}{2}\right)$  is the observable energy of an insect. Consistency contributions require that  $a = (1 - q)\omega^2$ ,  $b = 1 - q$  and that  $k = 1$ . Notice that the noise intensity is seen, in retrospect, to be proportional to the joint distribution of  $x$  and  $u$  raised to the power of  $(1 - q)/q$ .

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Gaussian distributions of positions and velocities are recovered from Eqn. S2 as  $q \rightarrow 1$ . More generally, when  $q < 1$ , the joint distributions of positions and velocities are more compact, having finite support. In the context of self-gravitating systems such cut-off corresponds, for each value of the radial coordinate  $x$ , to the corresponding gravitational escape velocity [Binney and Tremaine 1987].

The modelling therefore predicts that swarms undergo a phase transition to more stable, more compact forms when they become sufficiently large; the findings of Puckett and Ouellette [2014] regarding the asymptotic character of laboratory swarms notwithstanding. Moreover, because the entropic parameter  $q$  and the polytropic index  $n$  are related by  $\frac{1}{1-q} = n - \frac{1}{2}$  (Taruya, and Sakagami 2004), the modelling also predicts that these newly identified putative phases of swarm can, for example, have similitude with fully convective star cores (like those of red giants), brown dwarfs, giant gaseous planets (like Jupiter), or even for rocky planets; self-gravitating systems that are characterized by polytropes with index  $n = 3/2$  [Chandrasekhar 2016]. This predictions mirrors the case of wild swarms of *Anopheles coluzzi* mosquitoes which can be driven into more robust states (characterized by  $n = 3/2$ ) by environmental perturbations [Reynolds 2018a].

It has been shown that as swarms grow, more cohesive states that are better able to withstand environmental disturbances become accessible even when individuals have the simplest possible (linear) flight dynamics. The swarms are predicted to become ever more stable, as they grow (as collisions become ever more likely) thereby making any potential gains from adopting non-linear dynamics redundant. Consequently, when swarms become sufficiently large, selection pressures for cohesiveness, could drive flight dynamics towards simplicity.

Enhanced stability is only required in the presence of perturbations. This may explain why natural swarms, which must contend with environmental disturbances, are typically much larger than laboratory swarms. The increasing simplicity that is predicted accompany the growth in swarm size may also account, in part, for why the largest, least agile males occur predominantly in larger swarms [Neems et al. 1992].

A second phase transition is predicted to occur when  $q < -1$ . In these cases, the joint distributions of positions and velocities are no longer polytropes. Instead, individuals are most

likely to be located in the outskirts of the swarms, rather than in the cores of the swarms. This is reminiscent of starling (*Sturnus vulgaris*) flocks, as the birds are more tightly packed at the border than at the centre of the flock [Ballerini et al. 2008]. Moreover, because the swarming insects are predicted to have relatively low velocities in the borders, the insects like flocking starlings [Cavagna et al. 2016] are predicted to stay at the borders longer than the way internal individuals keep their position inside the collective. Although accidental this trait could be advantageous as males in the outskirts of swarms may be the first to detect the presence of incoming females. If this is the case, then there could be selection pressures of maintaining high density borders. But so far, such behaviour in insect swarms has not been reported on.

The two predicted phase transitions, from extensive to compacted density profiles, and from low density to high density borders, are not specific to noise intensities of the form  $B = 1 - a\frac{x^2}{2} - b\frac{u^2}{2}$ , and in this sense are robust model predictions. The predicted phase transitions do, for example, also arise when the noise intensities  $B = \exp\left(-a\frac{x^2}{2} - b\frac{u^2}{2}\right)$ , in which case the joint distributions of positions and velocity are Gumbel-like (extreme value distribution-like),  $P(u, x) \propto \exp\left(a\frac{x^2}{2} + b\frac{u^2}{2} - c * \exp\left(a\frac{x^2}{2} + b\frac{u^2}{2}\right)\right)$  where consistency conditions require that  $a/b = \omega^2$  and  $bc = k$ . More generally, Okubo's [1987] model predicts the occurrence of the phase transitions whenever it is driven by multiplicative noise that is a monotonically decaying function of  $a\frac{x^2}{2} + b\frac{u^2}{2}$ . Forms of multiplicative noise that are not functions of  $a\frac{x^2}{2} + b\frac{u^2}{2}$  are incompatible with Okubo's [1987] model. The phase transitions are also predicted by second-order variants of Okubo's [1987] model in which the positions, velocities and accelerations of simulated swarming insects evolve jointly as Markovian processes [Reynolds 2024], when these models are driven by multiplicative noise that is a monotonically decaying function of  $a\frac{x^2}{2} + b\frac{u^2}{2} + c\frac{\dot{A}^2}{2}$  where  $\dot{A}$  are the fluctuations in the accelerations above and below that mean acceleration that effectively bind simulated individuals to the centres of the swarms (see above). This is biologically plausible because these fluctuations arise, in part, from collision avoidance manoeuvres.

Finally, note that polytropic distributions albeit with  $q > 1$  and with more complicated expressions for the observable energies can accurately characterise the properties of laboratory swarms of the midge *Chironomus riparius*, as reported on by Kelley and Ouellette [2013]. The added complexity is necessary because the effective forces that bind individuals

to the centre of the swarm centre (and so the effective potential energies) are speed-  
dependent [Reynolds et al. 2017, see below].

