Eur. Phys. J. Plus (2024) 139:610
https://doi.org/10.1140/epjp/s13360-024-05401-x

THE EUROPEAN PHYSICAL JOURNAL PLUS

Regular Article

Why insect swarms seem unduly complicated

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Received: 10 May 2024 / Accepted: 24 June 2024
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Abstract Mating swarms of flying male insects are a form of collective behaviour, albeit one different from flocks and schools as they do not display ordered collective movements. In recent years, much progress has been made in uncovering the emergent mechanical-like and thermodynamic-like of such swarms. Nonetheless, two basic properties of this swarming behaviour remain unexplained. Namely, why do individual insects have erratic rather than regular flight patterns? And why are the swarms elliptical rather than circular? Here I account for this seemingly undue complexity. I show that regular flight patterns weaken an individual's attraction to the swarm centre, making swarms less resilient to the presence of environmental disturbances. I then show that the elliptical shape of swarms of the non-biting midge *Chironomus riparius* optimizes the trade-off between maximizing swarm size (target size for females) and maximizing swarm stability. Finally, I show that the observed excess velocity kurtosis of swarming *C. riparius* maximizes swarm cohesiveness. Taken together the new results provide the first tentative evidence for fine-tuning in insect mating swarms driven by selection pressure for advantageous behaviours.

1 Introduction

Collective motion of social animals is ubiquitous in nature. Birds, fish, ungulates, and other species of animal routinely exhibit coherent and often organized movement. These striking examples of self-organization in natural far-from-equilibrium systems are drawing the attention of physicists [1]. With very few exceptions, animal groups have been characterized almost exclusively by their morphology and by their degree of directional order.

Not all collective animal groups, however, show macroscopic order. The most notable outliers are mating swarms of flying insects which are generally assumed to be collective, but which can nonetheless lack positional and orientational order [2–8]. These stationary swarms are usually comprised almost entirely of males and typically form over prominent visual features known as swarm 'markers'. They function as leks, i.e. as areas where males congregate to secure mates [8]. Many species of insect form mating swarms and do so in a variety of ways [8]. But in all cases their lack of order challenges conventional notion of collective behaviour. Here I show how this lack order together with the incumbent complexity of swarming can be understood and brought into the fold of collective behaviour studies. For the most part attention is focused on recordings of laboratory swarms of the non-biting midge *Chironomus riparius* made under carefully controlled conditions, free from environmental disturbances [5, 9].

Mating swarms of flying insects typically show a high degree of spatial cohesion and are a form of collective animal behaviour, albeit one different from flocks and schools as they do not display ordered collective movements [2, 3, 5–7]. Flying insects do not circulate around the centre of the swarm in an orderly fashion but instead have more complicated erratic flight patterns [4–6, 8]. I show that this may be attributed to circular trajectories weakening an individual's attraction to the swarm centre, making the swarm less resilient to the presence of environmental disturbances. I then show that the elliptical shape of laboratory swarms of the non-biting midge *Chironomus riparius* [5, 9], an emergent collective property of the swarming behaviour, can be attributed to swarms optimizing the trade-off between maximizing their perimeter/major axis length and maximizing their resilience to environmental disturbances. Maximizing perimeter length/major axis length increases the likelihood that the swarm is detected by females that are close by/far afield. The modelling predicts that the trade-off is optimized when, as observed [9], the swarm aspect ratio is about 1.2. The much larger elongation in the vertical direction can be attributed to the stacking of near circular swarms [10]. Finally, I show that the observed value of the excess velocity kurtosis laboratory swarms of *C. riparius* midges maximizes swarm cohesiveness. From a physical perspective, the swarm aspect ratio and excess velocity kurtosis are free parameters and so, in principle, can take on any values. Herein, their values are determined by purely biological considerations. The new results thereby provide the first provisional evidence for fine-tuning in insect mating swarms driven by selection pressure for advantageous behaviours. Remarkably, this fine-tuning first occurs when swarms of *C. riparius* midges contain order 10 individuals, i.e. when all statistics saturate, and the

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Published online: 13 July 2024

swarms enter an asymptotic regime [9]. It occurs even though individuals are sporadically entering and exiting the swarm [5], and despite the fact that swarm dynamics are inherently noisy [10, 11].

