Regular Article

Velocity correlations in laboratory insect swarms

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Abstract. In contrast to animal groups such as bird flocks or migratory herds that display net, directed motion, insect swarms do not possess global order. Without such order, it is difficult to define and characterize the transition to collective behavior in swarms; nevertheless, visual observation of swarms strongly suggests that swarming insects do behave collectively. It has recently been suggested that correlation rather than order is the hallmark of emergent collective behavior. Here, we report measurements of spatial velocity correlation functions in laboratory mating swarms of the non-biting midge *Chironomus riparius*. Although we find some correlation at short distances, our swarms are in general only weakly correlated, in contrast to what has been observed in field studies. Our results hint at the potentially important role of environmental conditions on collective behavior, and suggest that general indicators of the collective nature of swarming are still needed.

1 Introduction

The large-scale coordinated motion of groups of social animals is one of the wonders of the natural world. Observations of the rapid aerial maneuvers of bird flocks or the splitting and re-forming of fish schools as they evade predators have led researchers to propose that these highly ordered groups may behave as "super-organisms," and may even be considered to possess group cognition [1]. Understanding and modeling collective behavior is thus a topic of great interest [2–4], and models have been successful in predicting the overall pattern and coherent motion that is typical of mobile animal aggregations [5,6].

It is easy to argue that the individuals in bird flocks or fish schools behave collectively because they all move in essentially the same way: up to small variations, all the birds in an organized flock fly in the same direction. In these cases, the overall order of the group can be viewed as a surrogate for the collective behavior itself.

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However, many animal groups, such as the social insects [7,8], certainly behave collectively without displaying this kind of coordinated motion. What then is the statistical signature of collective behavior in these disordered systems?

It has recently been suggested that local correlation rather than global order should be seen as the hallmark of collective behavior [9]. This criterion is certainly fulfilled for groups such as bird flocks (which show a great deal of correlation), but also may hold even for globally disordered aggregations such as insect swarms. Additionally, systems with strong correlations often show enhanced responses to external stimuli [9,10], a property that is also thought to be true for many animal aggregations [11,12].

Here, we therefore consider the pairwise velocity correlation between individuals in laboratory mating swarms of the non-biting midge *Chironomus riparius*. Recent work has reported surprisingly large correlations in swarms of similar insects in the wild [9], suggesting that such swarms may be nearly critical [10]. In contrast, we find very weak inter-individual correlation in our swarms, with correlation lengths on the order of a single body length. We find some dependence of the correlations on swarm size, with small swarms behaving differently from large swarms, but the trend is not sufficient to explain the discrepancy between our results and those previously reported [9]. Although we discuss other possible factors that could be responsible for these differences, our results clearly call both for further parametric study of environmental influences on collective behavior and for more work to define quantitative metrics to characterize the degree of collective behavior in animal groups.

2 Methods

We maintain a laboratory colony of *C. riparius* midges that was initiated from egg sacs purchased from Environmental Consulting and Testing, Inc. The midges spend their entire life cycle in a closed acrylic cubical box measuring 91 cm on a side. The enclosure contains 9 separate tanks, each containing 7 L of oxygenated, dechlorinated water and a cellulose substrate, in which eggs are laid and larvae develop. The water is changed twice weekly, after which the larvae are fed crushed commercial rabbit food. Once the larvae emerge as flying adults (after a period of about two weeks), they remain in the box, typically sitting on the floor or walls unless actively participating in swarming or mating. We note that the emergence of adults is not synchronized; midges at all life cycle stages are always present in the enclosure.

The environmental conditions in the enclosure are controlled. Temperature and humidity are fixed by the laboratory climate-control system; the enclosure is maintained at a constant 21 °C, with no thermal gradients. The solid walls of the enclosure prevent any air currents in the box that could affect swarming behavior. The entire enclosure is illuminated from above by a light on a circadian timer, providing 16 hours of light and 8 hours of darkness daily. Swarming events most frequently occur when the light turns on and off (that is, at "dawn" and "dusk"). Swarms are well known to nucleate over visual features on the ground [13]; in the wild, these features can range from stumps to stream banks. In the laboratory, we provide a $31{\times}31\,cm^2$ black felt "swarm marker" for this purpose. As we have shown previously, the size and shape of the marker can affect the behavior of small swarms (with fewer than 10 or so individuals), but does not play a strong role in the morphology or behavior of larger swarms [14]. We also note that swarms do not tend to fill the entire enclosure, but rather remain far from the walls [15].

