



# Intrinsic stochasticity and the emergence of collective behaviours in insect swarms

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**Abstract** Intrinsic stochasticity associated with finite population size is fundamental to the emergence of collective behaviours in insect swarms. It has been assumed that this intrinsic stochasticity is purely additive (position independent) in quiescent (unperturbed) swarms. Here, I identify the hallmarks of intrinsic multiplicative (position dependent) stochasticity and show that they are evident in quiescent laboratory swarms of the non-biting midge *Chironomus riparius*. In accordance with theoretical expectations, the smallest well-documented laboratory swarms (containing between 14 and 46 individuals) are found to have  $q$ -Gaussian density profiles with  $q > 1$ , whereas larger laboratory swarms have Gaussian ( $q = 1$ ) density profiles. I show that these newly identified states are analogous to interstellar clouds and thereby extend a long-standing analogy between insect swarms and self-gravitating systems. Smaller laboratory swarms have been observed and are predicted to be gas-like, filling the available space rather than occupying just a small proportion of it. The new results unify laboratory swarms with wild swarms. Unlike laboratory swarms, wild swarms must contend with environmental (extrinsic) noise and have density profiles that are accurately represented by  $q$ -Gaussians with  $q < 1$ . Finally, it is shown how intrinsic multiplicative noise allows for the nucleation of swarms away from prominent visual features (basins of attraction) known as swarm markers.

## 1 Introduction

Insect swarms have been the subject of extensive experimental studies [1–12]. Many of their properties are well represented by stochastic trajectory models [11–18]. Interactions between individuals are not explicitly modelled; rather, their net effect is subsumed in a restoring force term. Fluctuations in this resultant internal force that arise partly because of the limited number of individuals in the grouping and partly because of the non-uniformity in their spatial distribution are represented by additive noise terms. Multiplicative noise has only featured once in these analyses and appears to be instrumental when swarms are pulled apart quasi-statically, accounting for the emergence of macroscopic mechanical properties, including a finite Young's modulus and yield strength [8, 16]. Here, I provide evidence that multiplicative noise is prevalent, more generally, in quiescent swarms. I also show how multiplicative noise can delocalize swarms driving a transition from a bounded state wherein individuals occupy a small proportion of the available space to a gas-like state wherein the individuals fill the available space. In accordance with theoretical expectations for the influence of multiplicative noise, aerial density profiles of laboratory

swarms of the non-biting midge *Chironomus riparius* are shown to be well represented by  $q$ -Gaussians with  $q > 1$ . This complements theoretical expectations and observations of wild swarms whose aerial density profiles are well represented by more compact  $q$ -Gaussians with  $q < 1$  [15]. Unlike laboratory swarms, wild swarms are subject to environmental (extrinsic) noise. Some but not all insect swarms form over prominent visual features known as 'swarm markers' (basins of attraction). I show how the presence of intrinsic multiplicative noise allows for the formation of swarms away from swarm markers as reported on by Poda et al. [19]. Poda showed 'that males of two species mosquitoes used visual markers but in different ways: *An. coluzzii* swarm right above the marker whereas *An. gambiae* (s.s.) locate their swarm at a constant distance of  $76.4 \pm 0.6$  cm from a  $20 \times 20$  cm marker in the laboratory setup and at  $206 \pm 6$  cm from a  $60 \times 60$  cm marker in the semi-field setup'.

## 2 Findings

The trajectories of individual insects within a swarm can be accurately represented by Okubo's [1] 1-dimensional stochastic model and 3-dimensional elaborations [11–18]. These models agree with numerous observa-

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tions from carefully controlled, high-precision laboratory experiments. They do, for example, account for the observed emergence of macroscopic mechanical properties similar to solids, including a finite Young's modulus and yield strength [8, 16]; for the observed collective viscoelastic response to applied oscillatory visual stimuli [11]; and for fact that laboratory swarms of the non-biting midge *Chironomus riparius* consist of a core 'condensed' phase surrounded by a dilute 'vapour' phase [9, 14]. These two phases maintain distinct macroscopic properties even through individuals pass freely between them.