Hereafter, unless stated otherwise, attention is focused exclusively on horizontal movements. Results are obtained with the aid of stochastic models for simulating the trajectories of individual insects within swarms. These models are generalizations of Okubo's [6] classic, pioneering model and are in close agreement with numerous measurements of swarming behaviours made in carefully controlled laboratory settings and in the wild [6, 10–20]. These models account for: laboratory swarms of the non-biting midge *Chironomus riparius* surprisingly having macroscopic mechanical properties similar to solids, including a finite Young's modulus and yield strength, and for the swarms not flowing like viscous fluids [14, 21]; swarms of *Chironomus riparius* midges displaying a collective viscoelastic response to applied oscillatory visual stimuli characterized by a negative storage modulus [19]; environmental perturbations inducing correlations in swarms of *Chironomus riparius* midges [20], thereby reconciling seeming contradictory observations of laboratory swarms [22] made under quiescent conditions with observations of wild swarms which must contend with environmental disturbances [2]; the ability of swarms of *Chironomus riparius* midges to be driven through 'thermodynamic cycles' by external perturbations, during which an equation of state holds throughout [10, 23]; the collective response of *Anopheles gambiae* mosquito swarms to environmental disturbances which resembles shear hardening [17]. By construction, simulated trajectories produced by these models are necessarily consistent with parameterizations of both observed swarm density profiles and observed velocity distributions of swarming insects; quantities that are used as model inputs and those functional forms are herein attributed fine-tuning for advantageous behaviours. This contrasts with bottom-up models, such as the Vicsek-type models [2, 24] and effective gravity models [25], in which the density profiles and velocity distributions are emergent properties of the modelled interactions between individuals. It should be noted, as emphasized by Bialek et al. [26], that the maximum entropy principle is not a 'modelling assumption'; rather, it is the absence of assumptions. Any other model that accounts for the observations will have more structure and hence (explicitly or implicitly) assumes something about the nature of the interactions in the swarms beyond what is required to match the data.

The new results stand apart from previous ones in that they are indicative of fine-tuning by selection pressures for advantageous behaviours. Previously identified emergent mechanical properties of insect swarms although potentially advantageous appear to arise as accidental by-products of swarming [6, 10–20], and consequently there could be selection *against* losing them.

2 Regular flight patterns

The least biased (maximum entropy) choice for the distribution of velocities characterizing a two-dimensional circular trajectory with radially independent average speeds Ω is a multivariant Gaussian distribution with mean velocity $\boldsymbol{\mu} = \Omega(-\sin\theta, \cos\theta)$ and covariance matrix $\delta_{ij}\sigma_s^2$ where θ is an angular coordinate specifying the orientation of the insect's position vector, δ_{ij} is a Kronecker delta function and where the subscripts equal to 1 or 2 denote Cartesian coordinates. The least biased choice for the distribution of individual positions (the density profile) given only that the swarm is localized (on the origin) and coherent is a Gaussian with mean zero and variance σ_r^2.

It follows from the analysis of Reynolds et al. [12] (see Supplementary Data for derivation) that the simplest radially symmetric two-dimensional minimally structured (maximum entropy) stochastic trajectory model for the joint evolution of the position, x and y, and velocity, u and v, of an insect within a swarm with the aforementioned Eulerian Gaussian position statistics and homogeneous (spatially independent) Gaussian velocity statistics is given by

$$\mathrm{d}u = -\frac{(u-\overline{u})}{T}\mathrm{d}t - \left[\frac{s^2}{r}\sin(\phi-\theta) + \frac{s\sigma_s^2}{\Omega}\left(\frac{r}{\sigma_r^2} - \frac{1}{r}\right)\right]\sin(\phi)\mathrm{d}t + \sqrt{\frac{2\sigma_u^2}{T}}\mathrm{d}W_1(t) \tag{1a}$$

$$\mathrm{d}v = -\frac{(v-\overline{v})}{T}\mathrm{d}t + \left[\frac{s^2}{r}\sin(\phi-\theta) + \frac{s\sigma_s^2}{\Omega}\left(\frac{r}{\sigma_r^2} - \frac{1}{r}\right)\right]cos(\phi)\mathrm{d}t + \sqrt{\frac{2\sigma_u^2}{T}}\mathrm{d}W_2(t) \tag{1b}$$

$$\mathrm{d}x = u\mathrm{d}t \tag{1c}$$

$$\mathrm{d}y = v\mathrm{d}t \tag{1d}$$

where $x = r\cos(\theta)$, $y = r\sin(\theta)$, $u = scos(\phi)$, $v = s\sin(\phi)$, r is the distance from the swarm centre, s is the individuals speed, ϕ is an angular coordinate specifying the orientation of the insect velocity vector, T is a velocity correlation timescale, σ_u^2 is the velocity variance, $\mathrm{d}\boldsymbol{W}(t)$ is an incremental Wiener process with correlation property $\overline{\mathrm{d}W_i(t)\mathrm{d}W_j(t+\tau)} = \delta(\tau)\delta_{ij}\mathrm{d}t$. Equation 1 is the simplest of two possible minimally structured models. The alternative model is not considered here because it is considerably more complicated and from a physical perspective seemingly natural because the position and velocity vectors are parallel rather than orthogonal. By construction the simulated trajectories are necessarily consistent with the Eulerian distributions of position and velocity that are used as model inputs.

