

Rothamsted Repository Download

A - Papers appearing in refereed journals

Van Der Vaart, K., Sinhuber, M., Reynolds, A. M. and Ouellette, N. T.
2020. Environmental Perturbations Induce Correlations in Midge Swarms.
Journal of the Royal Society Interface. 17 (164), p. 20200018.

The publisher's version can be accessed at:

- <https://dx.doi.org/10.1098/rsif.2020.0018>

The output can be accessed at:

<https://repository.rothamsted.ac.uk/item/9755w/environmental-perturbations-induce-correlations-in-midge-swarms>.

© 25 March 2020, Please contact library@rothamsted.ac.uk for copyright queries.

Environmental Perturbations Induce Correlations in Midge Swarms

Kasper van der Vaart,¹ Michael Sinhuber,^{1,*} Andrew M. Reynolds,² and Nicholas T. Ouellette^{1,†}

¹*Department of Civil and Environmental Engineering,
Stanford University, Stanford, California 94305, USA*

²*Rothamsted Research, Harpenden, AL5 2JQ, United Kingdom*

Although collectively behaving animal groups often show large-scale order (such as in bird flocks), they need not always (such as in insect swarms). It has been suggested that the signature of collective behavior in disordered groups is a residual long-range correlation. However, results in the literature have reported contradictory results as to the presence of long-range correlation in insect swarms, with swarms in the wild displaying correlation but those in a controlled laboratory environment not. We resolve these apparently incompatible results by showing the external perturbations generically induce the emergence of correlations. We apply a range of different external stimuli to laboratory swarms of the non-biting midge *Chironomus riparius*, and show that in all cases correlations appear when perturbations are introduced. We confirm the generic nature of these results by showing that they can be reproduced in a stochastic model of swarms. Given that swarms in the wild will always have to contend with environmental stimuli, our results thus harmonize previous findings.

Microscopic interactions in many-body systems generically lead to emergent behavior at the macroscale [1]. In the context of animal behavior, social interactions within animal groups drive phenomena such as flocking [2, 3], where potentially vast numbers of animals move in a directed, coordinated fashion even when executing group-level maneuvers despite the lack of internal leadership or external direction [4–7]. This kind of ordering has been well studied and can be described, at least at a semi-quantitative level, by spin-like models [8–10]. In particular, the degree of order, and thus the effective strength of the collective behavior, can be captured by a simple order parameter, namely the polarization of the group.

Not all collective animal groups, however, show macroscopic order. In particular, although insect swarms are generally assumed to be collective, they lack positional or orientational order. Thus, no meaningful order parameter can be defined to describe the degree of collectivity. It has been proposed that instead the relevant property to look for in swarms is long-range correlation of the velocity fluctuations [11], since such correlations are also observed in other collective animal groups such as bird flocks [12, 13]. However, seemingly contradictory results for the presence of correlations in swarms have been reported: insect swarms observed in the wild appear to exhibit the anticipated long-range correlations [11, 14], while those observed in a controlled laboratory environment do not [15].

Here, we reconcile this apparent contradiction by showing that externally applied perturbations stimulate the appearance of long-range correlation in laboratory midge swarms. The development of correlation is surprisingly insensitive to the type of perturbation applied: we find qualitatively similar results when we subject the swarms to air flows, motion cues, varying illumination, or acoustic signals. This phenomenon is strikingly universal, arising from both behavioral and sensory cues and physical, force-based perturbations. We explain these results in

the context of a generic stochastic swarming model [16–18] that makes no assumptions about the details of how midges respond to specific stimuli. Since swarms in the wild unavoidably experience a dynamic external environment, our findings harmonize what has been reported previously in the literature. The picture that emerges from our results is that long-range correlation is not a result of the interaction between individuals per se but rather arises from the additional influence of the external environment on the swarm. Our results add further support to recent arguments that collective behavior cannot be understood in isolation without considering its environmental context [19, 20].

