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14. ABSTRACT In this report, we describe the results of the research completed with support from this grant. The results are organized along three broad themes: studies of the interactions between individual insects in a swarm; studies of the swarm as a whole; and swarm modeling. At the individual level, we showed that the typical modeling assumption of force-like pairwise interactions is invalid in our swarms, but that more subtle interactions can be identified. At the swarm level, we showed that the swarm state is robust with a surprisingly small number of individuals. We also developed methods for conducting controlled perturbation/response experiments that allow us to extract material					
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Report Title

Final Report: Laboratory and Modeling Studies of Insect Swarms

ABSTRACT

In this report, we describe the results of the research completed with support from this grant. The results are organized along three broad themes: studies of the interactions between individual insects in a swarm; studies of the swarm as a whole; and swarm modeling. At the individual level, we showed that the typical modeling assumption of force-like pairwise interactions is invalid in our swarms, but that more subtle interactions can be identified. At the swarm level, we showed that the swarm state is robust with a surprisingly small number of individuals. We also developed methods for conducting controlled perturbation/response experiments that allow us to extract material-like properties for the swarm. And we began work on a new, data-driven swarm model based on the sensory capabilities of the insects. Copies of all papers written with support from this award are included with this report.

Enter List of papers submitted or published that acknowledge ARO support from the start of the project to the date of this printing. List the papers, including journal references, in the following categories:

(a) Papers published in peer-reviewed journals (N/A for none)

<u>Received</u>	<u>Paper</u>
03/07/2016	7.00 James G. Puckett, Rui Ni, Eric R. Dufresne, Nicholas T. Ouellette. Intrinsic Fluctuations and Driven Response of Insect Swarms, Physical Review Letters, (09 2015): 118104. doi: 10.1103/PhysRevLett.115.118104
03/07/2016	8.00 Rui Ni, Nicholas T. Ouellette. Velocity correlations in laboratory insect swarms, The European Physical Journal Special Topics, (12 2015): 3271. doi: 10.1140/epjst/e2015-50077-5
08/18/2015	3.00 NICHOLAS T OUELLETTE. Empirical questions for collective-behaviour modelling, Pramana, (02 2015): 353. doi: 10.1007/s12043-015-0936-5
08/18/2015	4.00 James G. Puckett, Rui Ni, Nicholas T. Ouellette. Time-Frequency Analysis Reveals Pairwise Interactions in Insect Swarms, Physical Review Letters, (06 2015): 258103. doi: 10.1103/PhysRevLett.114.258103
08/21/2014	1.00 James G. Puckett, Douglas H. Kelley, Nicholas T. Ouellette. Searching for effective forces in laboratory insect swarms, Scientific Reports, (04 2014): 4766. doi: 10.1038/srep04766
08/21/2014	2.00 James G. Puckett, Nicholas T. Ouellette. Determining asymptotically large population sizes in insect swarms, Journal of the Royal Society Interface, (08 2014): 20140710. doi: 10.1098/rsif.2014.0710
TOTAL:	6

Number of Papers published in peer-reviewed journals:

(b) Papers published in non-peer-reviewed journals (N/A for none)

<u>Received</u>	<u>Paper</u>
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TOTAL:

Number of Papers published in non peer-reviewed journals:

(c) Presentations

"Yale-Weizmann Encounter in the Biological, Physical, and Engineering Sciences," Weizmann Institute of Science, Israel (January, 2014) (Invited presentation)

Department of Mechanical Engineering, Stanford University (February, 2014) (invited seminar)

Department of Physics, Duke University (February, 2014) (invited seminar)

APS March Meeting, Denver, Colorado (March, 2014) (2 presentations; 1 invited, 1 contributed)

Conference on "Interaction and Collective Movement Processing," Schloss Dagstuhl, Wadern, Germany (March, 2014) (Invited presentation)

17th US National Congress of Theoretical and Applied Mechanics, East Lansing, Michigan (June, 2014) (contributed presentation)

SIAM Annual Meeting, Chicago, Illinois (July, 2014) (contributed presentation)

School of Mathematical and Statistical Sciences, Arizona State University (September, 2014) (invited seminar)

Department of Physics, University of Massachusetts, Amherst (October, 2014) (invited seminar)

Center for the Study of Ecological Perception and Action, Department of Psychology, University of Connecticut (October, 2014) (invited seminar)