To quantify the behavior of the midges in the swarms, we track their motion using three hardware-synchronized 1-megapixel Point Grey Flea 3 cameras arranged outside the enclosure. Each camera captures images at a rate of 100 Hz, sufficient to

resolve the most intense accelerations of individual midges [15]. We typically record images for times between 30 and 60 s. The relative coordinates of the cameras are calibrated using a pinhole camera model and Tsai's method [16], so that the locations of midges found on each camera's image plane (determined via simple thresholding and intensity weighted centroid-finding) can be combined to produce three-dimensional midge coordinates using standard stereoimaging methods [17]. We then combine these three-dimensional positions together in time to generate midge trajectories using a multiframe predictive method described in detail elsewhere [17]. These trajectories can be differentiated numerically to produce the midge velocities and accelerations; to do so, we convolve them with a smoothing and differentiating filter that produces highly accurate results [14,18].

For the results presented here, we analyze the trajectories from 126 swarming events. Most of the swarms are small, containing only a few individuals. 33 of the swarms, however, contain 10 or more individuals, and so are approximately "asymptotically" large, as we have demonstrated previously [14].

3 Results

We are primarily concerned here with the spatial velocity correlations between midges, as an indicator of potential dynamical structure in the swarms. Since we are interested in the relative behavior of the midges, we follow Attanasi et al. [9] and work in the reference frame of the center of mass of the swarm. For each time t, we compute the center-of-mass velocity

$$\mathbf{V}_{CM}(t) = \frac{1}{N(t)} \sum_{\alpha=1}^{N(t)} \mathbf{v}_\alpha(\mathbf{x}, t), \tag{1}$$

where $N(t)$ is the number of midges in the swarm at time t and $\mathbf{v}_\alpha(\mathbf{x}, t)$ is the velocity of midge α (located at spatial position $\mathbf{x}$ at time t) in the laboratory reference frame. We note that $N(t)$ is a time-dependent quantity; the number of midges in the swarm is not fixed, as midges are free to enter or leave the swarm at any time. For each data set, however, the mean value of $N(t)$ is statistically stationary. The velocity of a given midge in the center-of-mass frame is then simply defined as

$$\mathbf{u}_\alpha(\mathbf{x}, t) = \mathbf{v}_\alpha(\mathbf{x}, t) - \mathbf{V}_{CM}(t). \tag{2}$$

With this definition, we write the correlation function of the center-of-mass velocity as

$$C_1(r) = \langle \mathbf{u}_\alpha(\mathbf{x}, t) \cdot \mathbf{u}_\beta(\mathbf{x} + \mathbf{r}, t) \rangle_{\alpha, \beta, t, \mathbf{x}, \hat{\mathbf{r}}}, \tag{3}$$

where the average is taken over midge identity (that is, α and β), time, $\mathbf{x}$ (the position of midge α), and the spatial orientation of the separation vector $\mathbf{r}$ (note that we define $\mathbf{r} = r\hat{\mathbf{r}}$, where r is the magnitude of $\mathbf{r}$ and $\hat{\mathbf{r}}$ is a unit vector in the direction of $\mathbf{r}$).

Even though there is typically no obvious coherent motion in our swarms, it is possible that there is instantaneously some net deformation (say, a global rotation or dilation) of the entire population. Thus, again following Attanasi et al. [9], we also define a second correlation function $C_2(r)$ that attempts to remove any such large-scale deformation. Instantaneously, the position of the center of mass of the swarm is given by