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

$$\begin{aligned} du &= -kudt - \omega^2 xdt + \sqrt{2B}d\xi(t) \\ dx &= udt \end{aligned} \quad (1)$$

The first term on the right-hand side of Eq. (1) tends to drive velocities back to their mean zero value.  $k$  is the 'frictional coefficient'. Interactions between the individuals are not explicitly modelled; rather, their net effect is subsumed in a restoring force term (the second term on the right-hand side of Eq. (1)), since observations have suggested that to leading order insects appear to be tightly bound to the swarm itself but weakly coupled to each other inside it [7]. Here, in accordance with observations [1, 2] 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  $\sigma_u^2 = \frac{B}{k}$ . This is consistent with observations of laboratory swarms of the non-biting midge *Chironomus riparius* [2, 13]. Positions are Gaussian distributed with mean zero and variance  $\sigma_x^2 = \frac{\sigma_u^2}{\omega^2}$ . At long times  $t \gg k^{-1}$ , Okubo's [1] model reduces to

$$dx = -k^{-1}\omega^2 xdt + k^{-1}\sqrt{2B}d\xi(t) \quad (2)$$

Okubo [1] tactfully assumed that the stochastic noise is position independent. Here, I assume that the stochastic noise, like the average restorative force, has an additional component that increases linearly with distance,  $x$ , from the swarm centre. In this case, Eq. (2) can be replaced by

$$dx = -k^{-1}\omega^2 xdt + k^{-1}\sqrt{2B}d\xi(t) + k^{-1}\sqrt{2F}xd\xi(t) \quad (3)$$

where  $Fx^2$  is the magnitude of the additional (multiplicative) component of the noise and  $d\xi(t)$  is a second

incremental Wiener process. As it stands, Eq. (3) is ambiguous because the magnitude of the multiplicative noise could be evaluated at the start of each time increment, their mid-points or even their end-points. Here, without loss of generality (see below), the Ito rather than the Stratonovich interpretation of the multiplicative noise is adopted, i.e. the magnitude of the noise is evaluated at the start of each time increment rather at their mid-points. The new term can be construed as noise in the effective spring constant,  $k^{-1}\omega^2$  (and more generally as noise in the strength of the restorative force). The modification is supported by an analysis of pre-existing data for laboratory swarms of *Chironomus riparius* [20] (Fig. 1). In accordance with theoretical expectations,  $\langle dx^2 \rangle = 2(B + Fx^2)dt$ , the laboratory swarms are characterized by  $\langle dx^2 \rangle$  that increase faster-than-linearly with  $x$  and as expected, the increases tend to be most pronounced in smaller, noisier swarms (Fig. 1a).

Probability density functions for position,  $p$ , i.e. density profiles, are determined by the Fokker–Planck equation

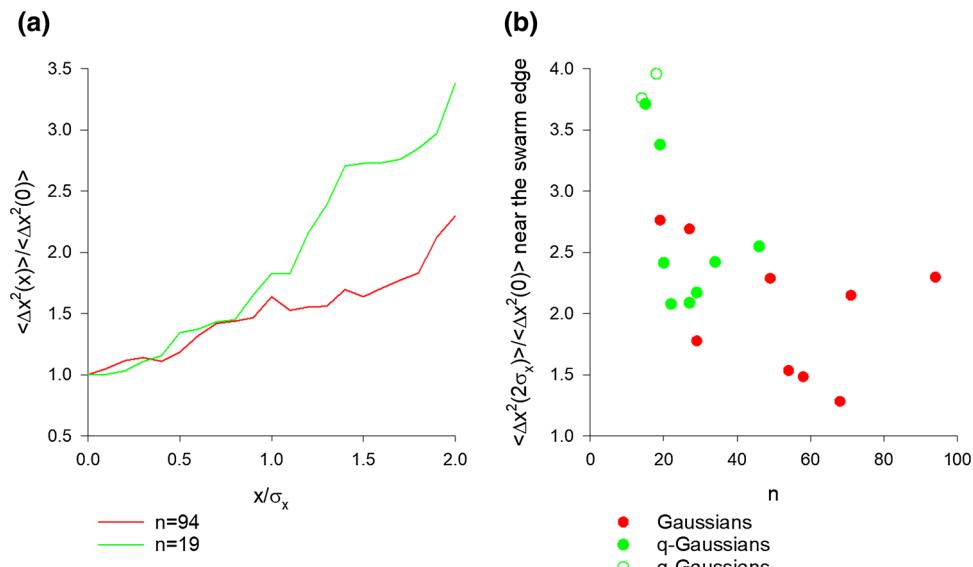
$$\frac{\partial p}{\partial t} = k^{-1}\omega^2 \frac{\partial}{\partial x} (xp) + k^{-2} \frac{\partial^2}{\partial x^2} ((B + Fx^2)p) \quad (4)$$

