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14. ABSTRACT

The goals of this project were to develop a laboratory system for quantitatively measuring the flight trajectories of swarming insects and to use the resulting data to evaluate currently used models of collective behavior. We were successful in completing both goals, leading to the first highly resolved, statistically robust data sets for insect swarms, which we mined for statistical information, and to an evaluation of canonical swarming models, which were shown to be lacking for describing real swarming data.

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Final Report: Characterization and Modeling of Insect Swarms Using tools from Fluid Dynamics

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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)

Received		Paper
06/03/2014	1.00	Nicholas T. Ouellette, Douglas H. Kelley. Emergent dynamics of laboratory insect swarms, Scientific Reports, (01 2013): 1073. doi: 10.1038/srep01073
06/03/2014	2.00	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
TOTAL:	**2**	

Number of Papers published in peer-reviewed journals:

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

Received	Paper
TOTAL:	

Number of Papers published in non peer-reviewed journals:

(c) Presentations

Invited presentations at:

Department of Mechanical Engineering, University of Pennsylvania
Max Planck Institute for Dynamics and Self-Organization, Goettingen, Germany
SIAM Conference on Applications of Dynamical Systems, Snowbird, Utah

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

<u>Received</u>   <u>Paper</u>

TOTAL:

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

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

<u>Received</u>   <u>Paper</u>

TOTAL:

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

(d) Manuscripts

<u>Received</u>   <u>Paper</u>

TOTAL:

Number of Manuscripts:

Books

<u>Received</u>   <u>Book</u>

TOTAL:

<u>Received</u>   <u>Book Chapter</u>

TOTAL:

Patents Submitted

Patents Awarded

Awards

Graduate Students

<u>NAME</u>	<u>PERCENT_SUPPORTED</u>	Discipline
Nidhi Khurana	0.30	
FTE Equivalent:	**0.30**	
Total Number:	**1**	

Names of Post Doctorates

<u>NAME</u>	<u>PERCENT_SUPPORTED</u>
James G. Puckett	1.00
FTE Equivalent:	**1.00**
Total Number:	1

Names of Faculty Supported

<u>NAME</u>	<u>PERCENT_SUPPORTED</u>	National Academy Member
Nicholas T. Ouellette	0.00	
FTE Equivalent:	**0.00**	
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

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

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Names of Personnel receiving masters degrees

NAME

Total Number:

Names of personnel receiving PHDs

NAME
Nidhi Khurana
Total Number: 1

Names of other research staff

NAME	PERCENT_SUPPORTED

FTE Equivalent:
Total Number:

Sub Contractors (DD882)

Inventions (DD882)

Scientific Progress

See Attachment

Technology Transfer

None.

Grant W911NF-12-1-0517
Characterization and Modeling of Insect Swarms Using Tools from Fluid Dynamics

Nicholas T. Ouellette
Department of Civil and Environmental Engineering, Stanford University
[Formerly Department of Mechanical Engineering and Materials Science, Yale University]

Overview

The large-scale scientific objective of this project was to develop tools to measure, characterize, and ultimately understand the collective behavior of animal groups. In nature, animal groups display collective motion at all size scales, from single-celled organisms to whales, and in all environments, on land, in the air, and underwater. Nature has found that collective motion is an efficient, robust solution to a wide range of biological problems. By studying a particular example of collective behavior—mating swarms of the flying midge *Chironomus riparius*—we aimed to understand how the large-scale behavior arises from the local interaction rules, to characterize what these rules are for this insect, and to lay the groundwork for harnessing this kind of collective behavior for engineering applications by developing models of swarm behavior. The specific goals of this project were to develop capabilities for acquiring high quality empirical data on the motion of *C. riparius* midges in laboratory swarms and to compare the results of these studies with canonical swarming models.

This project was successful in both of these goals, and led to the publication of two journal articles acknowledging support from the grant. The research was carried out at Yale University in the lab of PI Nicholas Ouellette (now an Associate Professor of Civil and Environmental Engineering at Stanford University), and the grant supported the training of postdoctoral researcher James Puckett (now an Assistant Professor of Physics at Gettysburg College) and graduate student Nidhi Khurana (now a researcher at the CDC).

Scientific Results

Empirical Measurements of Swarms

With support from this grant, we developed a laboratory experiment that allowed us to measure quantitatively the trajectories and associated kinematics of each individual midge in swarms ranging from a few individuals up to nearly one hundred. The results of our experiments represent the most highly resolved data on swarming insects ever recorded to date.