The first terms on the right-hand sides of Eqs. 1a, b are memory terms that causes velocity fluctuations to relax back to their mean value. Interactions between individuals are not explicitly modelled; rather, their net effect is subsumed in a restoring force term, since observations have suggested that to leading order swarming *Chironomus riparius* midges appear to be tightly bound

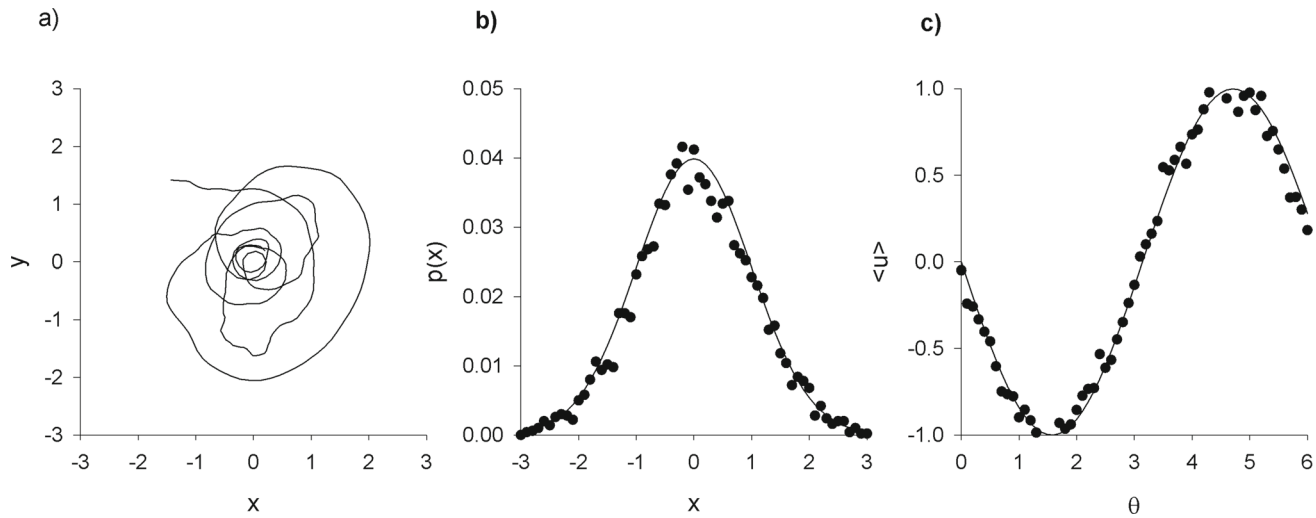

Fig. 1 Model trajectories have the prescribed behaviours and statistics. **a** Simulated trajectories are circular and most frequently are within the core of the swarm. **b**, **c** The predicted positions and mean velocities of individual insects (•) match the prescribed distributions (solid lines). Predictions were obtained using the stochastic trajectory model, Eq. 1, with $\Omega = 1$, $\sigma_u = 1$, $\sigma_r = 1$ and $T = 1$ a.u. Results shown in **b** and **c** were obtained by ensemble averaging over 5000 trajectories each of duration 60 a.u.

to the swarm itself but weakly coupled to each other inside it [5]. These restorative forces are given by the second terms on the right-hand sides of Eqs. 1a, b. In contrast with these model terms, individual *Chironomus riparius* midges, which have erratic rather than regular trajectories, behave on the average as if they are trapped in an elastic potential well (since the effective force is linear in position) that keeps them bound to the swarm [5, 6]. Nonetheless, the simulated insects like the swarming midges are on average accelerating towards the centre of the swarm. Functionally, an average acceleration towards the centre keeps the swarm intact. The noise term models a stochastic component of the internal forces that arise partly because of the limited number of individuals in the grouping and partly because of nonuniformity in their spatial distribution [6]. It also arises because of chance encounters with other individuals, and perhaps because of the inherent uncertainties in the detection of the 'swarm marker'.

The results of numerical simulations confirm that model predictions (model outputs) for the distributions of individual positions and speeds match the prescribed distributions (model inputs) (Fig. 1), i.e. they confirm that the model has been formulated correctly and has been implemented correctly in the computer code.

Compared with the case of non-circulating insects, circulating insects within the core of the swarm are more strongly bound to the swarm centre, whilst those in the outskirts of the swarm are less strongly bound to the swarm centre (Fig. 2). The steep change in the mean acceleration that occurs at $x = 0$ arises because the x-component of the mean speed changes sign at $x = 0$. The weakening of the binding in the outskirts of the swarm makes the swarm more susceptible to environmental perturbations because the effective spring constant is smaller. Consequently, there will be selection pressures for non-circulating trajectories because this allows swarming insects to better stabilize themselves against environmental perturbations. As shown below, this is a robust finding that also applies to swarms of non-interacting individuals with inhomogeneous Gaussian velocity statistics.