We addressed these questions by measuring the behavior of laboratory mating swarms of the nonbiting midge *Chironomus riparius*. Full details of our methods, along with data sets for the unperturbed swarms analyzed here, are given in ref. [21]; here, we only describe the laboratory setup briefly. The midges spend their entire life cycle in an acrylic cube measuring 122 cm on a side. In their larval state, the midges live in nine tanks containing water and a cellulose substrate. Near the end of their life cycle, they emerge as flying adults. When not actively swarming, midges sit still on the walls or floor of the enclosure. At laboratory “dawn” and “dusk” (as controlled by a timed circadian overhead light source), male midges spontaneously form swarms, nucleating over a ground-based swarm marker. We image these swarms with three synchronized PointGrey Flea3 cameras positioned outside the enclosure, illuminating the midges with near-infrared LED lamps at a wavelength that they cannot see. 1280×1024 pixel images are acquired at a rate of 100 frames per second; these images are then processed with a predictive particle tracking algorithm to produce three-dimensional trajectories along with time-resolved velocities and accelerations for each midge in the swarm [21].

Given the velocities of all the individual midges, we can

compute the single-time correlation function of the velocity fluctuations (sometimes called the connected correlation function) for our swarms in this controlled environment. Following previous work [11, 14, 15], we define this correlation function as

$$C(r) = \frac{\sum_{i \neq j}^N \delta \mathbf{v}_i \cdot \delta \mathbf{v}_j \delta(r - r_{ij})}{\sum_{i \neq j}^N \delta(r - r_{ij})}. \quad (1)$$

Here, $\delta \mathbf{v}$ is the velocity fluctuation of midge i relative to the instantaneous center-of-mass velocity of the swarm, r_{ij} is the distance between midges i and j , and N is the instantaneous number of midges in the swarm, which changes only slowly with respect to any dynamical timescales of the swarm. As we have reported before [15], correlation functions for these unperturbed swarms have small magnitudes and fall off very rapidly, with correlation lengths on the order of the body length of individual midges. **Although perturbations can, in general, induce global modes such as net compression that would induce spurious correlations, we find that these modes are not present for all of our perturbations. For the other perturbations, these modes only have negligible effect on the respective correlation functions.**

The length scale over which the correlation function decays has played a particularly central role in describing the physics of collective behavior. In flocks of starlings [12] and jackdaws [13], for example, correlations have been reported to be both long-range (persisting over the entire flock) and scale-free (increasing proportionally with the flock size). Similar results have been reported for insect swarms in the wild [11, 14]. Although there is no precise, general definition of a correlation length, we here follow previous work and take the distance r_0 at which $C(r)$ first crosses zero as a measure of this length scale. Although there is some increase of r_0 with swarm size, even for our largest swarms it is still always smaller than the typical nearest-neighbor distance, and thus only a fraction of the total swarm size R_S (defined as the standard deviation of the midge positions relative to the center of mass of the swarm). This result is in agreement with our previous findings for laboratory swarms observed in a smaller enclosure [15].

Swarms in the wild and in the laboratory, however, need not be the same: in natural conditions, insects must contend with a host of externally imposed stimuli that are not present in the controlled laboratory environment. It is possible that at least some of these additional perturbations may induce the longer-range correlations observed in wild swarms. To test this hypothesis, we introduced various types of externally imposed stimuli on our swarms. Midges are sensitive to many external factors, including light [22], sound [23], and motion [18], giving us a range of possible stimuli to test. Here, we report the results of five different applied stimuli.

Chironomids are quite sensitive to sound at frequencies

of a few hundred Hz, near their natural wingbeat frequency. Previously, we showed that playing sinusoidally modulated sound signals to midge swarms induced coherent motion of the swarm center of mass [23]. Here, we drove the swarms with an acoustic signal consisting of pulses of telegraph noise with varying length and amplitude. The telegraph noise was constructed by passing a white-noise signal through a low-pass 700 Hz filter. The pulse length ranged from 0.1 s to 0.3 s and the pause between pulses ranged from 0.25 s to 0.5 s. The noise amplitude was clearly audible over the ambient sound levels in the laboratory, and we varied it only slightly.