$$\mathbf{X}_{CM}(t) = \frac{1}{N(t)} \sum_{\alpha=1}^{N(t)} \mathbf{x}_\alpha(t). \tag{4}$$
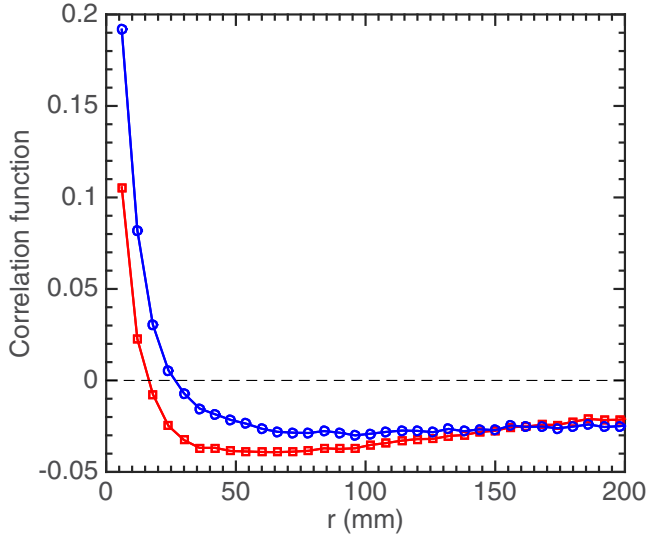
Fig. 1. Velocity correlation functions as measured for the entire ensemble of 126 swarms as a function of the pair separation r. Circles show C_1 (see Eq. (3)), and squares show C_2 (see Eq. (7)). For reference, the typical body length of a male *C. riparius* midge is about 7 mm.

The position of each midge in the center-of-mass frame is therefore

$$\mathbf{y}_\alpha(t) = \mathbf{x}_\alpha(t) - \mathbf{X}_{CM}(t). \tag{5}$$

The quantity $(\mathbf{y}_\alpha(t + \Delta t) - \mathbf{y}_\alpha(t))/\Delta t$, where Δt is the time between two camera frames, is a two-frame estimate of the velocity of midge α in the center-of-mass frame (albeit one that is more susceptible to noise than the multi-frame value computed from our convolution method above). By working directly with the positions, though, we can estimate any large-scale deformation of the swarm, which is more evident from the displacement of the midges than from their velocities [19]. This deformation can be expressed in terms of a rotation $\mathbf{R}$ and a dilation $\mathbf{D}$. We calculate the best-fit $\mathbf{R}$ and $\mathbf{D}$ that map the positions of the ensemble of midges at time t onto those at time $t + \Delta t$ [9] using the Kabsch algorithm (for $\mathbf{R}$) and a subsequent least-square fit (for $\mathbf{D}$). We then define a velocity fluctuation for each midge that removes any net (linear) deformation of the swarm as

$$\delta\mathbf{u}_\alpha(t) = \frac{1}{\Delta t} \left(\mathbf{y}_\alpha(t + \Delta t) - \mathbf{D}\mathbf{R}\mathbf{y}_\alpha(t) \right) \tag{6}$$

and a new correlation function

$$C_2(r) = \langle \delta\mathbf{u}_\alpha(\mathbf{x}, t) \cdot \delta\mathbf{u}_\beta(\mathbf{x} + \mathbf{r}, t) \rangle_{\alpha,\beta,t,\mathbf{x},\hat{\mathbf{r}}}, \tag{7}$$

where the average is taken in the same way as in Eq. (3).

We show both correlation functions computed for the entire ensemble of 126 swarms in Fig. 1. Though there are slight differences between C_1 and C_2, the trend for both is very similar. In each case, the correlation function rapidly decays, crosses zero, and then shows a region of weak anti-correlation. This anti-correlation is likely a signature of the binding of the midges to the swarm. As midges come close to the swarm edge, they tend to turn and fly back toward the swarm center. Conversely, midges near the center of the swarm will typically be oriented outward toward the
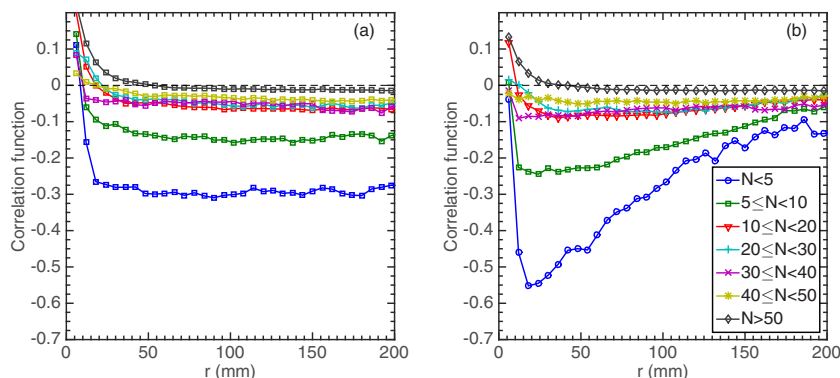
Fig. 2. Velocity correlation functions conditioned on the number of individuals N participating in the swarm, for (a) C_1 and (b) C_2.

swarm edge. Thus, for separations on the order of the swarm radius (typically about 100 mm in our experiments), the correlation function will be negative, since the velocities of pairs with those separations tend to be anti-parallel.

