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Intrinsic Fluctuations and Driven Response of Insect Swarms

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Animals of all sizes form groups, as acting together can convey advantages over acting alone; thus, collective animal behavior has been identified as a promising template for designing engineered systems. However, models and observations have focused predominantly on characterizing the overall group morphology, and often focus on highly ordered groups such as bird flocks. We instead study a disorganized aggregation (an insect mating swarm), and compare its natural fluctuations with the group-level response to an external stimulus. We quantify the swarm's frequency-dependent linear response and its spectrum of intrinsic fluctuations, and show that the ratio of these two quantities has a simple scaling with frequency. Our results provide a new way of comparing models of collective behavior with experimental data.

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From schools of fish to flocks of birds, collective action [1, 2] conveys many advantages to social animals [3–6]. The emergence of collective behavior from the underlying dynamics of individuals is a central question for understanding the evolution of sociality in animals [7] and for controlling engineered distributed systems [8, 9].

The sight of hundreds or thousands of animals moving in a coordinated way is visually striking [1], and has inspired many models of collective animal behavior. For strongly correlated aggregations such as bird flocks, models often aim to reproduce the observed group-level coherent motion and to characterize the conditions under which ordering will emerge [10]. But some animal groups, such as insect swarms, can behave collectively without ever exhibiting large-scale order [11], and for such cases different descriptions may be needed. Materials, both ordered and disordered, are typically characterized by measuring their response to controlled external perturbations. Probing animal groups in this way, however, is difficult to do. In the field, predator attacks have been used as natural experiments [12, 13], but neither the environmental conditions nor the behavior of the predators can be controlled. Clever laboratory experiments have used robots to perturb aggregations [14, 15], but as such visual stimuli may be highly screened in dense groups [16], it can be difficult to know which animals are aware of the perturbation directly and which are responding only to their neighbors. New techniques are therefore needed to move past purely observational studies of collective animal behavior.

In this Letter, we quantify both the intrinsic fluctuations of laboratory swarms of the non-biting midge *Chironomus riparius* and their response to a natural but controlled external signal—the amplitude-modulated hum of recorded midge wingbeats—that is applied to all of the individuals in the swarm in the same way. Although

these perturbations weakly affect the behavior of individuals, we show that they can strongly impact collective movement. Intriguingly, the swarm response mimics certain features of materials—the microscopic motion of strongly fluctuating individuals produces a macroscopic linear response of the swarm over a range of driving frequencies. Since individual midges inject energy into the swarm, the fluctuation-dissipation theorem for a passive material in equilibrium is unsurprisingly violated. However, by comparing the response of the swarms to driving and the internal fluctuations of free swarms, we can still define a state variable, similar to a frequency-dependent effective temperature, that characterizes their dynamical state. Surprisingly, this state variable has a relatively simple form: a monotonic decay that is consistent with power-law scaling. Our analysis provides a coarse-grained description of the microscopic fluctuations and macroscopic response of a swarm. And by characterizing more subtle information about the swarm dynamics than is contained in the overall group morphology, our results will allow a more detailed comparison between models and experiments.

Mating swarms of *C. riparius* are composed exclusively of males, and can range from a few individuals to many thousands in the wild. These swarms are epigamic; when females approach the swarm, they are chased by nearby males and captured. It is thought that males locate females within the swarm by listening for their characteristic wingbeat sounds [17]: the sound of female wingbeats has its fundamental frequency at about 275 Hz, while the fundamental frequency of male wingbeats is about 575 Hz. Males are thus highly sensitive to acoustic stimuli, a feature we can exploit to perturb them with an external, controlled signal—in this case, the recorded hum of a male midge. Acoustic signals also provide a nearly uniform stimulus to the swarm as a whole, since the speed