Midges are also sensitive to light signals, and dynamically varying illumination tends to change both the kinematics of individual and the swarm density [22]. We applied illumination perturbations by exposing the swarms to an array of LEDs with a periodically varying brightness level controlled by a function generator. We varied both the period of the illumination changes over a wide range (with a median of 2.25 s) and the difference in brightness between bright and dim phases. Neither the period nor the brightness difference had a noticeable effect on the correlations, and so below we simply consolidate all of the data.

In the wild, midge swarms nucleate over ground-based visual features known as swarm markers [24]. In the lab, we position our swarms with an artificial swarm marker—in our case, a simple square of black felt. By mounting this marker on a movable stage, however, we have shown that we can dynamically move and manipulate the swarm by applying an effective shear stress to its base [18, 25]. The marker was attached to a linear stage with a position accuracy of 14 μm (CS Series Belt Drive with NEMA 23 Brushless Servo Motor, Newmark Systems). We moved the marker in two distinct ways: a single abrupt movement, which we refer to as a step shear, and a continuous oscillatory shear. For the step shear experiments, the marker was displaced at a speed of 140.6 mm/s over a distance of 40 cm. After a 5 s pause, it was then displaced in the same fashion in the opposite direction. Data was only analyzed during the movement of the marker and not during the pause. For the oscillatory shear experiments, the marker was moved sinusoidally with frequencies between 0.05 Hz and 0.45 Hz and amplitudes between 2 cm and 10 cm (see ref. [18] for more details). The correlations were again not noticeably affected by the details of the oscillatory shear, and so again we average all of the data together in our analysis.

Finally, wild swarms must also contend with direct mechanical perturbations in the form of, e.g., wind. Thus, we also subjected our laboratory swarms to wind produced by a commercially available fan. The fan was positioned outside of the midge enclosure (with one of the acrylic walls replaced by a plastic mesh) and was pointed directly at the center of the swarm. The mean horizontal wind speed at the center of the swarm was 280 mm/s

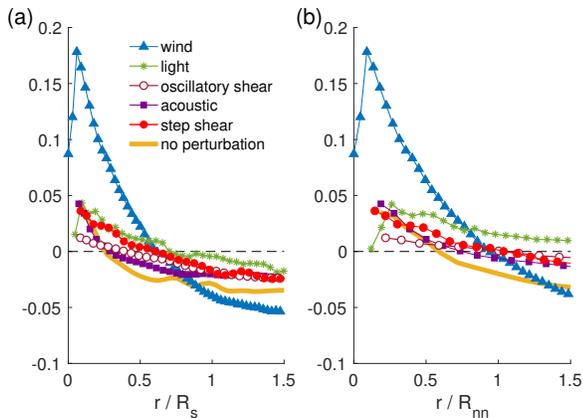


FIG. 1. Correlation functions (as defined in eq. 1) for unperturbed swarms and swarms subjected to various external stimuli. All swarms, perturbed and not, have $N \approx 45$. Data are shown as a function of distance normalized by (a) the swarm radius R_s and (b) the typical body length of a midge, $R_b = 7\text{mm}$. Note that laboratory swarms are typically dilute, resulting in swarm radii that are often of comparable order of the typical nearest-neighbor distances. In all cases, correlation lengths are longer for perturbed swarms.

with small angular and temporal variances, as measured by a two-dimensional sonic anemometer.

In fig. 1, we show correlation functions for swarms with comparable numbers of midges for all of these different stimuli. Although the details of these correlation functions are different for each stimulus, they show a number of similarities. In all cases, they fall off more slowly and have longer correlation lengths than the data for unperturbed swarms of a similar size, suggesting that the presence of the perturbations is inducing longer-range correlation in the swarms. This effect is particularly noticeable for the wind-perturbed swarms, which also show a much stronger degree of correlation in addition to a longer correlation length.

