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Formation and Dissolution of Midge Swarms

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Using external illumination cues, we induce the formation and dissolution of laboratory swarms of the non-biting midge *Chironomus riparius* and study their behavior during these transient processes. In general, swarm formation is slower than swarm dissolution. We find that the swarm property that appears most rapidly during formation and disappears most rapidly during dissolution is an emergent mean radial acceleration pointing toward the center of the swarm. Our results strengthen the conjecture that this central effective force [may be used as an indicator to distinguish when the midges are swarming from when they are not](#).

I. INTRODUCTION

Collective behavior in groups of social animals is widespread in nature, occurring across taxa, in a host of ecological contexts, and for animals with a vast range of degrees of individual intelligence [1]. Biologists have long studied collective behavior, with the goal of understanding why and how animals engage in it and what kinds of advantages it brings both for the individual and the group [2–5]. More recently, physical scientists have also become interested in collective behavior [6], as it is a beautiful example of self-organization far from equilibrium [7] and a strong motivation for studying active matter [8]. This endeavor has been supported by the increasing availability of quantitative empirical measurements of the dynamics of animals engaged in collective behavior. These data have revealed a wide range of non-trivial properties of animal groups, such as scale-free correlations [9, 10] and lossless information transfer [11] in bird flocks and emergent effective viscoelasticity [12, 13] in groups of insects.

Nearly all of these physics-inspired descriptions of collective behavior, however, stem from measurements of animal groups that are either known or assumed to be in steady state. Little is known quantitatively about how animal groups form or disperse and how their properties may vary during these processes. Studying animal groups during these transient periods may help to reveal how the remarkable collective properties of animal groups emerge from the interactions among individuals. More broadly, such studies may help to answer fundamental questions about appropriate signatures of collective behavior [14].

To make progress toward these goals, we studied laboratory swarms of the non-biting midge *Chironomus riparius* during swarm formation and dissolution. In the wild, these midges tend to form swarms at dawn and dusk, and environmental illumination levels provide a behavioral cue to individuals for when to swarm. We were

thus able to induce or disrupt swarming using illumination cues in the laboratory, allowing us to repeatedly generate and dissipate swarms on demand. We find that various swarm properties evolve with similar functional forms during swarm formation and dissolution, but that in general dissolution is much faster than swarm formation. We also find that the formation and dissolution of the swarms is clearly reflected in the rapid establishment and disappearance of an emergent central potential that binds individuals to the swarm. Our results [suggest that this central potential is a good candidate for an indicator of when the midges are actively swarming](#).

II. METHODS

Our laboratory setup and measurement techniques have been documented in detail elsewhere [15], so we describe them only briefly here. Our self-sustaining colony of *C. riparius* midges spend their entire life cycle contained in a cubic enclosure measuring 122 cm on a side. The enclosure contains eight 10-liter tanks filled with dechlorinated, oxygenated water and a cellulose substrate in which midge larvae develop. Adult midges emerge from the development tanks but remain within the enclosure, where they live for a few days before dying; when not swarming, they simply sit still on the walls or floor. The emergence of adults is not synchronized or controlled, so at any given time the enclosure contains a population of an unknown number of adults (not all of whom may participate in swarming) of varying ages.

In the wild, male midges spontaneously form swarms at dawn and dusk that are thought to act as targets for females to find mates [16]. Swarms tend to nucleate over ground-based visual features such as tree roots or bushes [17]. To simulate similar conditions in the laboratory, we illuminate the enclosure on a circadian cycle with an overhead lamp, providing 16 hours of “daytime” (with the lamp on) and 8 hours of “nighttime” (with the lamp off) every day. To encourage swarm nucleation and position the swarms in the enclosure, we place a black metal swarm marker in the center of the floor of the enclosure.

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The location of the swarm marker is fixed for the duration of each experiment. With this setup, we have found that we can reliably generate swarming events that persist for times on the order of 30 minutes when unperturbed.