[21]. Stationary solutions of Eq. (4) are given by

$$p(x) = N \left( 1 + \frac{F}{B} x^2 \right)^{-\frac{\omega^2 k}{2F} - 1} \quad (5)$$

where  $N$  is a normalization constant chosen so that probabilities sum to unity. These solutions are so-called  $q$ -Gaussians with  $\frac{1}{1-q} = -\frac{\omega^2 k}{2F} - 1$ .  $q$ -Gaussians are also obtained under the Stratonovich interpretation but in this case  $\frac{1}{1-q} = -\frac{\omega^2 k}{2F} - \frac{1}{2}$ . This illustrates how the results of one calculus can easily be mapped onto results of the other calculus.  $q$ -Gaussians came to the fore as probability distributions that maximize Tsallis entropy under appropriate constraints. Tsallis entropy is a possible generalization of the standard Boltzmann–Gibbs entropy [22]. A Gaussian distribution is obtained when  $F \rightarrow 0$ , i.e. when  $q \rightarrow 1^+$ . Note also that swarms are predicted to be localized even when the restorative force has mean zero, i.e. when  $\omega = 0$ .

Support for these predictions was found in an analysis of pre-existing data for laboratory swarms of the non-biting midge *Chironomus riparius* [20]. Sinhuber et al. [20] imaged the swarms using 3 hardwired-synchronized cameras located outside of the flight chamber and recording at a rate of 100 Hz. Sinhuber et al. [20] then exploited the redundant information recorded by the cameras, to extract the 3-dimensional positions of each individual in the swarm. Here, these trajectories were used to calculate the distribution of distances of each individual from the swarm centre. These 'density profiles',  $p$ , were then fitted to  $q$ -Gaussians and to Gaussians using maximum likelihood estimation methods,



**Fig. 1** **a** Mean square incremental displacements made in 1 s time increments as functions of distance from the swarm centres,  $x$ , prior to the displacement. Data are shown for laboratory swarms of the non-biting midge *Chironomus riparius* containing on average  $n = 94$  individuals (red line) and  $n = 19$  individuals (green line). Similar results are found for  $\frac{1}{2}$ s and 2 s time increments. Note that the typical speed of a midge in these swarms is about 100 mm/s, and the swarm diameter is about 200 mm. Very similar results are obtained for the y-direction. The vertical (z-) direction was not considered because swarms are elongated in that direction, perhaps because individuals tend to enter and leave

the swarms from above [2]. Data are taken from Sinhuber et al. [20] (Ob1 and Ob18). **b** Mean square incremental displacements made in 1 s time increments near the swarm edges (i.e. at  $x = 2\sigma_x$ ) as a function of the average population size,  $n$ . Data are taken from all 17 dusk time swarms (solid circles) and the 2 daytime swarms (open circles) in the dataset of Sinhuber et al. [20]. The magnitudes of the multiplicative noise and the prevalence of  $q$ -Gaussian density profiles tend to decrease as the average population size increases (see text). Note that smaller stable swarms have been observed in the laboratory but the data have not been published [Private Communication, Michael Sinhuber]

and the best model distribution was identified objectively using the Akaike's information criterion (AIC) which is widely used for statistical inference [23]. The relative likelihoods of the data being either  $q$ -Gaussian or Gaussian distributed are given by the Akaike weights which sum to unity. The Akaike weights vary between 0 (indicating no support for the given distribution) and 1 (indicating complete support for the given distribution).  $q$ -Gaussian density profiles were prevalent in swarms with small population sizes (with less than around 50 individuals) (Figs. 1b, 2a, b). Swarms with larger population sizes have density profiles that are closer to being Gaussian (Figs. 1b, 2c, d). In these asymptotically large swarms [6], the presence of relatively weak multiplicative noise (Fig. 1a) does not result in statistically significant departures from Gaussian density profiles.