The methodology of Reynolds et al. [12] [see 17] can be used to devise more complicated models that can account for radially dependent mean speeds, $\Omega(r)$. The simplest radially symmetric two-dimensional minimally structured (maximum entropy) stochastic model for the joint evolution of the position, x and y, and velocity, u and v, of an insect within such a swarm is given by

$$\mathrm{d}u = -\frac{(u-\overline{u})}{T}\mathrm{d}t - \left[\frac{s^2}{r}\sin(\phi-\theta) + \frac{s\sigma_s^2}{\Omega}\left(\frac{r}{\sigma_r^2} - \frac{1}{r}\right) - s\frac{\partial\Omega}{\partial r}\frac{\sigma_s^2}{\Omega^2}\left(\frac{s\Omega}{\sigma_s^2}\sin(\phi-\theta) - 1\right) + s\frac{\partial\Omega}{\partial r}\right]\sin(\phi)\mathrm{d}t + \sqrt{\frac{2\sigma_u^2}{T}}\mathrm{d}W_1(t) \quad (2a)$$

$$\mathrm{d}v = -\frac{(v-\overline{v})}{T}\mathrm{d}t + \left[\frac{s^2}{r}\sin(\phi-\theta) + \frac{s\sigma_s^2}{\Omega}\left(\frac{r}{\sigma_r^2} - \frac{1}{r}\right) + s\frac{\partial\Omega}{\partial r}\frac{\sigma_s^2}{\Omega^2}\left(\frac{s\Omega}{\sigma_s^2}\sin(\phi-\theta) - 1\right) + s\frac{\partial\Omega}{\partial r}\right]cos(\phi)\mathrm{d}t + \sqrt{\frac{2\sigma_u^2}{T}}\mathrm{d}W_2(t) \quad (2b)$$

$$\mathrm{d}x = u\mathrm{d}t \quad (2c)$$

$$\mathrm{d}y = v\mathrm{d}t \quad (2d)$$

This model reduces to Eq. 1 when $\frac{\partial\Omega}{\partial r} = 0$. The results of numerical simulations confirm that model predictions (model outputs) for the distributions of individual positions and speeds match the prescribed distributions (model inputs) (Fig. 3). The results of numerical simulations (Fig. 2) with such models reveal that radial-dependent mean speeds either have no discernible impact on the central attraction or as with constant mean speeds, weaken the central attraction. This is true irrespective of whether mean speeds increase or decrease with distance from the swarm centre.

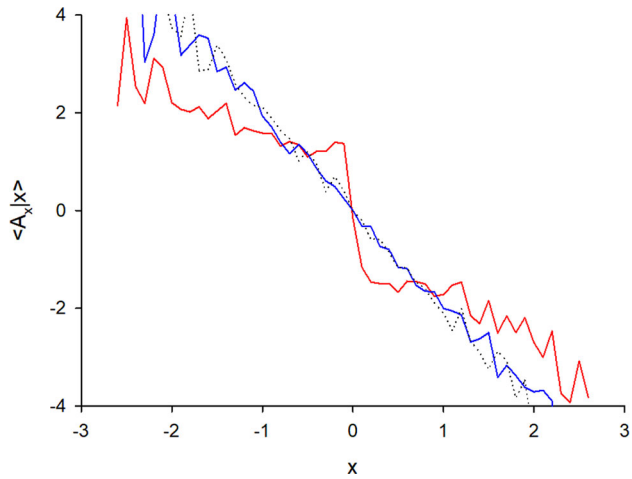

Fig. 2 Predicted mean value of a single component of the mean acceleration, $\langle A_x \rangle$, conditioned on an insect's distance from the centre of the swarm, x. Predictions are shown for non-circulating (blue) and circulating (red) insects. Predictions for non-circulating and circulating insects were obtained using the model of Reynolds [17] and Eq. 1 respectively with all parameters (mean speed, velocity variances, swarm size, velocity autocorrelation timescale) set to unity a.u. Shown for comparison (black dotted line) are predictions obtained using Eq. 2 for a radial-dependent mean speed, $\Omega(r) = r$ and with all other parameters set to unity a.u. Results were obtained by ensemble averaging over 10,000 trajectories each of duration 60 a.u.

3 Elliptical swarms

Laboratory swarms of *C. riparius* midges are elliptical [5, 9]. That is, individuals break rotational symmetry in the same way, making the symmetry breaking a collective property of swarming.

