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Dynamics of mosquito swarms over a moving marker

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Abstract. Insect swarms are a model system for understanding collective behavior where the collective motion appears in disorder. To initiate and maintain a swarm in place, flying insects often use a visual external cue called a marker. In mosquitoes, understanding the swarming behavior and its relation to the marker has an additional medical relevance since swarming often precedes mating in the wild, thus constituting an important stage to intercept for controlling mosquito population. In this paper, we conduct experiments to characterize the visual coupling between a swarm of mosquitoes and a marker. A laboratory microcosm with artificial lighting was built to stimulate swarming in the malarial mosquito *Anopheles stephensi*. The microcosm was used to film a mosquito swarm with a stereo camera system as a marker was moved back-and-forth with five different frequencies. System identification analysis of the frequency response shows that the relationship between the swarm and the marker can be described by delayed second order dynamics in a feedback loop. Further, the length of the internal time delay appears to correlate with the number of mosquitoes swarming on the marker indicating that such a delay may be able capture social interactions within swarming systems. For insect swarms, model fitting of trajectory data provides a way to numerically compare swarming behaviors of different species with respect to marker characteristics. These preliminary results motivate linear dynamic systems as a modeling framework for flying insect swarms.

Keywords: swarming, feedback control, delay, mosquito, marker

1 Introduction

Among the variety of collective behaviors demonstrated by different animal species, swarming in flying insects occupies a unique position [12]. Unlike fish schools and bird flocks, which often appear to be coordinated, insect swarms appear disorganized. Yet, insect swarming is far from a random process as was shown in one of the first works by Okubo [23], who studied collective motion of midge swarms and showed that swarming in insects is distinct from gaseous diffusion. With the ability to reconstruct three-dimensional motion, varying levels

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of coordination have been reported in mosquito swarms filmed in the wild [5, 28], and midge swarms filmed in the laboratory [20, 25]. In terms of the order parameter that is often used to describe coordination in collective behaviors, insect swarms have been shown to lie at the edge of the phase transition between order and disorder [1].

Among insects that swarm, the mosquito holds a special position in context of its role as a vector for many deadly diseases including malaria and dengue fever [2]. Mosquitoes often swarm during twilight over high contrast regions called markers [13, 11, 31]. These swarms are composed almost entirely of males with females entering at different times to mate [17, 7]. Females typically get inseminated only once [14], even though they lay eggs multiple times during their lifetime. From a malaria control perspective, this makes mosquito swarming, and the environmental cues that induce the same, an important feature to understand in order to intercept reproduction.

Example of markers that induce swarms in the wild include a pile of trash or a patch of grass [13, 11, 17, 5, 10]. Left undisturbed, these markers serve as consistent swarming sites every day, year after year, during the wet season [17, 5]. While experiments have been performed in the past to isolate the possible role of marker color, size, and movement on mosquito swarming [19, 21], most of these studies were purely observational; the visual marker was found to play a crucial role in eliciting different sized and shaped swarms in different species [24]. More recently, van der Vaart et al. [32] use experiments with oscillating visual markers to characterize laboratory midge swarms in a rheological sense, showing the existence of high viscosity and low structure within such swarms. These properties were found to vary with frequency and contribute to the general damping of the external perturbations.

Compared to previous studies on insect swarms, here we seek to model and validate marker following behavior as a feedback mechanism with linear system dynamics and the effect of social influence acting as a time delay within the dynamics of the response. We use this framework to test several hypotheses regarding the nature of the response dynamics, the existence of a delay term, and the dependence of the delay on the size of the swarm. Additionally, we experiment with swarms of mosquitoes, which have medical significance due to their role as disease vectors.