Department of Physics, University of California, Merced (January, 2015) (invited seminar)

American Physical Society Editorial Offices (February, 2015) (invited seminar)

APS March Meeting, San Antonio, Texas (March, 2015) (contributed presentation)

Conference on "Collective Dynamics and Model Verification: Connecting Kinetic Modeling to Data," Arizona State University (April, 2015) (invited presentation)

Okinawa Institute of Science and Technology, Okinawa, Japan (June, 2015) (invited seminar)

EquaDiff 2015, Lyon, France (July, 2015) (invited presentation)

Center for Nonlinear Dynamics, Department of Physics, University of Texas, Austin (October, 2015) (invited seminar)

Conference on "Geometric and Graph-Based Approaches to Collective Motion," Schloss Dagstuhl, Wadern, Germany (January, 2016) (invited presentation)

Department of Physics, Emory University (February, 2016) (invited seminar)

Number of Presentations: 20.00

Non Peer-Reviewed Conference Proceeding publications (other than abstracts):

Received Paper

TOTAL:

Number of Non Peer-Reviewed Conference Proceeding publications (other than abstracts):

Peer-Reviewed Conference Proceeding publications (other than abstracts):

Received Paper

TOTAL:

Number of Peer-Reviewed Conference Proceeding publications (other than abstracts):

(d) Manuscripts

Received Paper

08/18/2015	5.00	Rui Ni, James G. Puckett, Eric R. Dufresne, Nicholas T. Ouellette. Intrinsic Fluctuations and Driven Response of Insect Swarms, Physical Review Letters (accepted) (03 2015)
08/18/2015	6.00	Rui Ni, Nicholas T. Ouellette. Velocity correlations in laboratory insect swarms, European Physical Journal Special Topics (submitted) (03 2015)

TOTAL: 2

Number of Manuscripts:

Books

Received Book

TOTAL:

Received Book Chapter

TOTAL:

Patents Submitted

Patents Awarded

Awards

N/A

Graduate Students

<u>NAME</u>	<u>PERCENT_SUPPORTED</u>
FTE Equivalent:	
Total Number:	

Names of Post Doctorates

<u>NAME</u>	<u>PERCENT_SUPPORTED</u>
Rui Ni	0.55
FTE Equivalent:	0.55
Total Number:	1

Names of Faculty Supported

<u>NAME</u>	<u>PERCENT SUPPORTED</u>	National Academy Member
Nicholas T. Ouellette	0.05	
FTE Equivalent:	0.05	
Total Number:	1	

Names of Under Graduate students supported

<u>NAME</u>	<u>PERCENT SUPPORTED</u>
FTE Equivalent:	
Total Number:	

Student Metrics

This section only applies to graduating undergraduates supported by this agreement in this reporting period

The number of undergraduates funded by this agreement who graduated during this period: 0.00

The number of undergraduates funded by this agreement who graduated during this period with a degree in science, mathematics, engineering, or technology fields:..... 0.00

The number of undergraduates funded by your agreement who graduated during this period and will continue to pursue a graduate or Ph.D. degree in science, mathematics, engineering, or technology fields:..... 0.00

Number of graduating undergraduates who achieved a 3.5 GPA to 4.0 (4.0 max scale):..... 0.00

Number of graduating undergraduates funded by a DoD funded Center of Excellence grant for Education, Research and Engineering:..... 0.00

The number of undergraduates funded by your agreement who graduated during this period and intend to work for the Department of Defense 0.00

The number of undergraduates funded by your agreement who graduated during this period and will receive scholarships or fellowships for further studies in science, mathematics, engineering or technology fields:..... 0.00

Names of Personnel receiving masters degrees

<u>NAME</u>
Total Number:

Names of personnel receiving PHDs

<u>NAME</u>
Total Number:

Names of other research staff

<u>NAME</u>	<u>PERCENT SUPPORTED</u>
FTE Equivalent:	
Total Number:	

Sub Contractors (DD882)

Inventions (DD882)

Scientific Progress

See Attachment.