To make the trend of increased correlation length more apparent, we plot in fig. 2 the correlation length r_0 as a function of swarm size N for both unperturbed swarms and swarms subjected to each of the different external stimuli. In all cases, r_0 is longer for perturbed swarms as compared with unperturbed swarms, and in some cases becomes comparable to the swarm size itself. In addition, for perturbed swarms, r_0 appears to grow roughly linearly with N , suggesting that it will continue to increase for larger swarms and remain appreciable compared to the swarm size. In contrast, the correlation length for unperturbed swarms saturates at a value much smaller than the swarm size (though still several body lengths). This result reconciles previously reported findings for laboratory and wild swarms, suggesting that the unavoidable external perturbations in the natural environment drive the emergence of long-range correlation in swarms. That the emergence of correlations appears to be essentially

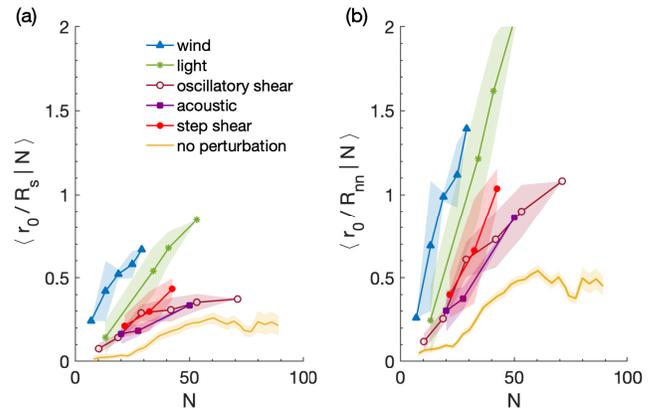


FIG. 2. Mean correlation lengths r_0 as a function of swarm size N for unperturbed swarms and swarms subjected to external stimuli. The shading shows the standard error. r_0 is shown normalized by (a) the swarm radius R_s and (b) the typical body length of a midge, $R_b = 7\text{mm}$. In all cases, correlation lengths are longer for perturbed swarms, and grown roughly linearly with N . In contrast, r_0 appears to saturate for unperturbed swarms.

independent of the type of perturbation strengthens this supposition even more.

Our assertion that long-range correlations are not the result of direct interactions between individuals but instead arise from perturbations finds strong support in the results of numerical simulations of the model of Reynolds *et al.* [26], which produces results that are consistent with numerous observations of laboratory swarms [16, 18]. This model generates positions and velocities of individual midges as solutions of a Langevin equation with an additional restoring force, given by

$$dv_i = \frac{v_i}{T} dt + \langle A_i | \mathbf{v}, \mathbf{x} \rangle dt + \sqrt{\frac{2\sigma_v^2}{T}} dW_i(t) \quad (2)$$

$$dx_i = v_i dt. \quad (3)$$

Here, v_i are the Cartesian components of the midge velocity \mathbf{v} , \mathbf{x} is the midge position, and A_i are the components of the midge acceleration. Given the simplicity of this model, we only seek a qualitative comparison between it and the experimental measurements; thus, we set the correlation timescale T and the root-mean-square speed σ_u to unity. $dW_i(t)$ is an incremental Wiener process that is δ -correlated in time. More details on the model can be found in Reynolds *et al.* [26] and van der Vaart *et al.* [18]. Note that interactions between the individuals are not explicitly modeled; rather, their net effect is subsumed into the restoring force term since, as we have argued previously [26–28], this restoring force is an emergent property of swarms and is the primary macroscopic consequence of the microscopic interactions. All simulated individuals will therefore respond in a similar way following global displacement of the swarm, thus