Here the methodology of Reynolds et al. [12] [see 17] is used to devise models for the trajectories of *C. riparius* midges within elliptically shaped swarms, wherein individual positions are distributed according to

$$p(x, y) \propto exp\left(-\frac{r^2}{2\sigma_r^2}\left(\frac{1}{\Lambda}cos^2\theta + \Lambda sin^2\theta\right)\right) \tag{3}$$

These modelled swarms have aspect ratio, Λ^2, cross-sectional areas πr^2 and to good approximation perimeters have length $\pi r \left[3\left(\Lambda + \frac{1}{\Lambda}\right) - \sqrt{\left(3\Lambda + \frac{1}{\Lambda}\right)\left(\Lambda + \frac{3}{\Lambda}\right)}\right]$ [27].

The simplest radially symmetric two-dimensional minimally structured (maximum entropy) stochastic model for the joint evolution of the position, x and y, and velocity, u and v, of an insect within such a swarm is given by

$$\mathrm{d}u = -\frac{u}{T}\mathrm{d}t - \frac{2\sigma_u^2}{\sigma_r^2}r\left[\frac{1}{\Lambda}\cos\phi\cos\theta + \Lambda\sin\phi\cos\theta\right]\cos(\phi)\mathrm{d}t + \sqrt{\frac{2\sigma_u^2}{T}}\mathrm{d}W_1(t) \tag{4a}$$

$$\mathrm{d}v = -\frac{v}{T}\mathrm{d}t - \frac{2\sigma_u^2}{\sigma_r^2}r\left[\frac{1}{\Lambda}\cos\phi\cos\theta + \Lambda\sin\phi\cos\theta\right]\sin(\phi)\mathrm{d}t + \sqrt{\frac{2\sigma_u^2}{T}}\mathrm{d}W_2(t) \tag{4b}$$

$$\mathrm{d}x = u\mathrm{d}t \tag{4c}$$

$$\mathrm{d}y = v\mathrm{d}t$$

By construction individual velocities are homogeneous and Gaussian distributed, as are the velocities of swarming of *C. riparius* midges, to good approximation [5, 9].

The results of numerical simulations confirm that model predictions (model outputs) for the distributions of individual positions and velocities match the prescribed distributions (model inputs) (Fig. 4), i.e. they confirm that the model has been formulated correctly and has been implemented correctly in the computer code.

Compared with the case of circular and nearly circular swarms with $\Lambda \leq 1.2$, individuals within more strongly elliptically shaped swarms are predicted to be less tightly bound (on average) to the centre of swarm (Fig. 5). The crossover is consistent with the observed aspect ratios of asymptotically large swarms of *C. riparius* [9], see also [5].

Laboratory swarms of *Anopheles gambiae* and *Anopheles coluzzii* mosquitoes that fly with near constant speed and have flight behaviours different from those of *Chironomus riparius* midges [4, 17, 18, 28], are also predicted, as observed [28], to be elliptical (Supplementary Data).

In Supplementary Data the modelling approach is used examine why swarms do not have 3 or higher fold rotational symmetries, and why swarms do not take spiral forms despite the long-standing analogy insect swarms have with self-gravitating systems [6, 13, 14, 16, 29, 30].