Technology Transfer

Final Report
Grant W911NF-13-1-0426
Laboratory and Modeling Studies of Insect Swarms

Nicholas T. Ouellette
Department of Civil and Environmental Engineering, Stanford University

Overview

The overarching goal of this project was to advance our understanding of collective behavior, in both natural and artificial systems, by acquiring highly resolved empirical data for swarming insects and then using these data to guide and validate models. The first year of the project was primarily devoted to data acquisition and the characterization of free swarms. Although we made progress on unraveling the local interactions that generate the global collective behavior, doing so proved to be quite challenging. Thus, in the second year of the project, we developed exciting new tools for *driving* the swarms with controlled perturbations and measuring the response. These novel methods allowed us for the first time to characterize precisely properties of the swarm at the group level, thereby providing much stronger constraints for models than had previously been available. Our results both provide deeper insight into the physics that governs insect swarming and point the way to a number of exciting new directions for future study.

Over the course of this award, the research was carried out by PI Nicholas Ouellette and postdoctoral researchers James Puckett (supported by internal Yale funds) and Rui Ni. All three have since left Yale; Ouellette is now an Associate Professor of Civil and Environmental Engineering at Stanford University, Puckett is now an Assistant Professor of Physics at Gettysburg College, and Ni is now an Assistant Professor of Mechanical and Nuclear Engineering at Pennsylvania State University.

Below, we summarize the principle results of the research supported by this grant, similar to what was reported earlier in the two Interim Progress Reports filed.

Scientific Results

Broadly, the results of this research are organized along several themes: studies of the interactions between individuals, studies of the swarm as a group, and work on modeling. Additionally, to enable the analyses discussed below, we collected a database of quantitative measurements several hundred swarming events, both free and subject to controlled perturbations. In addition to what we have learned so far from studying this database, we anticipate that more can be gleaned from it; and additionally, we have begun to share this data with other researchers, in an effort to build a strong community of like-minded researchers to make progress on the challenging questions posed in this field.

1. Interaction Rules

The generally accepted picture of collective animal behavior is that low-level, *local* interactions between individuals percolate upscale and lead to the

macroscopic behavior of the aggregation. Animal aggregations are thus expected to be distinct from other distributed systems (particularly engineered systems) that are organized around top-down control. Understanding how animals achieve robust, stable macroscopic states with only bottom-up self-organization is thus one of the holy grails of the field, with the hope that understanding this process in animal groups will allow us to exploit it in engineered applications.

But as discussed by the PI in an essay published with support from this award [Ouellette 2015], determining the interaction rules from empirical measurements of real animals is a challenging inverse problem: we must use the information about how each animal moved to understand *why* it moved in the way it did. This problem is made yet more difficult to solve if the interaction rules are not constant in time—that is, if the individuals have behave in different ways at different times. Models can thus be a useful guide in approaching this complex problem: if we have an expectation for what we are looking for, we can constrain the way we try to solve it.

Many different models of collective animal behavior have been proposed, but most share several common features. The field is currently dominated by models that treat each individual in the group as a point agent that interacts with others via social “forces” that take the same form as physical Newtonian forces. This kind of model is very appealing, since we have a great deal of intuition about how forces behave and how to treat them mathematically. Additionally, it has been shown that effective-force-based models can qualitatively reproduce many of the morphologies seen in animal groups in nature by tuning the balance of a long-range attraction (keeping the group bound together), a short-range repulsion (keeping the group from collapsing to a point), and an intermediate-range tendency toward alignment (promoting overall ordering of the group) [Couzin *et al.* 2002].

Since in these models social interactions are treated as forces, their effect should be apparent in the acceleration of the individuals, via an assumed form of Newton’s second law. We therefore studied the acceleration statistics of the midges to look for signatures of social interactions, and to calibrate the strength and balance of any effective forces in our swarms [Puckett *et al.* 2014]. Our results, however, were somewhat surprising. We found clear evidence for a very short-range (about a wingspan distance) repulsion; however, these repulsive events were extremely rare. We also found no evidence for a long-range attraction to other insects (see Fig. 1a), even though the swarms remained tightly bound together. And, in addition, our results for the real swarms are significantly different from simulations of a swarming model (Fig. 1b). Instead, our results paint an unexpected picture of the swarm behavior. Insects remain bound to the swarm via some kind of effective attraction, though this attraction is not pairwise. Inside the swarm, however, the insects behave as nearly free particles, and at the mean-field level are very close to particles in an ideal gas. Measurements of the mean-free path suggest that the swarms are at the same time tightly confined (since the mean-free path is on the order of the swarm size) and dilute (since the mean-free path is on the order of the mean inter-insect spacing).