To measure the behavior of swarming individuals, we use optical imaging. We illuminate the swarm region with LED banks that emit in the near infrared; this wavelength is not visible to the midges [18, 19], but is detectable by our cameras. We image the swarms with three Point Grey Flea 3 1-megapixel cameras arranged in a horizontal plane outside the enclosure. Note that the volume imaged by the camera array is much smaller than the full size of the enclosure. For the results described here, we acquired images at a rate of 100 pictures per second, sufficient to resolve not only the midge position but also their velocity and acceleration [15]. Using the information from the three cameras, we use stereovision and particle tracking to reconstruct the time-resolved kinematic properties of each individual in the swarms [15, 20, 21]. We refer the reader to ref. [15] for sample images and trajectories measured from laboratory swarms, along with available data sets.

As mentioned above, swarm formation in the wild is at least partially cued by the ambient illumination; thus, midges are sensitive to the illumination level. We have shown previously that small changes in background illumination can modulate swarm properties [22]. Here, we impose stronger illumination perturbations that act to disrupt or trigger swarm formation. To do so, we simply mounted an additional ambient light source below the enclosure and turned off the overhead circadian light. Turning this additional light on then triggered the formation of swarms; when it was turned off, swarms dispersed.

Here, we report results for 15 swarm formation experiments and 15 swarm dissolution experiments. To avoid possible memory effects, we conducted formation and dissolution experiments on different days. For the formation experiments, we began recording data as soon as the ambient light was turned off and continued to acquire data for 80 seconds, by which point we observed that the swarms had stabilized to a steady state. For the dissolution experiments, we waited for swarms to form and stabilize and then turned off the light, continuing to record data until the swarms had completely dispersed (after about 20 seconds). The stable swarm sizes are not controllable and were different (though comparable) for each experiment. For the formation experiments, the stable swarm sizes N_∞ were 24, 24, 24, 26, 27, 27, 27, 27, 28, 28, 28, 29, 31, 32, and 33 individuals, where N_∞ was computed by averaging the number of participating individuals over the final 5 seconds of the measurement period. For the dissolution experiments, the initial swarm sizes N_0 were 28, 29, 30, 32, 36, 37, 37, 37, 38, 39, 40, 40, 41, 42, and 52 individuals, where N_0 was computed by averaging the number of individuals over the time span before the light was turned off.