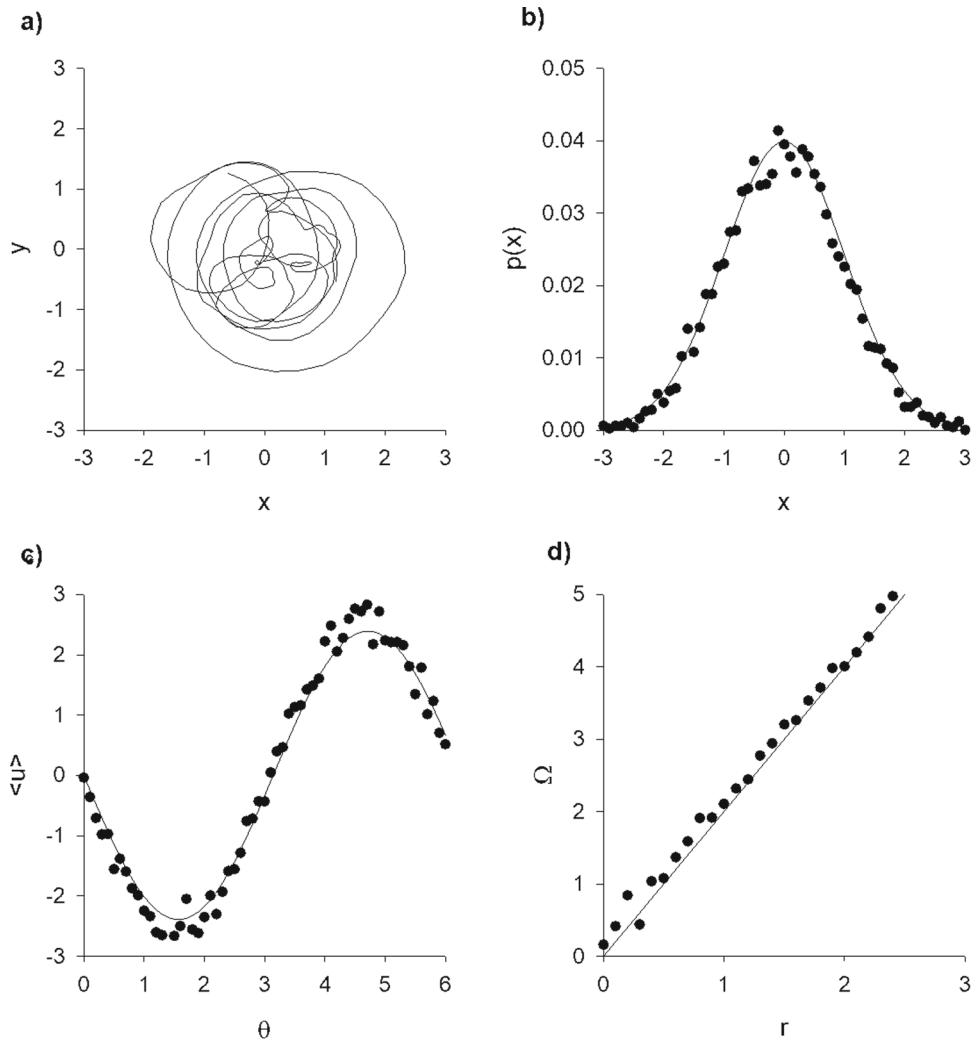

Fig. 3 Model trajectories have the prescribed behaviours and statistics. **a** Simulated trajectories are circular. Circulation is most evident in the outskirts of the swarm where the speeds are highest. **b**, **c** and **d** The predicted positions, mean velocities, and mean speeds of individual insects (•) match the prescribed distributions (solid lines). Predictions were obtained using the stochastic trajectory model, Eq. 2, with $\Omega(r) = 2r$, $\sigma_u = 1$, $\sigma_r = 1$ and $T = 1$ a.u. Results shown in **b**, **c** and **d** were obtained by ensemble averaging over 5000 trajectories each of duration 60 a.u.

4 Excess velocity kurtosis

The speed distributions of C. *riparius* midges in small swarms agree well with Maxwell–Boltzmann statistics [5, 6]; for asymptotically large swarms (containing more than 20 individuals), however, the speed distributions have long, nearly exponential tails [5]. The measured velocity is kurtosis about 3.4 [9]. The least biased (maximum entropy) choice for such leptokurtic distributions, and the one adopted here, is given by,

$$P(s) = N_{\exp}\left(-As - Bs^2\right) \tag{5}$$

where N is a normalization constant and where the values of the parameters A and B are found numerically so that each component of velocity as unit variance and a prescribed kurtosis.

The methodology of Reynolds et al. [12] [see Reynolds 17] can be used to devise models that can account for such non-Gaussian velocity statistics. In the simplest such models, individuals are, as observed [5, 6], on the average, accelerating towards the centre of the swarm thereby keeping the swarm intact. The magnitude of this mean acceleration is given by,

$$A_s = \frac{r}{\sigma_r^2} A_s^*$$

where

$$A_s^* = -\sqrt{\pi}\frac{A}{4B^{3/2}} exp\left(\frac{A^2}{4B}\right)\frac{1}{P(s)}\left(erf\left(\frac{A+2Bs}{2\sqrt{B}}\right) - 1\right) - \frac{1}{2B} \tag{6}$$

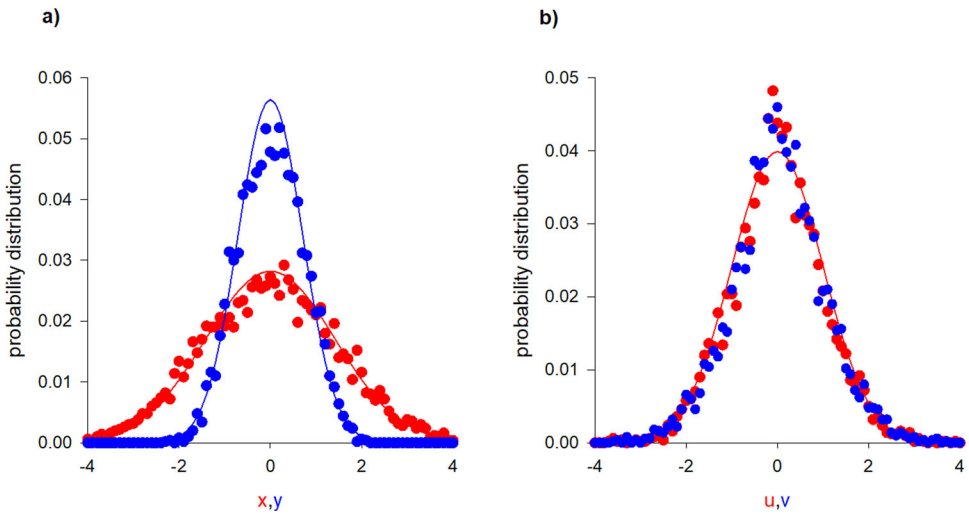

Fig. 4 Model trajectories have the prescribed statistics. The predicted positions and mean velocities of individual insects (•) match the prescribed distributions (solid lines). Predictions were obtained using the stochastic trajectory model, Eq. 4, with $\Lambda = 2$, $\sigma_u = 1$, $\sigma_r = 1$ and $T = 1$ a.u. Results shown were obtained by ensemble averaging over 5000 trajectories each of duration 60 a.u.