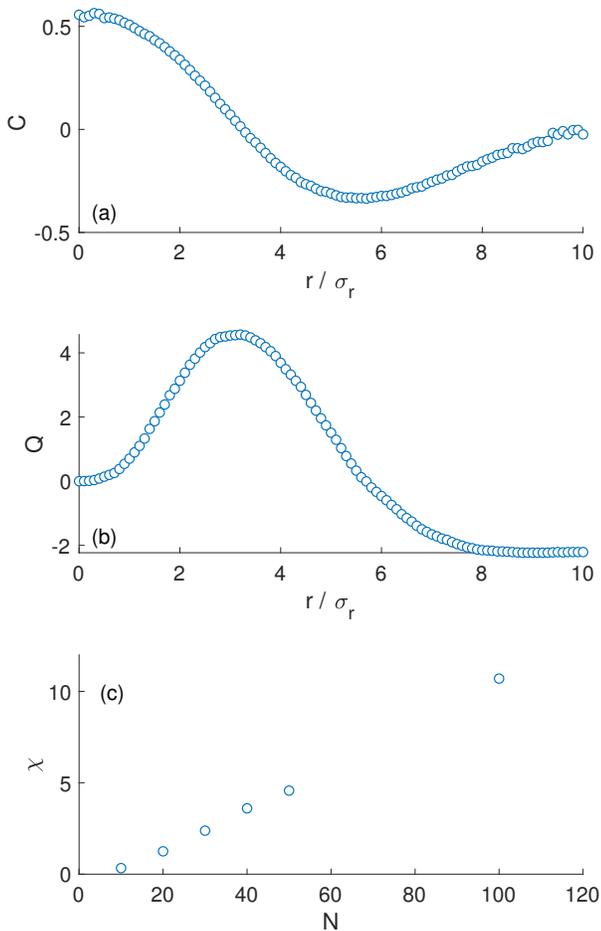


FIG. 3. Emergent correlations in a simulated swarm relaxing back to equilibrium after being instantaneously displaced horizontally from its equilibrium position by 5 a.u. Data were computed from simulations of the model of Reynolds *et al.* [26] with root-mean-square velocity $\sigma_u = 1$, root-mean-square size $\sigma_r = 1$, and velocity autocorrelation timescale $T = 1$, all in a.u. The (a) connected correlation function $C(r)$ and (b) cumulative correlation function $Q(r)$ are shown for swarms containing $N = 50$ individuals. (c) The susceptibility χ increases with swarm size N .

leading to the emergence of correlations in the system. Thus, to model the effect of perturbations on the swarm corresponding to the oscillatory shear experiments, we simulated how swarms relax back to their equilibrium positions (that is, just above their swarm markers) after being displaced simply by forcing the horizontal position of the swarm to oscillate along the horizontal axis.

On short distances the model produces strong positive correlation, indicating that simulated individuals have common velocity fluctuations (fig. 3a). After some neg-

ative correlation at intermediate distances, the correlations relax to zero at large distances. The correlation length r_0 is seen to extend across the entire core of the swarm. Such correlations are entirely absent at equilibrium in the model when no perturbations are applied.

The collective response of the simulated swarm depends on both the span and intensity of the correlation. Attanasi *et al.* [11, 14] combined these two factors into a single calculable property, namely the cumulative correlation up to a scale r . Defined as

$$Q(r) = \frac{1}{N} \sum_{i \neq j}^N \delta \mathbf{v}_i \cdot \delta \mathbf{v}_j \theta(r - r_{ij}), \quad (4)$$

where $\theta(r - r_{ij})$ is the Heaviside function, $Q(r)$ reaches a maximum at r_0 . The maximum $\chi = Q(r_0)$ is a measure of the total amount of correlation present in the swarm, and, if the swarm satisfied the fluctuation-dissipation theorem, would be equivalent to a susceptibility. The large value of χ observed in the simulations (fig. 3b) indicates that despite the lack of collective order, large clusters of simulated midges move coherently when the swarms are displaced and recovering. Moreover, χ for the simulated swarms increases linearly with the swarm size (fig. 3c). The simulated displaced swarms therefore exhibit a near-maximal degree of correlation at all sizes, mirroring observations of swarms in the wild [11, 14].