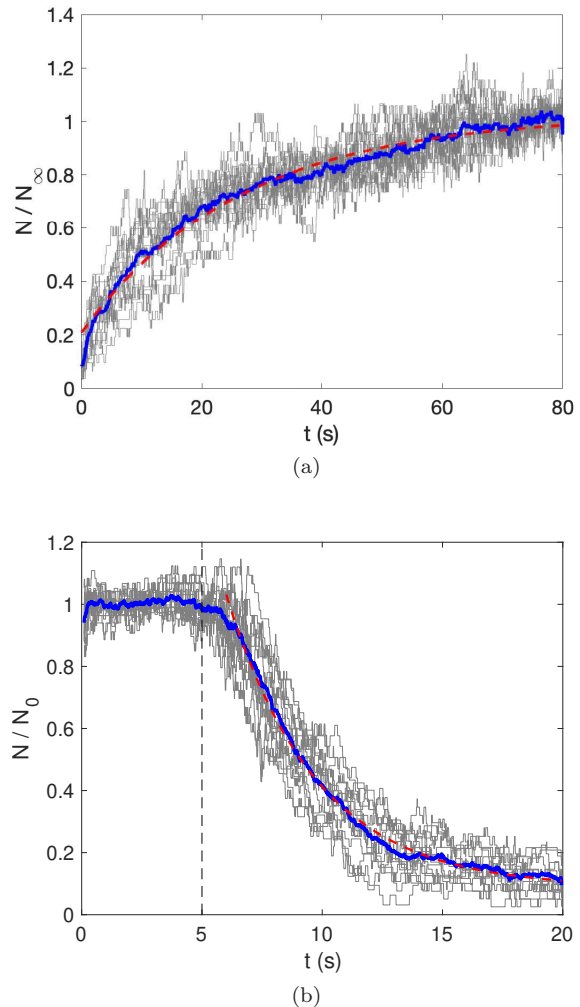


FIG. 1. The number N of individuals in the measurement volume as a function of time for (a) swarm formation and (b) dissolution. Data are normalized by the steady-state swarm sizes given in Sec. II. For formation (a), the light was turned on at $t = 0$; for dissolution (b), it was turned off at $t = 5$ s, as indicated by the vertical dashed line. The data for each individual swarming event are shown by the thin gray lines; the thick blue line is the ensemble average of the individual swarming events. The red dashed lines are fits of eq. 1.

III. RESULTS

In fig. 1, we show the number N of swarming midges as a function of time t for both formation and dissolution. For each swarm, we normalize N by its steady-state value (that is, the values given in the previous section) so that we can meaningfully average the different swarming events together. As can be observed in fig. 1, the shape of the formation and dissolution curves is similar for all swarms regardless of their size. In the formation experiments (fig. 1(a)), the ambient light source was turned on at $t = 0$ s; in the dissolution experiments (fig. 1(b)), the light was turned off at $t = 5$ s. We include data be-

fore turning off the light in the dissolution experiments to confirm that the swarm was in a steady state before the perturbation was applied. As soon as the light turns on in the formation experiments, the number of midges in the swarm steadily grows until saturating. Similarly, the number of midges participating in the swarming steadily diminishes after the light is turned off in the dissolution experiments, after a short time lag. The rate at which the swarm size changes appears to be much faster for dissolution than formation.

To quantify our results, we fit the mean formation and dissolution signals with simple exponential functions of the form

$$f(t) = C \pm e^{-(t-t_0)/\tau}, \quad (1)$$

where C is the asymptotic value of the curve, t_0 is the time at which the growth or decay begins, and τ is the characteristic time scale of the growth or decay. The sign of the exponential term is positive for decay and negative for growth. Although we do not have an *a priori* argument for exponentials, they are convenient choices here because they allow us to extract the characteristic times τ as a way to compare the rates of formation and dissolution quantitatively. From fitting the data in fig. 1, we find τ values of 26.3 ± 0.2 s for formation and 3.75 ± 0.04 s for dissolution. Thus, in agreement with our qualitative observations, swarm dissolution appears to be a much faster process than swarm formation, by a factor of roughly 7.

The evolution of the physical size of the swarm tells a similar story. We quantify the size of the swarm by computing the root-mean-square radial distance $\langle r(t)^2 \rangle^{1/2}$ of each individual in the swarm from the time-averaged center of mass at each time step. The time evolution of $\langle r(t)^2 \rangle^{1/2}$ is shown in fig. 2, where again we have normalized the data for each individual swarm by its steady-state value and then averaged the individual swarming events together. For reference, the steady-state values $\langle r_\infty^2 \rangle^{1/2}$ (for formation) and $\langle r_0^2 \rangle^{1/2}$ (for dissolution) vary with the number of individuals in the swarm, but all lie between roughly 17 and 21 cm in the data sets analyzed here (so that the swarming midges remain far from the enclosure walls at all times during swarming).

Figure 2(a) shows that the swarm radius starts at a large value when the ambient light is turned on, and then relaxes to its steady-state value. This behavior is to be expected, since individuals join the swarm from the outside; while the swarm is forming, most of the individuals are still arriving from outside the bounds of the eventual steady-state swarm and so are at larger-than-normal radial distances. The evolution of $\langle r(t)^2 \rangle^{1/2}$ for swarm dissolution, as plotted in fig. 2(b), shows that once the ambient light is turned off, the reverse process occurs (again after a short time lag). The maximum values of the formation and dissolution curves are roughly the same because they are constrained by the size of our measurement volume. As with the data for the number of individuals shown in fig. 1, the evolution of $\langle r(t)^2 \rangle^{1/2}$