It follows from Eq. (5) that as the intrinsic noise,  $F$ , diminishes, there is a transition at  $\omega^2 k = F$  (i.e. at  $q = 5/3$ ) from scale-free,  $\langle x^2 \rangle \rightarrow \infty$ , to scale-finite behaviour, i.e. there is a transition from unbounded spacing-filling swarms to bounded swarms whose size is determined intrinsically. This is broadly consistent with the observations of Puckett and Ouellette [6] who reported that the volume occupied per individual decreases exponentially with population size. Note also that it follows from Eq. (5) that Eq. (4) is effectively a

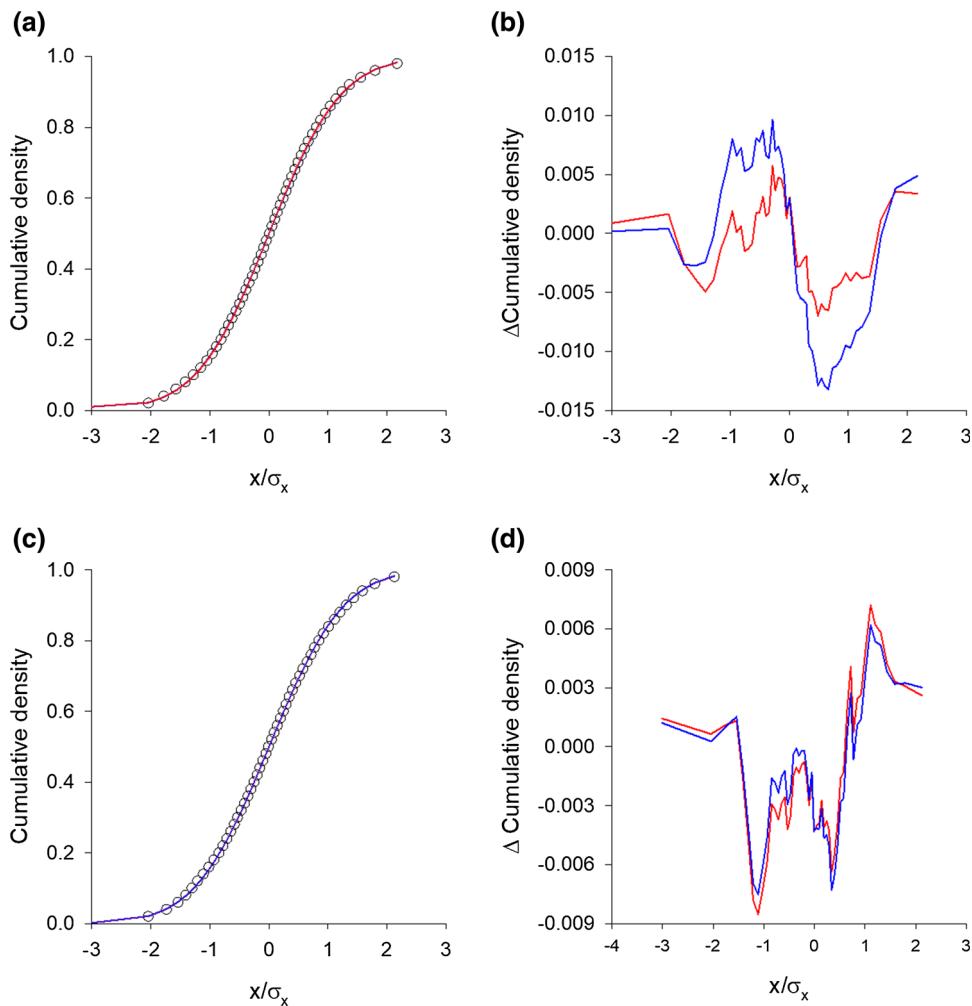
nonlinear Fokker–Planck equation

$$\frac{\partial p}{\partial t} = k^{-1} \omega^2 \frac{\partial}{\partial x} (xp) + k^{-2} \frac{\partial^2}{\partial x^2} (p^\nu) \quad (6)$$

where  $\nu = \frac{k\omega^2}{k\omega^2 + 2F} = 2 - q$ . Similarly, the stochastic model, Eq. (3), can be rewritten as