The midges spent their life cycle inside a cubic enclosure measuring 91 cm on a side. The floor of the enclosure held 9 open tanks containing several liters of dechlorinated, aerated water, a cellulose substrate, and midge larvae. When the midges matured, they emerged as flying adults; during this life cycle stage, they typically spent their time resting on the walls of the enclosure. Twice a day, at "dawn" and "dusk" (indicated by the cycling of circadian light source above the enclosure), male midges

spontaneously formed mating swarms. During these mating displays, females occasionally entered the swarms, were caught by males, and subsequently deposited fertilized egg masses back in the development tanks. The swarms were allowed to develop freely with no external controls; the one exception was the introduction of a ground-based "swarm marker" to encourage swarm nucleation and to place the swarm in a convenient location.

Once swarms were established, they were imaged at 100 frames per second by a set of three Photron Fastcam SA-5 cameras arranged outside the enclosure. These images were processed using algorithms originally designed to study turbulent fluid flows [Ouellette *et al.* 2006] to reconstruct the trajectories of each individual in the swarm. From these time-resolved trajectories, accurate velocities and accelerations could be computed, allowing us access to all the kinematic information in the swarm.

These methods and the results of an initial analysis of 10 swarming events were reported in [Kelley & Ouellette 2013]. This study laid the groundwork for our future exploration of insect swarms. We considered the essential statistical properties of the swarm at three different kinematic levels: the statistics of swarm structure and midge positions, the velocity statistics, and the acceleration statistics.

We found that the gross structure of the swarm was highly repeatable, and that they are somewhat elongated along the vertical (gravity) axis. The number density of the swarms appeared to be dynamically set and constant across swarming events of different sizes. However, even though the swarms appeared highly disordered by eye, the distribution of midges inside them was not random, but rather showed statistical evidence of internal spatial structure. In subsequent work [Puckett *et al.* 2014], we showed that the spatial structure of swarms is well described by the same distribution as one would expect for randomly packings of hard spheres, indicating that the midges prefer a region of excluded volume—a "personal space"—around them.

In keeping with the appearance of randomness in the swarms, the midge velocities followed a distribution that was nearly Maxwellian near its peak, indicating that to a good approximation the midges behave like particles in an ideal gas. As the swarm size grew, however, the velocity distribution developed a heavy, exponential tail, indicating the appearance of interactions (as one would expect). But these interactions do not dominate the swarm behavior, as their signature appears only in the tail of the distribution. Thus, it appears that statistically significant interactions may be somewhat rare events in these swarms, with implications for modeling (see below).

Finally, we considered the acceleration statistics in the swarms. The most interesting result of this part of the study was the spatially resolved mean acceleration showed that midges feel an effective force per unit mass (that is, an acceleration) that increases linearly with the distance from the swarm center and that is pointed toward the center, so that the swarm itself creates an effective harmonic trap for the midges. The slope of the acceleration curves gives the trap stiffness; and, intriguingly, this stiffness *decreased* monotonically with the size of the swarm, so that larger swarms counterintuitively behaved as weaker traps.

Comparison with Models

The dominant paradigm for modeling collective behavior at the moment is a framework that assumes that social interactions can be represented as "effective forces" that affect the motion of individuals through Newton's second law. Typically, these forces are given by some blend of a short-range repulsion, a long-range attraction, and (for ordered groups such as bird flocks) an intermediate-range alignment, as described by the classic model of [Couzin *et al.* 2002]. To analyze empirical data, it has become relatively standard practice simply to fit the data to the model parameters [Lukeman *et al.* 2010], without necessarily analyzing the underlying model assumptions.

We considered the Couzin model, and effective-force models more generally, in the context of our midge swarms in [Puckett *et al.* 2014]. If such models are to be correct, then the signatures of the effective forces ought to be apparent in the acceleration statistics. When we considered such statistics for our midges, we found evidence for a short-range repulsion (confirmed by spatial statistics, as mentioned above), but little else. Aside from a general tendency to be bound to the swarm, the midge acceleration statistics are inconclusive at best for fitting to models. And, when comparing to the results of running the Couzin model in its swarming regime, the empirical statistical from the real swarms are completely different. Thus, we conclude that such models are a poor choice for capturing the dynamics of real swarms, even though their results are visually reasonable. The primary conclusion of this paper was that interactions, although clearly present in the swarm, are very subtle, and are not well modeled as forces.

Summary

With support from this STIR award, we were successful in achieving our two goals: we built an experimental system capable of extracting highly detailed kinematic information for individual insects in swarms, and we used this data to assess canonical models. Although the data showed that the models were not appropriate and therefore raised significant new questions, this award allowed us to lay the groundwork to study many new and exciting aspects of swarms.

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

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[Puckett *et al.* 2014] J. G. Puckett, D. H. Kelley, and N. T. Ouellette, "Searching for effective forces in laboratory insect swarms," *Sci. Rep.* **4**, 4766 (2014).