The strong static correlations and critical-like behavior of wild swarms reported by Attanasi *et al.* [11, 14] prompted Cavagna *et al.* [29] to go one step further and examine fully spatiotemporal correlations. They presented empirical evidence for the emergence of so-called dynamic scaling in wild swarms. We note that we find the same dynamic scaling in our simulations of displaced swarms with no direct interactions. Following Cavagna *et al.* [29], we tested for dynamic scaling in our model by computing the spatiotemporal correlation functions of velocity fluctuations in Fourier space, given by

$$C(k, t) = \left\langle \frac{\sin(kr(t_0, t))}{kr(t_0, t)} \delta \mathbf{v}(t_0) \cdot \delta \mathbf{v}(t_0 + t) \right\rangle, \quad (5)$$

where $r(t_0, t) = |\mathbf{r}(t_0) - \mathbf{r}(t)|$ and associated characteristic timescales τ_k were determined by

$$\int_0^\infty \frac{\sin(t/\tau_k) C(k, t)}{t} dt = \frac{\pi}{4}. \quad (6)$$

For exponential correlation, τ_k is the exponential decay time; and even for more complex forms, τ_k is the most relevant timescale of the system. Cavagna *et al.* [29] evaluated $C(k, t)$ at $k = 1/\xi$, where ξ is the correlation length. Here, the root-mean-square swarm size was used as a proxy for the correlation length. This is reasonable because correlation lengths of wild swarms grow linearly with swarm size [11, 14]. The results (fig. 4)

do not change significantly when the proxy for ξ is increased or decreased by a factor of two. In the simulations, the only other model parameters (the velocity autocorrelation timescale and the root-mean-square velocity) were kept constant across differently sized swarms because they are assumed to be characteristics of individual midges.

In accordance with the analysis of Cavagna *et al.* [29], we find that the spatiotemporal correlation functions collapse onto a single curve when plotted as functions of $k^z t$ and $\tau_k \sim k^{-z}$, where the dynamic critical exponent $z = 1$ (fig. 4). This result suggests that the wild swarms studied by Cavagna *et al.* [29] and our simulated swarms belong to the same dynamic universality class. Here, however, we attribute this dynamic scaling to the effects of perturbations rather than to interactions between the individuals per se.

Externally induced perturbations are inevitable for wild swarms that must contend with a host of environmental disturbances. Here, we have shown that such disturbances generically tend to induce the emergence of correlations in laboratory swarms that closely resemble those reported for wild swarms by Attanasi *et al.* [11, 14]. Such correlations were interpreted as evidence that wild swarms are nearly critical, and tune themselves to be close to a phase transition from disorder to order (though always remaining on the disordered side). Our findings here suggest instead that even when the intrinsic dynamics are always disordered with no hint of criticality, external perturbations can impose an ordered response—perhaps indeed poisoning swarms near a phase transition, though one different from that envisioned by Attanasi *et al.* In this regard, it is interesting to note that the emergent solid-like properties observed in laboratory swarms [18, 25] have also been attributed to the presence of perturbations that move the swarm center of mass [30]. More work thus remains to be done to disentangle the roles of intrinsic dynamics and external stimuli in producing correlations in collective animal groups, and thus to interpret such correlations properly.

The research at Stanford was sponsored by the Army Research Laboratory and accomplished under grant no. W911NF-16-1-0185. The views and conclusions in this document are those of the authors and should not be interpreted as representing the official policies, either expressed or implied, of the Army Research Laboratory or the U.S. government. K.V. acknowledges support from an Early Postdoc.Mobility fellowship from the Swiss National Science Foundation, and M.S. acknowledges support from the Deutsche Forschungsgemeinschaft under grant no. 396632606. 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.

K.V. and M.S. contributed equally to this work.

A.M.R. conceived of the initial idea for unifying laboratory and wild swarm results, and undertook the numerical simulations. K.V. and M.S. ran the experiments and analyzed the data. All authors interpreted the data and wrote the paper.