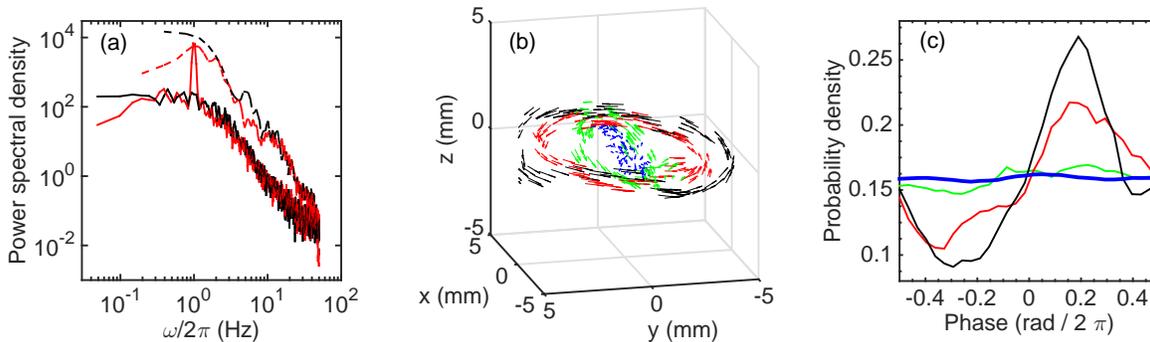


FIG. 1. (color online) (a) Power spectra of one component of the velocity for an individual midge in a swarm (dashed lines) and the center of mass of the swarm (solid lines). Data are shown for the undriven case (black) and for swarms excited by the sound of a male midge sinusoidally modulated at a frequency of $\omega_d/2\pi = 1$ Hz and a maximum intensity of $h_0 = 75$ dB (red). (b) Phase-averaged velocities and trajectories of the center of mass (see eq. (1) for the definition of phase averaging) for swarms driven at $\omega_d/2\pi = 1$ Hz with $h_0 = 0$ (i.e., undriven; blue), 63 dB (green), 68 dB (red), and 75 dB (black). The length of each arrow shows the instantaneous magnitude of the center-of-mass velocity normalized by the maximum observed value for that data set (green: 19 mm/s; red: 35 mm/s; black: 44 mm/s). The sound source lies along the y -axis and points in the positive y direction. (c) Probability density functions (PDFs) of the relative phase of the component of individual midges' motion at the driving frequency for the same cases as in (b). The driving signal is defined to have a phase of 0.

of sound is very fast compared to the speed of a midge, attenuation is weak over the size of a swarm, and the sound arriving at a single midge is negligibly screened by other midges since the size of a midge is very small compared to the sound wavelength. We were therefore able to study laboratory swarms of *C. riparius* under both driven and undriven conditions.

We maintain a laboratory colony of *C. riparius* in a closed cubic enclosure measuring 91 cm on a side. The enclosure contains 9 tanks of dechlorinated, oxygenated water in which larvae develop; adults live in the same enclosure once they emerge. Details of our husbandry procedures are given elsewhere [18, 19]. Adult males spontaneously form swarms twice a day, with sizes ranging from a few individuals up to about 100. Using three hardware-synchronized Point Grey Flea3 cameras, we captured movies of swarms at a rate of 100 frames per second, which we then processed to obtain time-resolved three-dimensional trajectories and kinematics of all the midges in the swarms using techniques we have described in detail before [18, 20].

Unperturbed swarms are roughly fixed in place: even though each individual midge traces out complex flight paths, their erratic motion averages out and produces no net drift. This is evident in, for example, the temporal velocity power spectra of the center of mass of the swarm as compared with single individuals (Fig. 1(a)): the power in the center-of-mass fluctuations is significantly damped relative to the case of a single midge, with no significant spectral peaks. The swarm behavior, however, changes when it is exposed to external acoustic signals. We excited the swarm by placing a speaker roughly a meter from its center (for comparison, typical swarm diameters

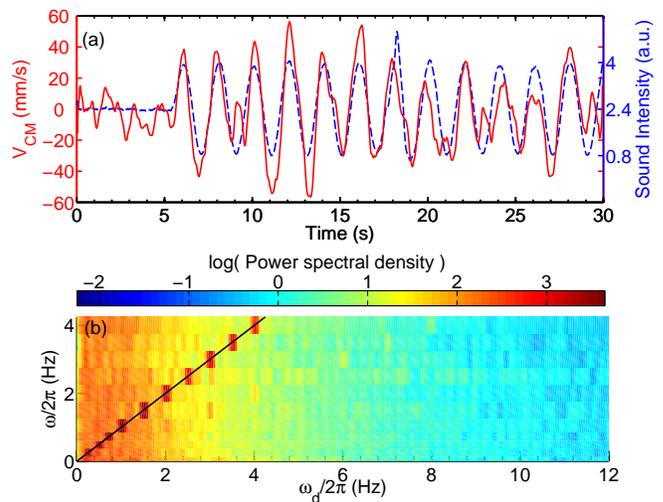


FIG. 2. (color online) (a) Component of the center-of-mass velocity V_{CM} projected along the direction toward the speaker for a sound signal with $h_0 = 75$ dB (4 a.u.) and a modulation frequency of $\omega_d/2\pi = 0.5$ Hz (left axes). The measured sound intensity is shown as a dashed line (right axes). Once the sound is initiated, the variation in V_{CM} tracks the modulation of the acoustic driving. (b) Temporal power spectra of V_{CM} for a range of driving frequencies. At all frequencies we tested, the peak response of the swarm was at the driving frequency. The solid line shows $\omega_d = \omega$.