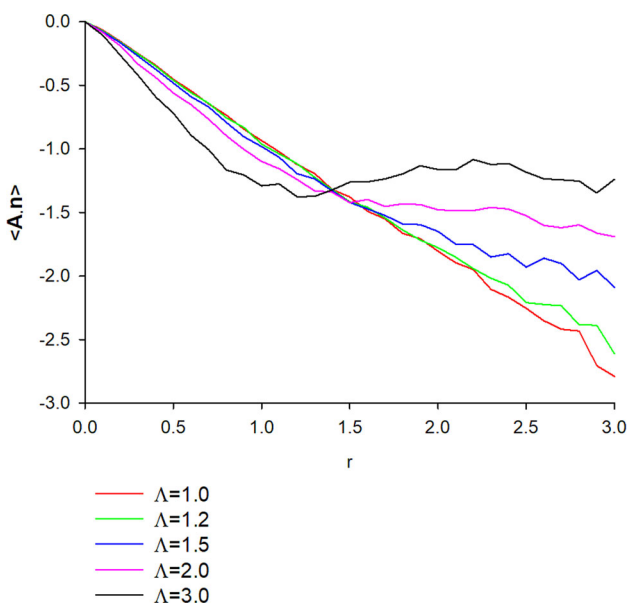

Fig. 5 The predicted strength of the effective force binding individuals to centres of elliptical swarms as a function of distance, r, from the swarm centre. A_x and A_y are given by the second terms on the right-hand sides of Eqs. 4a and b. n is a unit vector pointing towards the swarm centre. Predictions were obtained using the stochastic trajectory model, Eq. 4, with $\sigma_u = 1$, $\sigma_r = 1$ and $T = 1$ a.u. Results were obtained by ensemble averaging over 100,000 trajectories each of duration 60 a.u.

As observed [12], the mean acceleration is predicted to increase monotonically with increasing speed (Fig. 6a). The average value of $-A_s^*$ is $-\sigma_u^2$. Nonetheless, the percentage of individuals that are momentarily bound (on average) to the centre of the swarm less tightly than $-\sigma_u^2 r/\sigma_r^2$ (i.e. are less tightly bound to the swarm centre than are individuals with Gaussian velocity statistics) increases monotonically with increasing kurtosis F, of one component of velocity and reaches 50% (the tipping point) when F reaches the observed value of 3.4 [9] (Fig. 6b). These findings do not depend sensitively on the functional form of the speed velocity, and do, for example, arise when the maximum entropy form, Eq. 5, is replaced by a linear combination of a Gaussian and an exponential (results not shown).

In Supplementary Data I examine the influence that anisotropic velocity statistics have on the cohesiveness of swarms. I also identify a new mechanism for the formation of transient, local order (synchronized subgroups) that is seen in wild swarms of *Anopheles gambiae* and *Anopheles coluzzii* mosquitoes [31].