We hypothesized the following: (h1) the open-loop swarm dynamics within the feedback loop that best fit the data will be in the form of a second order system; this was based on existence of such feedback loops in several other biological systems [8], and on prior work [5] which showed that the interaction of mosquitoes within a swarm can be described as a damped harmonic oscillator; (h2) the best-fit swarm dynamics will consist of a non-zero delay term; this hypothesis rests on the assumption that intra-swarm interactions have the same general effect on swarm response as that of neural processing delay modeled in individual systems [30]; and (h3) the existence of a dependence of the delay on the average number of positions tracked per time step—in other words, more the number of mosquitoes following the marker, higher the intensity of social

interaction and therefore longer the delay in how the swarm responds to the marker.

2 Methods

2.1 Mosquitoes

Mosquitoes for the experiments were obtained from a cyclic colony of *An. stephensi* maintained in the insectary at the National Institute of Malaria Research, Dwarka, India. The temperature and relative humidity were maintained at $27\pm 1^\circ$ and $70\pm 5\%$ respectively. Eggs were obtained from an insect colony in a petri dish containing water and lined with blotting paper on the inner side. Eggs were allowed to hatch and then transferred to enamel trays containing de-chlorinated tap water. Larvae were fed upon a mixture of powdered yeast and dog biscuits in a 60:40 ratio. The water in the rearing trays was replaced daily.

2.2 Experimental setup

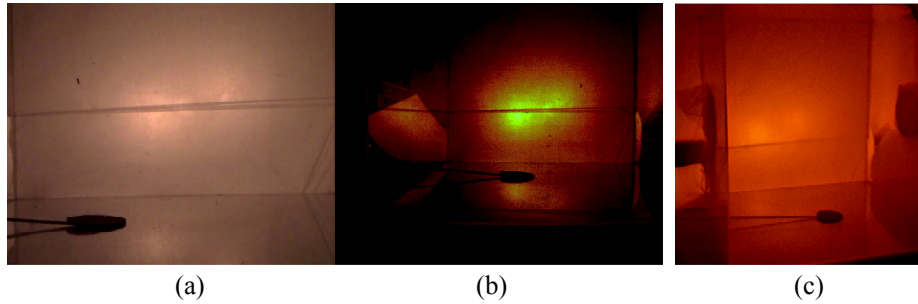


Fig. 1. Left (a) and right (b) camera image of a mosquito swarm over the circular black disc that served as a marker; the disc was connected to a white colored stick (appearing dark because of backlighting) that was moved by hand. A third perspective (c) of the setup is also shown.

The experimental setup consisted of a clear acrylic cube cage with 61 cm side, and a stereo camera setup for filming the mosquitoes (Fig.1). A custom diurnal lighting system was made using an incandescent bulb and a triac switch connected to a microcontroller and a real-time clock. This provided 10.5 hours of day and night times with dawn and dusk periods simulated by gradually increasing and decreasing the light intensity over a 1.5 hour period. The incandescent bulb was placed 20 cm from on one side of the clear acrylic cage. The efficacy of the diurnal lighting system in terms of eliciting swarming behavior was evaluated and confirmed by filming the mosquitoes in a netted cage over

successive days and confirming the presence of swarming during the artificially induced dusk and dawn periods. The stereo camera system was placed facing the opposite side of the cage so that a back-lighting effect was created. The cage had two 15.2 cm diameter sized circular holes on opposite sides of the cage for ventilation, cleaning, and placing moist raisins as food. Nets were used to cover the two holes and were set in place with a 3D printed plastic ring. The side of the cage facing the bulb was covered with parchment paper sheet to diffuse the light and avoid glares. A small hole in the side of the cage was made to allow moving the marker from outside the cage with a stick.

The stereo camera setup consisted of two cameras (Flea3, Edmund Optics, Singapore, recording 1280×1024 pixel resolution frames at 60 frames per second, and a Canon Vixia HFR500 recording 1920×1024 at 30 frames per second) mounted on a custom stereo bar and a tripod (Gorillapod, Vitec Imaging Inc, USA). The cameras were mounted parallel to each other with a baseline of 23 cm. Cameras were calibrated using a calibration toolbox (MATLAB Calibration toolbox [3]) to obtain the intrinsic (focal length and camera center) and extrinsic (relative position and orientation) parameters.