ters are about 200 mm) and playing back the recorded sound of flying midges. When we played the sound of a female midge, the swarm immediately dissolved as all the males flew toward the speaker and landed on it. When we played the sound of a male midge at a constant inten-

sity, we observed no change in the swarm behavior after a brief, transient dilation at the initiation of the playback. But when we modulated the intensity of the male sound in time by multiplying it by a sinusoidally varying signal of angular frequency ω_d , we observed a clear and repeatable response. The trajectories and power spectra (Fig. 1(a)) of individuals did not significantly change; however, when we averaged over all the individuals, we observed a net response that was manifest as a strong peak in the power spectrum of the swarm's center of mass at the modulation frequency of the external sound (Fig. 1(a)). In space, the center of mass traced out elliptical, oscillatory trajectories with the long axis oriented toward the speaker, moving away from the speaker as the volume increased and toward it as the volume decreased (Fig. 1(b)). Moreover, as the overall sound intensity increased, both the displacement and the speed of the center of mass also increased. This behavior is qualitatively different from the nearly random (although with slightly larger fluctuations in the vertical, gravity direction) dynamics of the center of mass in undriven swarms (Fig. 1(b)).

What is the origin of this group-level response? Figure 1(a) shows that power spectra of individual midges does not significantly change under external driving; additionally, the nature and frequency of pairwise interactions, computed via a time-frequency analysis of relative positions [21], were also unchanged. However, the signature of the driving is quite evident when averaging over the entire swarm. These observations suggest that the swarm-level response may be due to a new coherence in the phases induced by the driving signal. To assess this hypothesis, we measured the probability density functions (PDFs) of the relative phase of the Fourier mode of individual midges at the driving frequency, as extracted from the cross wavelet transform of the midge motion with an appropriate sine wave [22]. As shown in Fig. 1c, this PDF changes from a uniform distribution (that is, phases that are incoherent over the population) with no driving to a distribution that is strongly peaked, albeit with a phase lag from the driving signal. Thus, the smooth orbits of the center of mass we observe under driving are likely due to a driving-induced ordering of the phases of each individual midge.

To examine the swarm-level response in more detail, in Fig. 2(a) we plot an example time series of the center-of-mass velocity V_{CM} projected in the direction of the external speaker for a driving signal modulated at a frequency of $\omega_d/2\pi = 0.5$ Hz. In this example, the peak intensity of the driving signal was $h_0 = 75$ dB, and the sound intensity varied from $0.2h_0$ to h_0 ; for comparison, the background sound level at the swarm location was measured to be roughly 48 dB. Although we measured sound intensities in dB, we set them using linear arbitrary units (a.u.). The scales are related by h_0 (dB) = $62.83(h_0$ (a.u.))^{0.13}, so that 75 dB corresponds

to about 4 a.u.

For the first 5 s of data shown in Fig. 2(a), when the external sound was played at a constant intensity, V_{CM} fluctuated with little temporal structure. But once we began to modulate the sound signal, V_{CM} exhibited clear oscillations at the same frequency as the driving. Power spectra of V_{CM} (Fig. 2b) show that the dominant response of the swarm is indeed at ω_d for all frequencies we tested (up to $\omega_d/2\pi = 32$ Hz). We find that the response is insensitive to the number of midges participating in the swarm, consistent with our previous results [23].

Since the response of the swarm to the driving is approximately periodic with angular frequency ω_d , we define the amplitude U of the response as the peak magnitude of the phase-averaged center-of-mass velocity $\bar{V}_{CM}(t)$, assuming a period of $2\pi/\omega_d$. More precisely, we define

$$\bar{V}_{CM}(t) = \frac{1}{N_T} \sum_{n=0}^{N_T-1} V_{CM} \left(t + \frac{2\pi n}{\omega_d} \right), \quad (1)$$

assuming that we measure for N_T total periods and where $0 \leq t \leq 2\pi/\omega_d$; the response amplitude is then $U = \frac{1}{2} (\max_t \bar{V}_{CM}(t) - \min_t \bar{V}_{CM}(t))$. In general, U is a function of both the frequency ω_d and the intensity h_0 of the driving sound. In Fig. 3a, we show the dependence of U on h_0 for a fixed frequency of $\omega_d/2\pi = 1$ Hz. For large values of h_0 , U is only weakly dependent on h_0 , with no clear trend. But for smaller values (up to about 4 a.u.), U varies linearly with h_0 .