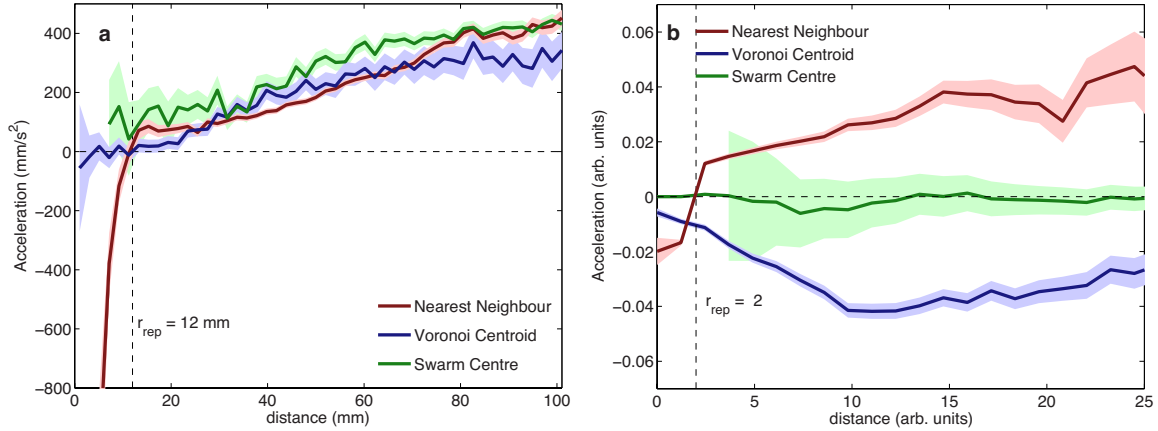


Figure 1. (a) Mean acceleration of one midge in the direction of its nearest neighbor (red), the most empty space nearby (blue), given by the nearest Voronoi centroid, and the center of the swarm (green), as a function of separation distance. Negative values indicate repulsive interactions, while positive values are attractive. Midges show a clear nearest-neighbor repulsion at very short range; these mean-field acceleration statistics, however, do not distinguish between the effects of other midges, empty space, or the center of the swarm. **(b)** The same statistics as calculated from a simulation of the swarm model of Couzin *et al.* 2002. The statistics from the model are qualitatively different from those measured in the experiment. Figure taken from Puckett *et al.* 2014.

But just because we could not identify simple, acceleration-level interactions does not mean that there are no interactions present in the swarms. And indeed, qualitative observations of the swarms did appear to suggest the existence of pairwise interactions. These interactions, however, also seem to be highly transient, which would explain why they did not have a strong effect on simple mean-field averages.

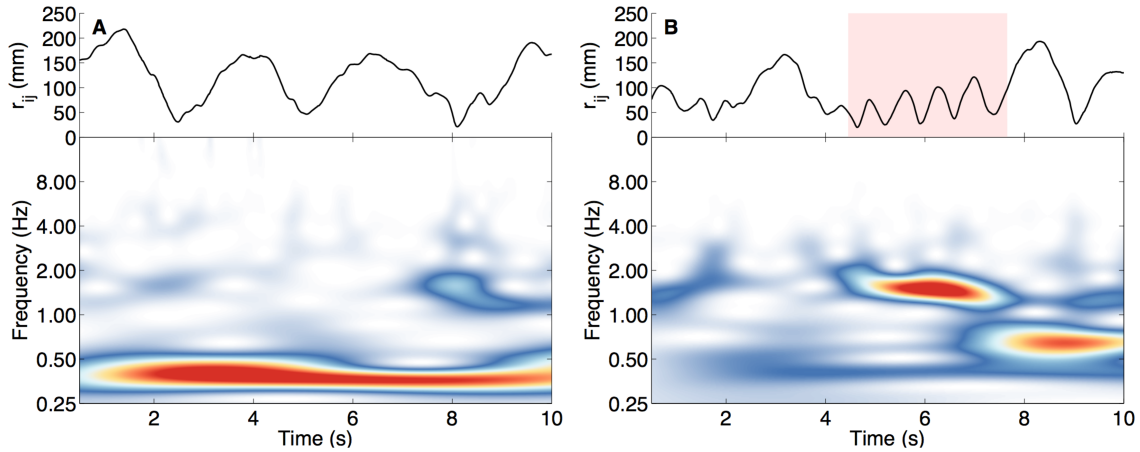


Figure 2. Time-frequency analysis of the relative distance between midge pairs. (A) Time series for a randomly chosen pair as well as its continuous wavelet transform (CWT; bottom panel). Nearly all of the power in the signal for this non-interacting pair is at low frequencies. **(B)** Time series and CWT for an interacting pair. In the shaded region, the distance oscillates nearly harmonically with significant power only at frequencies higher than 1 Hz. Figure taken from Puckett *et al.* 2015.