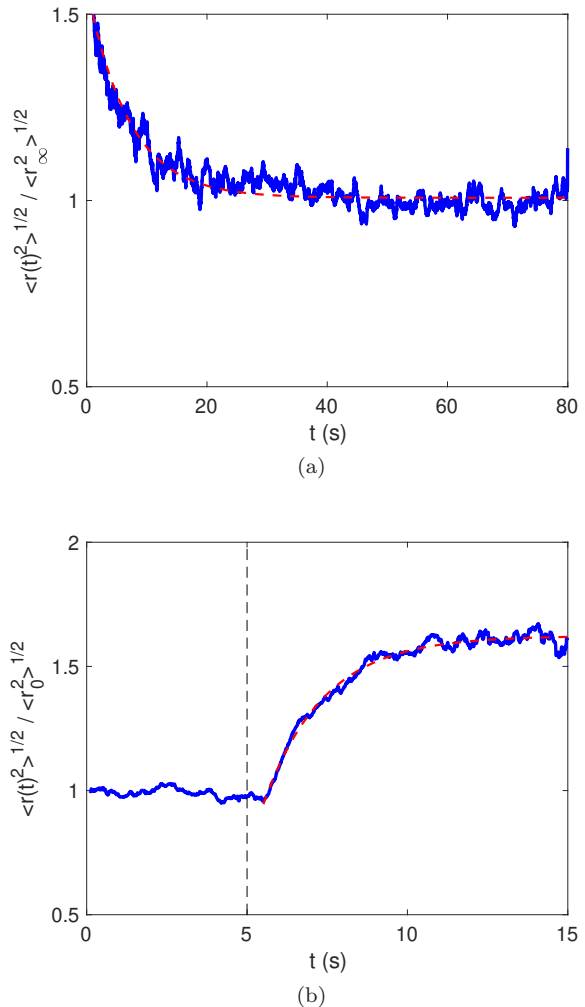


FIG. 2. The swarm physical size, as quantified by the root-mean-square distance of individuals from the time-averaged center of mass $\langle r(t)^2 \rangle$, as a function of time for (a) swarm formation and (b) dissolution. As in fig. 1, the blue solid lines show the ensemble average over all the (normalized) swarming events, and the red dashed lines are fits of eq. 1. Note that we limit the time span over which we report statistics for the dissolution experiments relative to what is shown in figs. 1 and 3 because at long times, there are very few individuals remaining in the measurement volume for some of our experiments. This paucity of samples makes the long-time statistics of the swarm size unreliable, since a single midge in a small swarm leaving the observable volume has a very large effect on the computed swarm size. Similar effects are not as significant for kinematic statistics like the acceleration, since each midge has statistically similar motion.

for both formation and dissolution are well fit by exponentials of the form given in eq. 1. Fits to the data show again that the approach of the swarm physical size to its steady-state value is much slower for formation than the rate at which it grows during dissolution, with characteristic times τ of 7.0 ± 0.1 s for formation and 1.87 ± 0.04 s for dissolution. Note, however, that the change in swarm

radius is significantly faster (by a factor of 2 to 3) than the rate of change of the number of participating individuals. This difference should be expected, though, since swarming midges do not explore the entire volume of the enclosure but rather only a much smaller volume. Thus, even a single midge flying from its perch on the wall to the swarm region in the center of the enclosure would show a rapid change in radial distance.

So far, we have considered only simple physical properties of the swarms that indicate that individuals enter the measurement volume when the light turns on and leave when it turns off. These quantities, however, do not directly give us information about the *collective* behavior of the midges. Indeed, midges must individually and independently make the decision to leave their perches and join the swarm. It is thus natural to ask when the growing number of midges in the measurement volume during swarm formation becomes a swarm and not simply an aggregation, and likewise when the group of midges stops being a swarm during dissolution.