Such linear response is typical of materials driven by external fields, and can be fully described by a single response function, the susceptibility χ [24]. Remarkably, since we observe linear response for the swarm, its dynamics can also be captured in this simple way, even though the swarm is composed of complex, living animals. We write the swarm response as

$$U \sin \omega_d t = \chi(\omega_d) h_0 \sin(\omega_d t - \phi), \quad (2)$$

where $\chi(\omega_d)$ is the susceptibility in the frequency domain (which may be a complex number) and ϕ is a possible phase shift between the driving and the response. Over the range of linear response, the magnitude of the susceptibility $|\chi(\omega_d)| = U/h_0$ is approximately independent of h_0 (Fig. 3(b)). We extract the phase lag ϕ by locating the peak of the temporal cross-correlation between the center-of-mass velocity and the driving sound. As shown in Fig. 3(c), ϕ is roughly independent of h_0 , and is consistent with the PDFs shown in Fig. 1c. We note that unlike in a previous study [11, 25], χ does not describe a tendency for the midges to align their flight directions (and indeed we do not observe any such alignment [18]); rather, it characterizes their mean-field response to the acoustic driving signal.

We next study the frequency dependence of the swarm response by fixing h_0 and varying ω_d . In Fig. 3(d), we

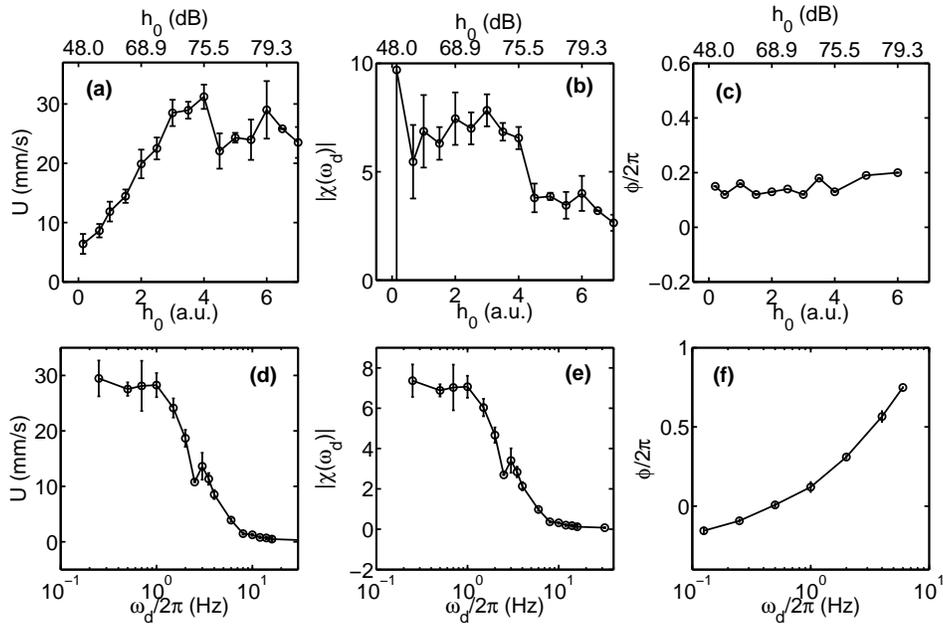


FIG. 3. (a-c) The amplitude U (a), magnitude of susceptibility $|\chi(\omega_d)|$ (b), and phase ϕ (c) of the response as a function of h_0 for a fixed driving frequency of $\omega_d/2\pi = 1$ Hz. h_0 is shown both in dB (top axes) and in arbitrary linear units (bottom axes). (d-f) U , $|\chi(\omega_d)|$, and ϕ as a function of ω_d for a fixed $h_0 = 4$ a.u. (75 dB). Error bars show the standard error computed from measurements of several swarming events.