We therefore designed a wavelet-based time-frequency analysis to identify such transient interactions, as long as they modified the frequency structure of the insect flight trajectories over some non-zero length of time. Using this method, we were indeed able to measure and characterize pairwise interactions in our swarms

[Puckett2015]. As shown in Fig. 2, these interactions took the form of relatively high-frequency and nearly harmonic oscillations in the relative distance between pairs of midges. And although they were transient, they were not necessarily rare; we found that midges spend about 15% of their time, on average, engaged in these interactions. We have hypothesized that these interactions serve the function of helping the midges to assess the gender of their interaction partner. Midges are known to do this by listening to wingbeat sounds, which occur at different frequencies for males and females. Our speculation (which remains to be tested) is that the midges may be using some kind of lock-in amplification by modulating their distance to their interaction partner at a controlled frequency in order to isolate its (quiet) wingbeat sounds.

In addition to this targeted study looking for a particular type of interaction with a specific frequency signature, we also looked more generally for evidence of coordination in the swarms by studying the spatial velocity correlation functions. We were motivated by recent work on wild insect swarms that reported surprisingly long-range correlations [Attanasi *et al.* 2014a,b]. In swarms of midges of similar species to ours, the authors observed correlation lengths of nearly 20 cm, more than 4 times the typical distance between nearest neighbors. Given this result, they suggested that such correlation is the true signature of collective behavior even in an animal group like an insect swarm that does not show overall order.

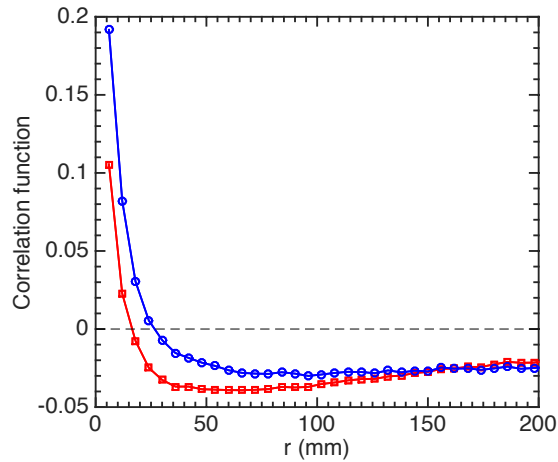


Figure 3. Spatial velocity correlation function measured in our swarms. Blue circles show the raw correlation function; red squares show the correlation function after accounting for large-scale rotation and dilation, as defined by Attanasi *et al.* [Attanasi *et al.* 2014a,b].

When we measured the identical statistics in our swarms, however, we found a very different result: our correlation lengths were an order of magnitude smaller [Ni & Ouellette 2015]. As shown in fig. 1, we measured a correlation length of 16 mm, or about two body lengths—and *smaller* than the typical nearest neighbor distance of about 35 mm. Thus, we find barely any correlation in the midge velocities. The difference between our results and those of Attanasi *et al.* remain something of a mystery. We believe, however, that the stronger correlation they observed may be due to external uncontrolled effects such as air currents or

light patterns, since their swarms were measured in the field whereas ours are in a controlled laboratory environment. Similar to the phase-locking we describe below, external effects can indeed lead to coherent signals in swarms.

2. Statistics at the Swarm Level

When the insects in our laboratory colony swarm, the number of participating individuals is not fixed or consistent; rather, each swarming event is different. Our enclosure does not allow us to reach extremely large swarms (the largest we have measured contained about 90 individuals); it does, however allow us to explore the *small* number limit. Using our swarm database, we therefore posed a simple but unexplored question: how many insects does it take to make a swarm? In other words, when do the statistics of the aggregation cease to depend on the number of individual insects present?