Directly assessing the degree of collectivity of a group of animals remains in general a challenge. For ordered groups like flocks, the net polarization is often used as an order parameter [23, 24]. Polarization, however, always remains low in a disordered group like a swarm [21], and so is not appropriate in this case. It has been argued that long-range velocity correlations are a better general hallmark of collective motion [25, 26]. However, correlations do not in general appear to be present in laboratory swarms [14], and may in fact be more indicative of the collective response to external perturbations rather than being an inherent feature of collective behavior per se [27].

We therefore turn to a simpler way of characterizing the group behavior. We have shown previously that individuals in midge swarms behave as if they are moving in a harmonic potential well with a strength that varies monotonically with the size of the swarm [21, 28]. This kind of emergent potential is not observed in all swarm models (see, e.g., [29]), and so can be seen as a nontrivial property that is associated with real swarms and not with any generic swarm-like system. One signature of this emergent potential well is an inward-pointing mean radial acceleration field with a strength that varies linearly with distance from the swarm center. We note that the shape and strength of this potential well are not set by the swarm marker for swarms that are not too small [30]; instead, the marker primarily sets the location of the center of the potential well [13, 31].

In fig. 3, we show the mean radial acceleration (with radial distance again measured from the time-averaged swarm center of mass) as a function of time for swarm formation and dissolution. Note that since, as a second derivative, the acceleration is a noisy signal, we smooth the acceleration with a running average over 0.2 s windows, close to the estimated response time of the midges [29]. The temporal behavior of the mean radial acceleration resembles that of the number of individuals and

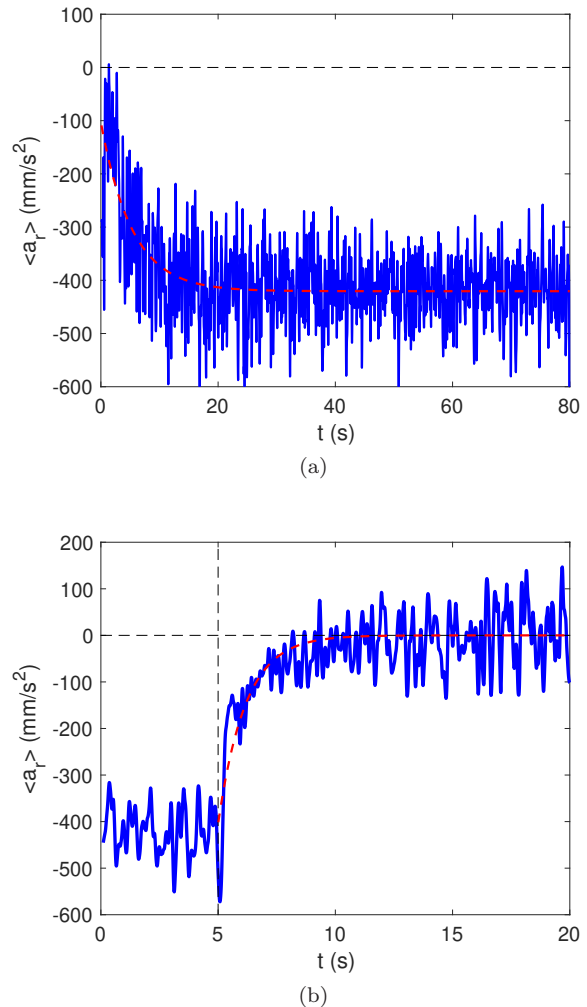


FIG. 3. Mean radial acceleration a_r as a function of time for (a) swarm formation and (b) dissolution. Acceleration signals are smoothed over 0.2 s windows to reduce noise. As in fig. 1, the blue solid lines show the ensemble average over all the (normalized) swarming events, and the red dashed lines are fits of eq. 1.