$$dx = -k^{-1} \omega^2 x dt + k^{-1} p(x)^{\frac{\nu-1}{2}} d\xi(t) \quad (7)$$

The same equations albeit with  $\nu < 1$  describe wild swarms that unlike the laboratory swarms must contend with environmental fluctuations and which display significant coordinated behaviour [3–5]. Reynolds [15] hypothesized that the presence of a fluctuating environment drives the formation of transient, local order (synchronized subgroups) and that this local order pushes the swarm into a new state that is robust to environmental perturbations. In accordance with theoretical expectations, density profiles were found to be well represented by  $q$ -Gaussians with  $q < 1$ . This pathway to  $q$ -Gaussians and stability is distinctly different from the one identified above. Together these results form a seemingly consistent, unified picture of insect swarms. They suggest that as the population size increases, intrinsic noise diminishes and swarms transi-



**Fig. 2** Cumulative density profiles of laboratory swarms of the non-biting midge *Chironomus riparius* are consistent with theoretical expectations. **a** Data (o) for a swarm (Ob18) containing on average 19 individuals are best represented by a  $q$ -Gaussian (red line) with  $q = 1.1$ . The Akaike weight for the  $q$ -Gaussian is 1.00. The best-fit Gaussian is shown for comparison (blue line). **b** Differences between the best-fit  $q$ -Gaussian and the observations (red line) and between the best-fit Gaussian and the observations (blue line). These differences are not discernible on the scale of panel **c**. **c** Data for a swarm (Ob1) containing on average

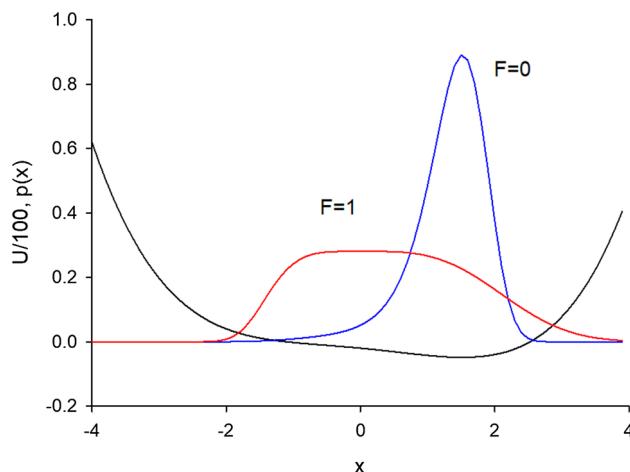
94 individuals are best represented by a Gaussian distribution (blue line). The Akaike weight for the Gaussian is 1.00. The best-fit  $q$ -Gaussian is shown for comparison (red line). **d** Differences between the best-fit  $q$ -Gaussian and the observations (red line) and between the best-fit Gaussian and the observations (blue line). These differences are not discernible on the scale of panel **c**. Cumulative density profiles,  $\int_{-\infty}^x p(\dot{x}) d\dot{x}$ , unlike density profiles *per se* can be plotted without binning of data which is arbitrary and can be distorting. Data are taken from Sinhuber et al. [20]

tion at  $q = 5/3$  from being gas-like to being bound collective states. This process culminates in the formation of Gaussian swarms ( $q = 1$ ). Further increases in stability cannot be brought by further increases in population size; instead, it requires the formation of local order which in turn results in swarms characterized by  $q < 1$ . This unification of laboratory and natural swarms complements that of van der Vaart et al. [12] who showed that environmental perturbations induced correlations. Such correlations are a hallmark of wild swarms [3–5] but are absent in quiescent laboratory swarms [12].

The results also contribute to a long-standing [1] and productive [15, 17, 18, 24–26] analogy between insect

swarms and self-gravitating systems. This is because  $q$ -Gaussians, also known as polytropic distributions, constitute the simplest, physically plausible models for self-gravitating stellar systems [27]. The smaller laboratory swarms with  $5/3 > q > 1$  have similitude with interstellar clouds [28, 29], whereas asymptotically large laboratory swarms with  $q = 1$  are more like globular clusters [27], as claimed by Gorbonos et al. [24].