We used trajectory data for swarms containing as many as 60 individuals and as few as a single insect. Calling a single insect a “swarm” is certainly questionable; however, we observed that these single insects executed trajectories and maneuvers that were qualitatively indistinguishable from the trajectories of individuals in much larger swarms. We then examined various statistics, including measures of the spatial structure of the swarms, the insect velocities, and the path lengths between large changes in direction, as a function of swarm size. In all cases, we found that as soon as the swarms contained about 10 individuals, the statistics saturated to a constant value. Statistically, then, our results show that a swarm of 10 is indistinguishable from a swarm of 60 or more. We also examined the effect of external visual cues on swarms of varying size, and found similar results [Puckett & Ouellette 2014].

These results have wide-ranging implications. From an experimental standpoint, they show that our relatively small laboratory experiments provide information that is also valid for the much larger swarms that can sometimes be observed in the wild. Our results impose a strong constraint on modeling as well, requiring that models converge to stable results with only a few individuals: a model that requires thousands of agents, for example, cannot accurately describe our swarms. And finally, from an engineering standpoint, our results are very promising and support the feasibility of using collective animal behavior as a design tool, since even a small number of agents can produce useful, stable collective behavior.

But perhaps the most exciting line of research we pursued during this award can be broadly categorized as exploring and defining a new kind of swarm “thermodynamics.” Traditionally, models of collective motion have been validated by studying the group morphology they produce: a model of flocking birds, for example, will be judged successful if each agent moves in the same direction. As we have shown, however, morphology alone is not a good indicator of model correctness [Puckett *et al.* 2014]: it is simply not sufficient or detailed enough information. Many different kinds of models can produce nearly identical group morphology, and they cannot all be simultaneously correct.

Animal aggregations are often considered to have well defined group-level properties and to behave as “super-organisms,” even though they are composed of individual, independent animals that do not behave according to simple physical laws. Aggregations have thus captured the attention of the community of physicists and applied mathematicians working on so-called active materials. Following some of their work, we were thus motivated to ask a simple question: if an insect swarm can be considered to be a kind of “material,” what are its material properties? As any materials engineer knows, this question cannot be answered by passive observations alone: for example, a cube of jello and a cube of acrylic can look similar, even though they have very different properties.

To describe a material properly, one needs to know various thermodynamic properties, such as state variables, response coefficients, and constitutive laws. Measuring such quantities requires true experiments rather than simple observations: we need to be able to perturb the system in a known way and measure its response. These kind of experiments are quite difficult to do for real animal groups, particularly in the wild. Over this past year, however, we have developed some ways to do them for our laboratory swarms, and have found fascinating results [Ni *et al.* 2015].

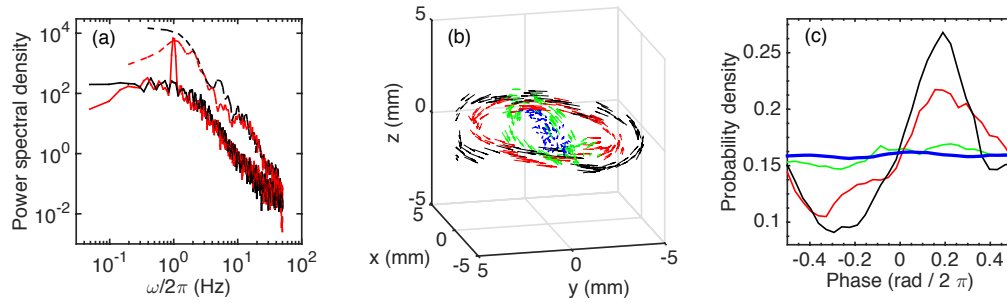


Figure 4. (a) Power spectra of one component of the velocity for an individual midge (dashed lines) and the center of mass of the swarm (solid lines). Data are shown for the undriven case (black) and for swarms excited by the sound of a male midge sinusoidally modulated at a frequency of 1 Hz and a maximum intensity of 75 dB (red). (b) Phase-averaged velocities and trajectories of the center of mass for swarms driven at 1 Hz with maximum intensities of 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. Figure taken from Ni *et al.* 2015.

Since midges respond to acoustic signals, our first set of experiments involved driving the swarms with sound. We recorded the sound of a flying male midge, and played it back to developed swarms via an external speaker. If we played the sound at a fixed volume, we saw no response (aside from a transient excitation and relaxation when the sound was initiated). But when we modulated the sound amplitude sinusoidally in time, we saw a clear signal at the group level: as shown in fig. 4, the motion of the center of mass of the swarm changed from being random to following well defined, smooth elliptical trajectories, and its power spectrum showed a strong peak at the driving frequency. We were able to

find evidence that the mechanism for this change was a kind of phase-locking of each individual to the external driving signal.