swarm radius. During swarm formation, the mean acceleration is initially close to zero, but rapidly saturates to a finite, negative value, where the negative sign indicates that it points toward the center of mass. This mean value was similar for all the swarms regardless of size, so it was not necessary to normalize the acceleration signals. (Note that even though the mean acceleration is roughly constant during steady-state swarming, the acceleration signals and trajectories of individual midges are highly variable [15, 30].) During swarm dissolution, this mean acceleration rapidly disappears. Fitting the acceleration curves with the exponential functions given in eq. 1, we find that the characteristic times τ are 5.3 ± 0.3 s for formation and 1.17 ± 0.09 s for dissolution—even faster than the change in swarm radial size. Note too that the exponential function in Eq. 1 fits less well to the mean ac-

celeration during swarm dissolution, so the time constant may actually be an overestimate of the time it takes for the binding potential to vanish once the light turns off. Indeed, an alternative description of the curve in fig. 3(b) could be to argue that the mean acceleration decreases by about a factor of two nearly instantaneously before decaying to zero on a slightly slower time scale.

IV. DISCUSSION AND CONCLUSIONS

By taking advantage of natural behavioral cues, we have shown that by manipulating background illumination levels we can both induce or disrupt laboratory swarms of *C. riparius* midges. This control allowed us to study the transient processes of swarm formation and dissolution in a robust, repeatable way.

During swarm formation, midges gradually entered the swarm from outside on a relatively slow time scale, with swarms reaching their steady-state size after a minute or two. The physical size of the swarm changed more rapidly, though this is to be expected given that midges do not explore the entire enclosure volume while swarming. Swarm formation was also associated with the emergence of a mean central acceleration, which reached its steady-state value on a much faster time scale than the physical size change of the swarm. Its rapid emergence and stabilization suggests that the aggregation of individuals during swarm formation becomes a real “swarm” very rapidly and even when it is composed of only a few individuals. This finding supports our earlier suggestions

that the effective “thermodynamic limit” for swarms is surprisingly small [30].

Swarm dissolution follows similar patterns (in reverse) as swarm formation, though on uniformly faster time scales. In particular, the central acceleration disappears very rapidly, suggesting that the group of midges stops being a “swarm” almost as soon as the external light is turned off and becomes simply a group of independent individuals flying away to rest.

Our results build on our previous findings of emergent central potentials in midge swarms [21, 28], revealing how this potential appears and disappears as swarms form and dissipate. It may be productive in future work to use the emergence of this potential to study, for example, how midges approach the stability boundary between normal swarming and swarm dissolution as illumination levels are varied.

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- [1] J. K. Parrish and L. Edelstein-Keshet, Complexity, pattern, and evolutionary trade-offs in animal aggregation, *Science* **284**, 99 (1999).
 - [2] W. D. Hamilton, Geometry for the selfish herd, *J. Theor. Biol.* **31**, 295 (1971).
 - [3] I. D. Couzin, Collective cognition in animal groups, *Trends Cogn. Sci.* **13**, 36 (2009).
 - [4] D. J. T. Sumpter, *Collective Animal Behavior* (Princeton University Press, Princeton, 2011).
 - [5] D. M. Gordon, The ecology of collective behavior, *PLoS Biol.* **12**, e1001805 (2014).
 - [6] A. Cavagna and I. Giardina, Bird flocks as condensed matter, *Annu. Rev. Condens. Matter Phys.* **5**, 183 (2014).
 - [7] D. J. T. Sumpter, The principles of collective animal behaviour, *Phil. Trans. R. Soc. B* **361**, 5 (2006).
 - [8] M. C. Marchetti, J. F. Joanny, S. Ramaswamy, T. B. Liverpool, J. Prost, M. Rao, and R. Aditi Simha, Hydrodynamics of soft active matter, *Rev. Mod. Phys.* **85**, 1143 (2013).
 - [9] 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 (2010).
 - [10] 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 (2019).
 - [11] A. Attanasi, A. Cavagna, L. Del Castillo, I. Giardina, T. S. Grigera, A. Jelić, S. Melillo, L. Parisi, O. Pohl, E. Shen, and M. Viale, Information transfer and behavioural inertia in starling flocks, *Nat. Phys.* **10**, 691 (2014).
 - [12] M. Tennenbaum, Z. Liu, D. Hu, and A. Fernandez-Nieves, Mechanics of fire ant aggregations, *Nat. Mater.* **15**, 54 (2016).
 - [13] K. van der Vaart, M. Sinhuber, A. M. Reynolds, and N. T. Ouellette, Mechanical spectroscopy of insect swarms, *Sci. Adv.* **5**, eaaw9305 (2019).
 - [14] R. Ni and N. T. Ouellette, Velocity correlations in laboratory insect swarms, *Eur. Phys. J. Special Topics* **224**, 3271 (2015).
 - [15] 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).
 - [16] J. A. Downes, The swarming and mating flight of Diptera, *Annu. Rev. Entomol.* **14**, 271 (1969).
 - [17] A. E. R. Downe and V. G. Caspary, The swarming behaviour of *Chironomus riparius* (Diptera: Chironomidae) in the laboratory, *Can. Entomol.* **105**, 165 (1973).