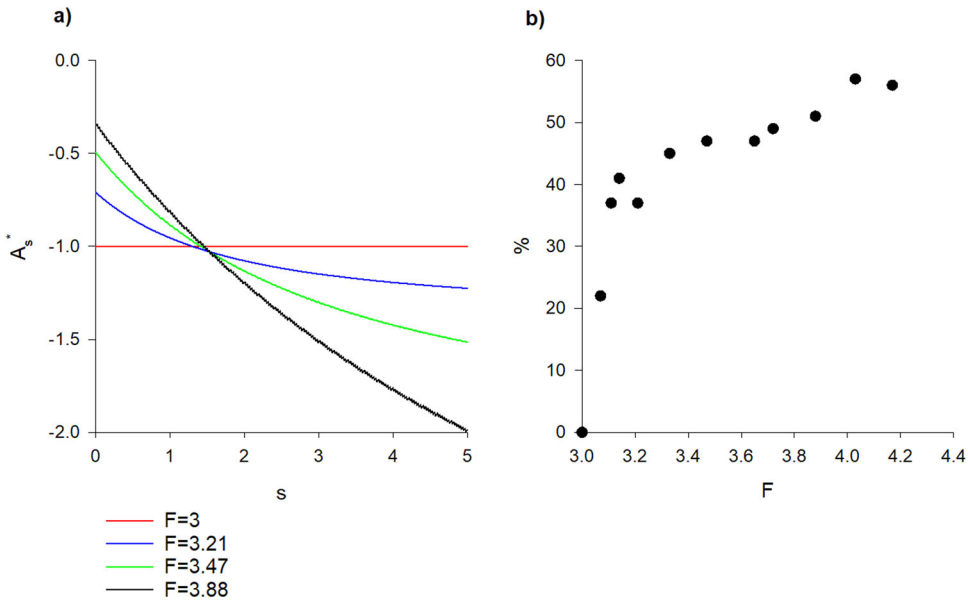

Fig. 6 Mean predictions for the mean acceleration of insects in swarms with leptokurtic velocity distributions. **a** As observed [12], mean accelerations increase monotonically with increasing speed when velocity distributions are non-Gaussian and have kurtosis (flatness) $F > 3$. **b** Predicted percentage of individuals that are momentarily bound to the centre of the swarm by an effective force less strong than that acting on individuals with Gaussian velocity statistics. Predictions for (**a**) were obtained by numerical evaluation of Eqns.5 and 6 for $\sigma_u = 1$ (making kinetic energy a constant across the simulations) and for (**b**) by numerical integration of Eq. 6

5 Discussion

Insect swarms have emergent macroscopic mechanical properties such as tensile strength [15, 21], viscoelastic behaviours [19], and shear hardening capabilities [17] that help to them resist environmental disturbances. Here I showed how the apparently unduly complicated nature of insect swarms contributes to this robustness. I showed that individuals within swarms of erratically flying insects are more tightly bound to the swarm centres than are individuals within swarms of circulating insects. I then showed how the observed elliptical shape of asymptotically large laboratory swarms of the midge *Chironomus riparius* allows for the maximum perimeter length without comprising swarm cohesiveness. Maximizing the perimeter may be crucial for mating success because females cannot detect mating swarms for afar. Although some swarming insects are known to be very sensitive to acoustic signals, acoustic communication is restricted to close range pair interactions [32]. Moreover, in two specifies of mosquitoes, at least, there is no evidence of long-range sex pheromones involved in swarm detection and recognition by females [33]. If females mating can detect mating swarms visually from afar then some fortuitously placed females would benefit considerably from the swarms having, as observed [5, 9] a major axis around 30% longer than a circular swarm containing the same number of males. If on the other hand, females can only detect mating swarms at close range then they benefit from the observed and predicted elliptical shapes of these swarms being 2.5% longer than the perimeter of circular swarms having the same cross-sectional area. The new result leaves open the question as to what, if anything, determines the orientations of the ellipses. In accordance with observations [28] swarms of the mosquito *Anopheles coluzziis* are also predicted to have elliptical cross sections with finely tuned aspect ratios. In the Supplementary Data I provide putative evidence for a distinctly different kind of fine-tuning in swarms of the mosquito *Anopheles coluzziis.* These presented in this paper were obtained with the aid of minimally structure models for the trajectories of swarming insects. The relationship between these models and bottom-up models is examined in the Supplementary Data where I provide an illustrative example of the pitfalls of bottom-up modelling.

The breaking of rotational symmetry, together with the erratic trajectories of individual insects, enriches a long-standing analogy that insect swarms have with self-gravitating systems [6, 13, 14, 16, 29, 30], (Supplementary Data). Swarms of the non-biting midge *Chironomus riparius* now appear to the analogous to 'elliptical galaxies' that are filled with old red stars that have random orbits, rather than to global clusters, as suggested previously [25].

I also showed that the observed departures from Maxwell–Boltzmann speed statistics, i.e. Gaussian velocity statistics [9], can be attributed to *C. riparius* midges in the laboratory maximizing their attraction to the swarm centre. Moreover, it was shown that somewhat fortuitously efficient horizontal flight, a biological constraint on individuals, does not impact adversely on the cohesiveness of swarms. This leaves open the question as to why of the three eigenvectors of the inertia tensor which specify the intrinsic orientations of midge swarms one is always nearly vertical, whilst the other two always deviate significantly and consistently from the horizontal [5].

Taken together, the results show how seemingly innocuous and until overlooked idiosyncratic properties of swarming (more generally collective animal behaviour) combined with physical modelling can provide information about biological function, as advocated by Ouellette [1]. They are indicative of fine-tuning due to selection pressures for advantageous behaviours. This interpretation could be tested by careful quantification of the emergent properties of swarms of insects with behaviours comparable to that of swarming *Chironomus riparius* midges. The new results also show how analogies with self-gravitating systems continue to deepen.

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1140/epjp/s13360-024-05401-x.

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.

Data Availability Statement Data sharing is not applicable to this article as no datasets were generated during the study.

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