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## 235 **Midges may maximize the cohesiveness of their swarms**

Here with the aid of stochastic modelling I show that the excess velocity flatness statistic of asymptotically large swarms of the non-biting midge *Chironomus riparius* may result in the maximum attainable cohesiveness of the swarm. One-dimensional stochastic models for the joint evolution of the positions,  $x$ , and velocities,  $u$ , are individual midges take the general form,

$$240 \quad du = a(u, x, t)dt + b(u, x, t)d\xi(t) \quad (1)$$

$$dx = udt$$

where  $d\xi(t)$  is an incremental Wiener process with correlation property  $\overline{d\xi(t)d\xi(t+\tau)} = \delta(\tau)dt$ . The simplest such model, Okubo's classic [1986] model, wherein  $a(u, x, t)$  is linear in both  $x$  and  $u$ , and  $b(u, x, t)$  is a constant, captures many of the properties of laboratory swarms of *Chironomus riparius* midges. The joint distribution of positions and velocities,  $p(x, u)$ , is a solution of the Fokker-Planck equation

$$\frac{\partial p}{\partial t} + u \frac{\partial p}{\partial x} = -\frac{\partial}{\partial x}(ap) + \frac{1}{2} \frac{\partial^2}{\partial x^2}(b^2 p) \quad (2)$$

Here for simplicity, I consider statistically stationary swarms with homogeneous velocity statistics and I consider models those deterministic terms are quadratic functions of  $u$  so that  
 250  $a(u, x, t) = \alpha(x)u^2 + \beta(x)u + \gamma(x)$  and those intensity amplitude is constant,  $b(u, x, t) = b_0$ . Following Franzese et al. [1999], a set of equations for the coefficients  $\alpha(x)$ ,  $\beta(x)$  and  $\gamma(x)$  is obtained by multiplying the Fokker-Planck equation by  $u^n$  and then averaging over all velocities:

$$-\langle u^{n+1} \rangle \frac{\partial \rho}{\partial x} = n[\alpha \langle u^{n+1} \rangle + \beta \langle u^n \rangle + \gamma \langle u^{n-1} \rangle] + \frac{b_0^2}{2} n(n-1) \langle u^{n-2} \rangle \quad (3)$$

255 where  $\rho(x)$  is the swarm's density profile. Evaluating this equation for  $n=1, 2$  and  $3$  provides expressions for  $\alpha(x)$ ,  $\beta(x)$  and  $\gamma(x)$ :

$$\alpha(x) = \frac{\partial \rho}{\partial x} \frac{\left[ \frac{\langle u^4 \rangle}{3} - \langle u^2 \rangle^2 \right]}{[\langle u^4 \rangle - \langle u^2 \rangle^2]} \quad (4)$$

$$\beta(x) = -\frac{b_0^2}{2\langle u^2 \rangle}$$

$$260 \quad \gamma(x) = \frac{\partial \rho}{\partial x} \langle u^2 \rangle \frac{\frac{2}{3} \langle u^4 \rangle}{[\langle u^4 \rangle - \langle u^2 \rangle^2]}$$

Such a prescription ensures that the position and velocity statistics of the simulated trajectories are approximately consistent with the model inputs, namely the moments of the velocity distribution and the swarm's density profile. For swarms with Gaussian position and velocity

statistics, the stochastic model reduces to Okubo's [1986] model:  $\alpha(x) = 0$ ,  $\beta(x) = -\frac{b_0^2}{2\langle u^2 \rangle}$ ,

$\gamma(x) = -\frac{\langle u^2 \rangle}{\langle x^2 \rangle}x$  wherein individuals behave on the average as if they are trapped in elastic

potential wells (since the effective forces are linear in position,  $x$ ) that keeps them bound to the swarms. This is consistent with early observations [Okubo 1986, Kelly and Ouellette 2013].

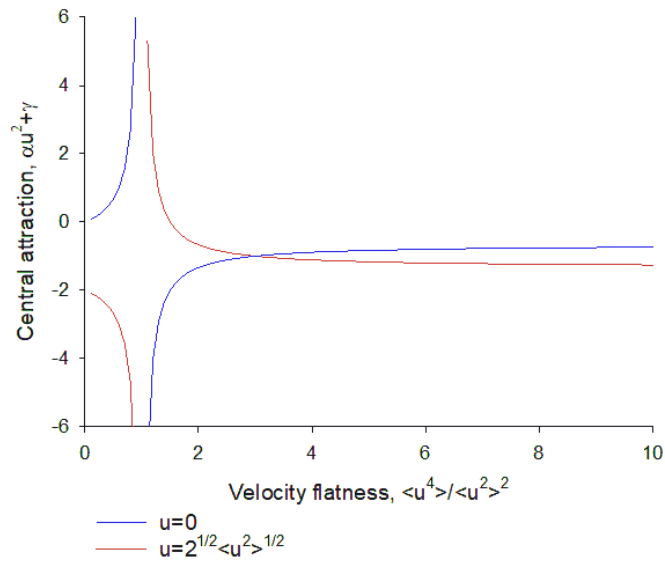
More generally, the effective forces that bind individuals to the swarms are predicted to be speed dependent, as observed by Reynolds et al. [2017]. As the velocity flatness increases

from unity, slower (faster) moving individuals become increasingly less (more) tightly bound to the swarm (Fig. 1). Nonetheless, the most slowly moving individuals are necessarily bound to

the swarm by virtue of their not moving whilst the fastest moving individuals may be most susceptible to environmental disturbances, and so could benefit from enhanced binding to

their swarms, i.e., could benefit from high excess velocity flatness values. In practice the excess velocity flatness values cannot be arbitrarily large because insects cannot fly arbitrarily

fast. This analysis may therefore account for the positive excess velocity flatness,  $\sim 0.4$ , of asymptotic large midge swarms [Puckett and Ouellette 2014].



**Figure 1. The predicted strength of the central attraction for slow- and fast-moving individuals as functions of the velocity flatness.** Without loss of generality results are shown for  $\frac{\partial \rho}{\partial x} = -1$ . Results for velocity flatness values less than unity are shown for completeness even though the associated velocity distributions are pathological.