* Present address: Max Planck Institute for Dynamics and Self-Organization, 37077 Göttingen, Germany

† nto@stanford.edu

- [1] P. W. Anderson, “More is different,” *Science* **177**, 393–396 (1972).
- [2] D. J. T. Sumpter, “The principles of collective animal behaviour,” *Phil. Trans. R. Soc. B* **361**, 5–22 (2006).
- [3] A. Cavagna and I. Giardina, “Bird flocks as condensed matter,” *Annu. Rev. Condens. Matter Phys.* **5**, 183–207 (2014).
- [4] H. Pomeroy and F. Heppner, “Structure of turning in airborne rock dove (*columba livia*) flocks,” *Auk* **109**, 256–267 (1992).
- [5] A. Attanasi *et al.*, “Information transfer and behavioural inertia in starling flocks,” *Nat. Phys.* **10**, 691–696 (2014).
- [6] A. Attanasi *et al.*, “Emergence of collective changes in travel direction of starling flocks from individual birds’ fluctuations,” *J. R. Soc. Interface* **12**, 20150319 (2015).
- [7] H. Ling, G. E. McIvor, J. Westley, K. van der Vaart, J. Yin, R. T. Vaughan, A. Thornton, and N. T. Ouellette, “Collective turns in jackdaw flocks: kinematics and information transfer,” submitted (2019).
- [8] T. Vicsek, A. Czirók, E. Ben-Jacob, I. Cohen, and O. Shochet, “Novel type of phase transition in a system of self-driven particles,” *Phys. Rev. Lett.* **75**, 1226–1229 (1995).
- [9] I. D. Couzin, J. Krause, N. R. Franks, and S. A. Levin, “Effective leadership and decision-making in animal groups on the move,” *Nature* **433**, 513–516 (2005).
- [10] W. Bialek, A. Cavagna, I. Giardina, T. Mora, E. Silvestri, M. Viale, and A. M. Walczak, “Statistical mechanics for natural flocks of birds,” *Proc. Natl. Acad. Sci. USA* **109**, 4786–4791 (2012).
- [11] A. Attanasi *et al.*, “Collective behaviour without collective order in wild swarms of midges,” *PLoS Comput. Biol.* **10**, e1003697 (2014).
- [12] A. Cavagna, A. Cimorelli, I. Giardina, G. Parisi, R. Santagati, F. Stefanini, and M. Viale, “Scale-free correlations in starling flocks,” *Proc. Natl. Acad. Sci. USA* **107**, 11865–11870 (2010).
- [13] H. Ling, G. E. McIvor, K. van der Vaart, R. T. Vaughan, A. Thornton, and N. T. Ouellette, “Costs and benefits of social relationships in the collective motion of bird flocks,” *Nat. Ecol. Evol.* **3**, 943–948 (2019).
- [14] A. Attanasi *et al.*, “Finite-size scaling as a way to probe near-criticality in natural swarms,” *Phys. Rev. Lett.* **113**, 238102 (2014).
- [15] R. Ni and N. T. Ouellette, “Velocity correlations in laboratory insect swarms,” *Eur. Phys. J. Special Topics* **224**, 3271–3277 (2015).
- [16] A. M. Reynolds, “Langevin dynamics encapsulate the microscopic and emergent macroscopic properties of midge swarms,” *J. R. Soc. Interface* **15**, 20170806 (2018).
- [17] A. M. Reynolds, “Fluctuating environments drive insect