Aside from the shape of density profiles, multiplicative noise also may account for the formation of swarms of mosquitoes away from swarm markers as reported by Poda et al. [19]. Perhaps for reasons noted above, wild swarms of mosquitoes unlike laboratory swarms



**Fig. 3** In the presence of multiplicative noise, swarms are not centred over asymmetric basins of attraction. In this example, the harmonic potential in Eq. (1) has been replaced by the asymmetric potential  $U = -\frac{1}{2}(x+2)^2 + \frac{1}{4}x^4$  (black line). When  $F = 0$  and  $B = 1$ , the probability density for position,  $p = e^{-U}$ , is centred over the well (blue line). When  $F = 1$  and  $B = 1$ , the probability density for position  $p = e^{-4\sqrt{2}\tan^{-1}(\frac{2+x}{\sqrt{2}})-(x-8)x}/(x^2+4x+6)^{10}$ , is not centred over the well (red line). In this case, the multiplicative noise is parametric noise: the coefficient of the  $(x+2)^2$ -term in  $U$  contains noise as well as a deterministic element

of midges form synchronized subgroups whose size and membership change rapidly over time [30]. These coordinated dynamics can be incorporated into Okubo's model [1], the model used here, through the addition of fission–fission terms [15]. These terms effectively strengthen (renormalize) the average restorative force in Okubo's [1] model.

The formation of swarms away from swarm markers may be of biological significance, allowing for spatial segregation and reproductive isolation of genetically distinct subgroups [31]. As noted by Okubo [1] and Reynolds [16], albeit in different contexts, additive noise spreads individuals around the bottom of a potential well but does not influence the potential well itself, whereas multiplicative noise can create new states of potential. This can occur when the noise-free well is asymmetric as illustrated in Fig. 3 or has multiple minimum. In the latter case, multiplicative noise causes the swarms to be pulled into the spaces between the minimum, as if they are tension [16].

### 3 Conclusions

Okubo's [1] stochastic model and subsequent refinements [11–18] predict accurately many of the properties of insect swarms. Accounting correctly for the emergence of one of the most intriguing properties—tension strength [8]—showed that the long-standing assumption that intrinsic noise is purely additive needed to

be revised [16]. Here, I presented evidence that the effects of multiplicative noise are evident even in the simplest case of quiescent swarms. I showed how this realization brings about a unification of laboratory and wild swarms which have distinctly different properties. In both cases, swarm dynamics are described by the nonlinear Fokker–Planck equation and density profiles are  $q$ -Gaussians. I predicted that as a consequence of multiplicative noise swarms transition from unbounded gas-like phases to bounded phases as their population size increases. In other words, bounded swarms are predicted to have a minimal population size. This may provide new insights into swarm formation, as might the association of the smaller laboratory swarms with interstellar clouds. Finally, I suggested that multiplicative accounts for the formation of swarms away from swarm markers. The various results old and new make clear that multiplicative noise like additive noise is fundamental to the characterization of emergent collective behaviours of insect swarms [32]. This may hold true across taxa, since intrinsic multiplicative noise also induces schooling in small-to-medium size groups ( $10 \leq N \leq 100$ ) of cichlid fish *Eretroplus suratensis*. Jhawar et al. [33].

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**Data Availability Statement** This manuscript has associated data in a data repository. [Authors' comment: The experimental data used in the present study was published by Sinhuber et al. [20].]

### References

1. A. Okubo, Dynamical aspects of animal grouping: swarms, schools, flocks and herds. *Adv. Biophys.* **22**, 1–94 (1986)
2. D.H. Kelley, N.T. Ouellette, Emergent dynamics of laboratory insect swarms. *Sci. Rep.* **3**(1073), 1–7 (2013)
3. A. Attanasi et al., Collective behaviour without collective order in wild swarms of midges. *PLoS Comput. Biol.* **10**, e1003697 (2014a)
4. A. Attanasi et al., Finite-size scaling as a way to probe near-criticality in natural swarms. *Phys. Rev. Lett.* **113**, 238102 (2014)
5. A. Cavagna et al., Dynamic scaling in natural swarms. *Nat. Phys.* **13**, 914–918 (2017)
6. J.G. Puckett, N.T. Ouellette, Determining asymptotically large population sizes in insect swarms. *J. R. Soc. Int.* **11**, 20140710 (2014)
7. J.G. Puckett, D.H. Kelley, N.T. Ouellette, Searching for effective forces in laboratory insect swarms. *Sci. Rep.* **4**, 4766 (2014)
8. R. Ni, N.T. Ouellette, On the tensile strength of insect swarms. *Phys. Biol.* **13**, 045002 (2016)