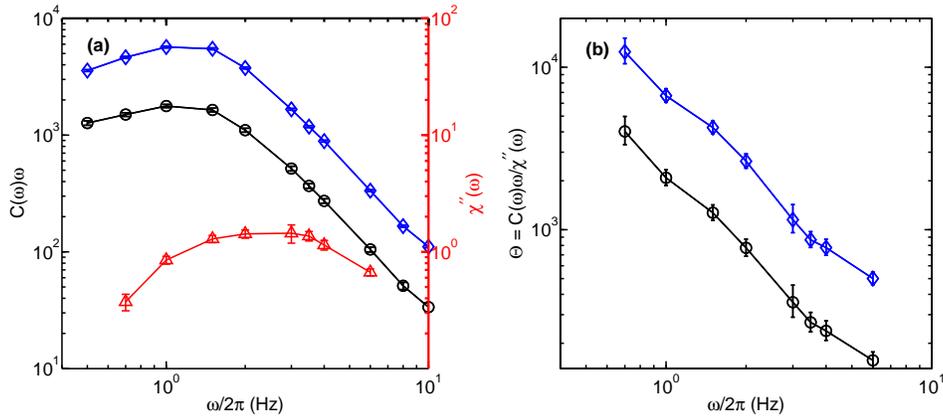


FIG. 4. (color online) (a) The power spectral density $\omega\tilde{C}(\omega)$ of the velocity fluctuations for undriven swarms (left axes). Data are shown for both the center of mass (circles) and individuals (diamonds). Also shown is $\chi''(\omega)$, the imaginary part of the susceptibility (triangles; right axes). $\omega\tilde{C}(\omega)$ and $\chi''(\omega)$ disagree, particularly at low frequencies, violating the fluctuation-dissipation theorem. (b) The ratio of $\omega\tilde{C}(\omega)$ and $\chi''(\omega)$ as a state variable Θ that characterizes the swarm. Θ decays roughly as $\omega_d^{-3/2}$.

show the dependence of U on ω_d for a fixed $h_0 = 4$ a.u. (the largest sound intensity in the linear response regime; results for smaller h_0 are similar). U is approximately independent of ω_d for small frequencies, but falls off rapidly as ω_d increases above 1 Hz. In Fig. 3(e,f), we show $|\chi(\omega_d)|$ and ϕ as functions of ω_d . Although it is insensitive to h_0 , the phase ϕ shows a clear dependence on ω_d ; the swarm response lags far behind the driving for high frequencies, but somewhat leads the driving at low frequencies.

The swarm's simple response to external driving mimics the response of a passive material in an external field. How far does this analogy extend? For a passive material near thermodynamic equilibrium, the fluctuation-dissipation theorem states that the relaxation after external forcing is the same as the relaxation of a spontaneous, intrinsic fluctuation [26]. In our case, it would suggest that $\omega\tilde{C}(\omega) \propto \chi''(\omega)$, where $\tilde{C}(\omega)$ is the Fourier transform of the velocity autocorrelation function in the

absence of driving and $\chi''(\omega) = |\chi(\omega)| \sin \phi$ is the imaginary part of the susceptibility. But in active systems, where the individual components locally inject and dissipate energy [27, 28], the fluctuation-dissipation theorem is often violated, since active processes can cause intrinsic fluctuations that are not related to the system relaxation. Such violations have been observed in living systems such as the cytoskeleton [29, 30], bundles of hair cells [31], and bacterial suspensions [32]. One would therefore expect similar, and likely larger, deviations for insects, as they are both macroscopic and athermal and display complex individual and social behavior.

We test the fluctuation-dissipation theorem in Fig. 4(a), where we plot both $\omega\tilde{C}(\omega)$ and $\chi''(\omega)$. We compute $\tilde{C}(\omega)$ for both the center of mass of the swarms and for individual insects (in each case averaging over 100 swarms), and find that the trends are similar, although the amplitude is higher for individuals. $\omega\tilde{C}(\omega)$ and $\chi''(\omega)$, however, are quite different, particularly at low frequencies. The fluctuation-dissipation theorem is thus violated, as one would expect: active processes that may be associated with individual behavior or social interactions lead to fluctuations that are larger than what they would be for a purely thermal system. Classically, the constant of proportionality between $\omega\tilde{C}(\omega)$ and $\chi''(\omega)$ is related to the temperature. Although swarms are athermal, the ratio of these two quantities can be used to define a state variable Θ , similar to an effective temperature, for the swarm [31]. As shown in Fig. 4(b), Θ falls off with frequency roughly as $\omega_d^{-3/2}$, though our dynamic range is too short to measure the decay rate precisely.

We have demonstrated quantitatively that swarms can exhibit a mean-field linear response to external stimuli, and that we can characterize this swarm-level response with a simple state variable that links the microscopic fluctuations of the swarm with the macroscopic behavior. These results suggest that we may be able to characterize the dynamics of animal groups in terms of macroscopic state variables and constitutive laws instead of low-level interactions, just as we can coarse-grain over molecular interactions in a classical material. And since such state variables are likely much more sensitive to the dynamical details of the aggregations than simply the overall pattern [1], this approach is a natural starting point for more stringent comparisons of models with experiments.

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