- [18] M. J. Kokkinn and W. D. Williams, An experimental study of phototactic responses of *tanytarsus barbitarsis* Freeman (Diptera: Chironomidae), *Aust. J. Mar. Freshwater Res.* **40**, 693 (1989).
- [19] A. Ali, G. Ceretti, L. Barbato, G. Marchese, F. D'Andrea, and B. Stanley, Attraction of *chironomus salinarius* (Diptera: Chironomidae) to artificial light on an island in the saltwater lagoon of Venice, Italy, *J. Am. Mosq. Control Assoc.* **10**, 35 (1994).
- [20] N. T. Ouellette, H. Xu, and E. Bodenschatz, A quantitative study of three-dimensional Lagrangian particle tracking algorithms, *Exp. Fluids* **40**, 301 (2006).
- [21] D. H. Kelley and N. T. Ouellette, Emergent dynamics of laboratory insect swarms, *Sci. Rep.* **3**, 1073 (2013).
- [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] 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 (1995).
- [24] 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).
- [25] A. Attanasi, A. Cavagna, L. Del Castillo, I. Giardina, S. Melillo, L. Parisi, O. Pohl, B. Rossaro, E. Shen, E. Silvestri, and M. Viale, Collective behaviour without collective order in wild swarms of midges, *PLoS Comput. Biol.* **10**, e1003697 (2014).
- [26] A. Attanasi, A. Cavagna, L. Del Castillo, I. Giardina, S. Melillo, L. Parisi, O. Pohl, B. Rossaro, E. Shen, E. Silvestri, and M. Viale, Finite-size scaling as a way to probe near-criticality in natural swarms, *Phys. Rev. Lett.* **113**, 238102 (2014).
- [27] K. van der Vaart, M. Sinhuber, A. M. Reynolds, and N. T. Ouellette, Environmental perturbations induce correlations in midge swarms, *J. R. Soc. Interface* **17**, 20200018 (2020).
- [28] D. Gorbonos, R. Iancu, J. G. Puckett, R. Ni, N. T. Ouellette, and N. S. Gov, Long-range acoustic interactions in insect swarms: An adaptive gravity model, *New J. Phys.* **18**, 073042 (2016).
- [29] J. G. Puckett, D. H. Kelley, and N. T. Ouellette, Searching for effective forces in laboratory insect swarms, *Sci. Rep.* **4**, 4766 (2014).
- [30] J. G. Puckett and N. T. Ouellette, Determining asymptotically large population sizes in insect swarms, *J. R. Soc. Interface* **11**, 20140710 (2014).
- [31] R. Ni and N. T. Ouellette, On the tensile strength of insect swarms, *Phys. Biol.* **13**, 045002 (2016).