9. M. Sinhuber, N.T. Ouellette, Phase coexistence in insect swarms. *Phys. Rev. Lett.* **119**, 178003 (2017)
10. M. Sinhuber, K. van der Vaart, N.T. Ouellette, Response of insect swarms to dynamic illumination perturbations. *J. R. Soc. Interface* **16**, 20180739 (2019)
11. K. van der Vaart, M. Sinhuber, A.M. Reynolds, N.T. Ouellette, Mechanical spectroscopy of insect swarms. *Sci. Adv.* **5**, eaaw9305 (2019)
12. K. van der Vaart, M. Sinhuber, A.M. Reynolds, N.T. Ouellette, Environmental perturbations induce correlations in midge swarms. *J. R. Soc. Interface* **17**, 20200018 (2020)
13. A.M. Reynolds, M. Sinhuber, N.T. Ouellette, Are midge swarms bound together by an effective velocity-dependent gravity? *Euro. Phys. J. E* **40**, 46 (2017)
14. A.M. Reynolds, Langevin dynamics encapsulate the microscopic and emergent macroscopic properties of midge swarms. *J. R. Soc. Int.* **15**, 20170806 (2018)
15. A.M. Reynolds, Fluctuating environments drive insect swarms into a new state that is robust to perturbations. *Europhys. Lett.* **124**, 38001 (2018)
16. A.M. Reynolds, On the origin of the tensile strength of insect swarms. *Phys. Biol.* **16**, 046002 (2019)
17. A.M. Reynolds, On the emergence of gravitational-like forces in insect swarms. *J. R. Soc. Int.* **16**, 20190404 (2019)
18. A.M. Reynolds, Insect swarms can be bound together by repulsive forces. *Euro. Phys. J. E* **43**, 39 (2020)
19. S.B. Poda et al., Sex aggregation and species segregation cues in swarming mosquitoes: role of ground visual markers. *Para. Vests.* **12**, 589 (2019)
20. M. Sinhuber, K. van der Vaart, R. Ni, J.G. Puckett, D.H. Kelley, N.T. Ouellette, Three-dimensional time-resolved trajectories from laboratory insect swarms. *Sci. Data* **6**, 190036 (2019)
21. L. Borland, Microscopic dynamics of the nonlinear Fokker–Planck equation: a phenomenological model. *Phys. Rev. E* **57**, 6634–6642 (1998)
22. C. Tsallis, Possible generalization of Boltzmann–Gibbs statistics. *J. Stat. Phys.* **52**, 479–487 (1988)
23. K.P. Burnham, D.R. Anderson, Multimodal inference: understanding AIC and BIC in model selection. *Soc. Methods Res.* **33**, 261–304 (2004)
24. Gorbonos, D. et al. Long-range acoustic interactions in insect swarms: an adaptive gravity model. *New J. Phys.* **18**, 073042 (2016)
25. D. Gorbonos, N.S. Gov, Stable swarming using adaptive long-range interactions. *Phys. Rev. E* **95**, 042405 (2017)
26. D. Gorbonos et al., Similarities between insect swarms and isothermal globular clusters. *Phys. Rev. Res.* **2**, 013271 (2020)
27. A.R. Plastino,  $S_q$  entropy and self-gravitating systems. *Europhys. News* **36**, 208 (2005)
28. F.H. Shu et al., Galactic shocks in an interstellar medium with two stable phases. *Astrophys. J.* **173**, 557–592 (1972)
29. Y. Viala, Structure et critères d’effondrement gravitationnel d’une sphère polytropique d’indice négatif. *Comp. Rend. Acad. Sci. (Paris)* **275B**, 117–120 (1972)
30. D. Shishika et al., Male motion coordination in anophe-line mating swarms. *Sci. Rep.* **4**, 6318 (2014)
31. A. Diabaté et al., Spatial swarm segregation and reproductive isolation between the molecular forms of *Anopheles gambiae*. *Proc. R. Soc. B.* **276**, 4215–4222 (2009)
32. C.A. Yates, Inherent noise can facilitate coherence in collective swarm motion. *Proc. Nat. Acad. Sci.* **106**, 5464–5469 (2009)
33. J. Jhawar et al., Noise-induced schooling of fish. *Nat. Phys.* **16**, 488–493 (2020)