The response of the center of mass we measured occurred at the same frequency as the external sound, and its amplitude increased linearly with the sound loudness. We were thus able to apply linear response theory to define a frequency-dependent susceptibility. Using a fluctuation-response relation, this susceptibility in turn allowed us to measure an effective temperature for the swarm, albeit one that was frequency dependent. The implications of the particular form of the effective temperature are not yet known; but this is, to our knowledge, the first such study in a real animal group, and provides data that can be used for a much more stringent test of models than anything that has been known previously.

3. Swarm Modeling

Since our swarms do not show clear signatures of interactions in the mean-field acceleration [Puckett *et al.* 2014a], their dynamics cannot be captured by traditional agent-based models that assume a combination of pairwise attraction, repulsion, and alignment social forces. And since a number of swarm-level statistics are reminiscent of an ideal gas (including a nearly Maxwell-Boltzmann speed distribution [Kelley & Ouellette 2013] and an exponential free-path distribution [Puckett *et al.* 2014]), it is tempting to model the swarm to leading order as a collection of essentially non-interacting random walkers in some kind of confining potential (to keep the swarm cohesive). In such a model, interactions would be essentially non-existent, and the insects would be only very weakly coupled.

An alternative, and we believe more biologically reasonable approach, is to instead realize that similar macroscopic effects can appear if all the insects are in fact *strongly* coupled, in the sense that each insect feels the effects of all the others. Working in collaboration with Prof. Nir Gov at the Weizmann Institute of Science in Israel, we have been developing such a model. Unlike earlier descriptions of collective motion that are based on high-level assumptions of social tendencies, our model is based on the actual sensing capabilities of the insects. As stated above, we know that midges are highly sensitive to sound, and that the inter-individual interactions are mostly likely acoustic. Over the size of a typical swarm, acoustic damping due to air friction is negligible; thus, the sound produced by one midge falls off only geometrically. If we model each individual as a point emitter, the acoustic intensity will thus decay according to an inverse-square law—just like a gravitational field. Making the additional ansatz that each midge is attracted to its neighbors with a strength that is proportional to the sound it detects, we can thus model the swarm as a self-gravitating cluster. The n -body gravity problem is well known to admit chaotic solutions, and so the model can reproduce complex individual trajectories; and in addition, an overall swarm cohesion is a natural consequence of the formulation of the model.

To make a tighter connection to the midge biology, we introduce one more feature to the model: as is often the case with biological sensors, we assume that

the midges adapt their acoustic sensitivity to the overall sound level. Specifically, we assume the common fold-change detection mechanism [Shoval *et al.* 2010], also known as Weber’s law. With this final assumption, the effective force on midge i due to midge j can be written as

$$\mathbf{F}_{\text{eff}}^i = C \sum_j \hat{\mathbf{r}}_{ij} \frac{1}{|\mathbf{r}_i - \mathbf{r}_j|^2} \left(\frac{R_{\text{ad}}^{-2}}{R_{\text{ad}}^{-2} + \sum_k |\mathbf{r}_i - \mathbf{r}_k|^{-2}} \right),$$

where C is an overall coupling strength, $\mathbf{r}_i$ is the position of midge i , $\hat{\mathbf{r}}_{ij}$ is a unit vector pointing from midge i to midge j , and R_{ad} is a length scale over which adaptivity occurs. Since this force involves a sum over all midges in the denominator of the term in parentheses, it is inherently many-body, and cannot be decomposed into a sum of pairwise interactions. Thus, the results from the model mirror what we observe in the swarms, where the acceleration statistics do not show a signature of pairwise interactions. With this model, however, we can reproduce more subtle features of the swarm, including the swarm-size scaling of the strength of the effective harmonic trap that binds the midges to the swarm [Kelley & Ouellette 2013] and the shape of the velocity and acceleration distributions. A paper outlining the model and these preliminary results is currently in preparation. With these model predictions in hand, we can then look for these effects in the actual insect swarms, as a way to benchmark the model much more carefully than would be possible from considering, e.g., swarm shape alone.

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*References marked with * acknowledge support from this award.*

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