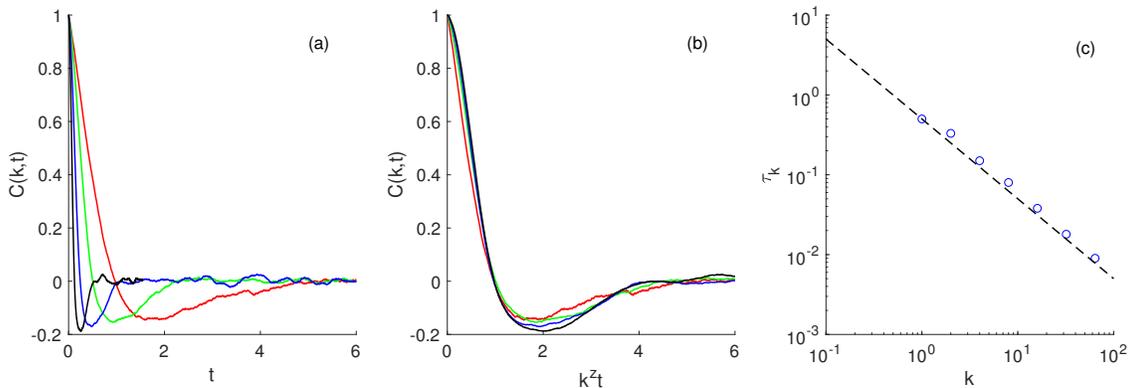


FIG. 4. Predicted dynamical scaling and critical exponent. (a) Normalized temporal correlation functions $C(k, t)$ evaluated at $k = 1/\xi$ where $\xi = \sigma_r$, the root-mean-square size of the swarm. The lines correspond to $\xi = 1$ (red), $1/2$ (green), $1/4$ (blue), and $1/8$ (black). (b) $C(k, t)$ as a function of the scaling variable $k^2 t$ for the same cases shown in (a). (c) Characteristic timescale τ_k computed at $k = 1/\xi$ as a function of k . Predictions are shown for the model of Reynolds *et al.* [26] with root-mean-square velocity $\sigma_u = 1$ and velocity autocorrelation timescale $T = 1$, and with root-mean-square sizes σ_r ranging from 1 to $1/64$ a.u.

- swarms into a new state that is robust to perturbations,” EPL **124**, 38001 (2018).
- [18] K. van der Vaart, M. Sinhuber, A. M. Reynolds, and N. T. Ouellette, “Mechanical spectroscopy of insect swarms,” *Sci. Adv.* **5**, eaaw9305 (2019).
- [19] A. J. King, G. Fehlmann, D. Biro, A. J. Ward, and I. Fürtbauer, “Re-wilding collective behaviour: an ecological perspective,” *Trends Ecol. Evol.* **33**, 347–357 (2018).
- [20] H. Ling, G. E. McIvor, J. Westley, K. van der Vaart, R. T. Vaughan, A. Thornton, and N. T. Ouellette, “Behavioural plasticity and the transition to order in jackdaw flocks,” *Nat. Commun.* **10**, 5174 (2019).
- [21] M. Sinhuber, K. van der Vaart, R. Ni, J. G. Puckett, D. H. Kelley, and N. T. Ouellette, “Three-dimensional time-resolved trajectories from laboratory insect swarms,” *Sci. Data* **6**, 190036 (2019).
- [22] M. Sinhuber, K. van der Vaart, and N. T. Ouellette, “Response of insect swarms to dynamic illumination perturbations,” *J. R. Soc. Interface* **16**, 20180739 (2019).
- [23] R. Ni, J. G. Puckett, E. R. Dufresne, and N. T. Ouellette, “Intrinsic fluctuations and driven response of insect swarms,” *Phys. Rev. Lett.* **115**, 118104 (2015).
- [24] A. E. R. Downe and V. G. Caspary, “The swarming behaviour of *chironomus riparius* (Diptera: Chironomidae) in the laboratory,” *Can. Entomol.* **105**, 165–171 (1973).
- [25] R. Ni and N. T. Ouellette, “On the tensile strength of insect swarms,” *Phys. Biol.* **13**, 045002 (2016).
- [26] A. M. Reynolds, M. Sinhuber, and N. T. Ouellette, “Are midge swarms bound together by an effective velocity-dependent gravity?” *Eur. Phys. J. E* **40**, 46 (2017).
- [27] Douglas H. Kelley and Nicholas T. Ouellette, “Emergent dynamics of laboratory insect swarms,” *Scientific Reports* **3**, 1073 EP (2013).
- [28] Dan Gorbonos, Reuven Ianconescu, James G Puckett, Rui Ni, Nicholas T Ouellette, and Nir S Gov, “Long-range acoustic interactions in insect swarms: an adaptive gravity model,” *New Journal of Physics* **18**, 073042 (2016).
- [29] A. Cavagna *et al.*, “Dynamic scaling in wild swarms,” *Nat. Phys.* **13**, 914–918 (2017).
- [30] A. M. Reynolds, “On the origin of the tensile strength of insect swarms,” *Phys. Biol.* **16**, 046002 (2019).