We can use the distance r_0 at which the correlation functions cross zero as a measure of the correlation length [9,10]. We find $r_0 = 26$ mm (for C_1) and $r_0 = 16$ mm (for C_2). For comparison, the typical body length of a male *C. riparius* midge is about 7 mm; thus, we observe correlations that decay on a length scale comparable to the body length of the individual. As we have previously reported [20], individuals only rarely come this close to one another; thus, we interpret our data as revealing that there is essentially no correlation between the velocities of different midges in our swarms. This result is markedly different from what was reported by Attanasi et al. [9,10], who found correlation lengths nearly an order of magnitude larger. We also note that the polarization reported by Attanasi et al. [9,10] (that is, the tendency of the full ensemble of individuals to be oriented in the same direction) is also significantly larger than what we find in our swarms [15].

There are many factors that may potentially lead to the differences we observe. One possibility is the size of the swarms. The largest swarms we measured contained fewer than 100 individuals, and on average our swarms were composed of about 20 individuals. In contrast, the swarms studied in the field by Attanasi et al. [9,10] contained up to 600 insects. To look for a possible systematic dependence of the correlations on the swarm size, we therefore computed the correlation functions conditioned on the number of individuals in the swarm. As shown in Fig. 2, we do see a size dependence of the behavior of the correlation functions: swarms with fewer than about 10 individuals look quite different from larger swarms, consistent with our earlier findings for other statistical measures [14]. In particular, these small swarms show much stronger anti-correlation. But, as we reported previously, swarms this small tend to be strongly influenced by the size and shape of the swarm marker; it may be that the anti-correlation seen in these small swarms is a result of the midges independently exploring the marker. For larger swarms, the size dependence is very weak; and, overall, the trend is not sufficient to explain the differences between our findings and those of Attanasi et al. [9,10].

4 Discussion and conclusions

Our results show that the midges in our swarms are very weakly correlated, with correlation lengths of only a few body lengths. These results are quite different from

what was observed in the swarms studied by Attanasi et al. [9,10]: our swarms appear to be much more disordered, in that any correlation lengths are very small. And yet it is not the case that our midges are not behaving collectively. Particularly for larger swarms, the outer boundary of the swarm is quite sharp (in a statistical sense) and does not line up with the boundary of the swarm marker [14], suggesting that the swarms are true self-organized states. Additionally, the ensemble statistics of the midges suggest the presence of interactions [15]. Thus, it would seem that long-range velocity correlation is not required for collective behavior, just as long-range order is not. Precisely defining what we mean by "collective behavior" via some kind of order parameter thus remains an open question.

The reason for the difference in observed correlations between the two data sets also remains to be determined. We observe very little size dependence on the correlation lengths (or on any other statistical quantities) for reasonably large swarms [14], though we cannot rule out a transition to a different regime for significantly larger swarms such as those studied by Attanasi et al. We have observed qualitatively, for example, that the morphology of large swarms is somewhat different from that of smaller swarms; large swarms are, for example, more columnar [15]. It is also possible that the differences in correlation are due to differences in species; after all, the behavior of different species need not be identical. But we suggest that a more likely explanation may be the influence of external environmental effects. As described above, our swarms form in very controlled conditions, with no temperature gradients, fluid flows, or other dynamic perturbations. In contrast, all of these effects are unavoidably present for swarms studied in the field. In models of collective behavior, the effects of such environmental perturbations can be significant [21], and correlated perturbations could potentially introduce correlated behavior among the individuals; and we have recently demonstrated the ability to induce large-scale coherent motion in our laboratory swarms via controlled external signals [22]. On the other hand, swarming in insects evolved in natural environments, and so the *un*perturbed laboratory situation is in a sense unnatural. Thus, our results indicate that further observation and experimentation are required both to disentangle intrinsic correlation from externally induced effects and to understand the role played by environmental cues in natural collective behavior.

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