We used a black cardboard disc as marker for the experiments (Fig.1). The disc was attached to a 1 m long stick made of bamboo through the circular hole. We tested three different discs with 4,8, and 16 cm diameter to assess ease of use in terms of moving the marker back and forth and the ability to attract large swarms and selected the 8 cm marker for experiments.

2.3 Experimental Procedure

Three days prior to an experimental trial approximately sixty male *An. stephensi* mosquitoes were introduced into the cage in a bowl. Male mosquitoes were selected as follows. Once larvae were transformed into pupae, they were transferred into an insect cage inside a plastic bowl containing 10% glucose or water-soaked raisin, food for emergence into adult mosquitoes. Since male mosquitoes emerged first, the early emergents were used for this study. Individual mosquitoes were sucked in a glass aspirator and checked for their sex under the illumination of a table lamp based on the physical appearance of antennae, which are bushy, and palpi, which are club-shaped in male mosquitoes.

A petri dish with raisins dipped in water was placed at the corner of the cage for feeding. On the day of the experiment, the petri dish was removed thirty minutes prior to filming. Although mosquitoes swarmed during dawn and dusk periods, the experiments were only carried out during the dusk. All experiments were conducted on a single batch of mosquitoes over a span of two days.

The experiment involved moving the marker back-and-forth along a single direction by hand with the attached stick. Markings on the stick were used to visually assist the experimenter to maintain a constant distance travelled within the cage. A checkerboard pattern was placed in the view of both cameras before the start of trials each day. This was done to perform extrinsic calibration separately for each day in the event that the cameras had moved.

The experimental procedure involved moving the marker back and forth for about a minute between two fixed points on the base of the cage, and then waiting for three minutes before moving the marker again with a different frequency. Care was taken to ensure that the marker movement did not cause any movement of the cage and produced minimal noise. The different frequencies ranged between moving the marker very slowly between the two extreme locations to moving it very fast so that the swarm could not follow it at all. A stopwatch was used to maintain the frequency of marker movement. Out of the eighteen total trials, five trials were selected for analysis based on the variability in marker driving frequencies.

2.4 Analysis

Reconstructing three dimensional trajectories from stereo videos We processed the videos from each camera to extract frames. Frames from the camera with the lower frame rate of 30 frames per second (with respect to 60 frames per second with the faster camera) were repeated so that the total number of frames for a given time were the same. Frames were then synchronized manually by ensuring that the marker movement and mosquito movement in the two frames were aligned. This was confirmed by creating a stereo video and watching it for the length of the video to ensure that no delay between the two camera views was observed (see <https://youtu.be/o5f383Unmas>). We note that the maximum delay that such an approach would introduce between two successive frames is 1/60th of a second. At a maximum speed of 1 m/s this would produce a reconstruction error of approximately 1.6 cm which is within one mosquito body length. To ensure consistent analysis, we selected a subset of the video that showed the marker moving for at least one back-and-forth cycle. Mosquitoes either swarmed over the marker or sat on the walls of the acrylic cage. All mosquitoes swarming over the marker during this video were tracked until they either disappeared from view or settled on the wall of the cage.

The synchronized stereo video data was then used to reconstruct three-dimensional trajectories of individual mosquitoes and the marker using a probabilistic multi-target tracking algorithm [4]. The algorithm was implemented in two stages. First, an automatic version ran a multi-hypothesis particle filter which reconstructed individual mosquito motion until it was lost due to occlusion between two or more mosquitoes that could not be resolved automatically, or change in brightness; in these situations the track was re-initiated with a different identity. The output of this first stage were a series of tracklets of length 4.5 ± 2.5 frames having different identities. Next, a graphical interface was used to manually verify and stitch together the tracklets into longer trajectories. The graphical interface also ran a particle filter to estimate three-dimensional position and velocity of a target based on user inputs. The final trajectories were smoothed using a Kalman filter and transformed so that three orthogonal axes corresponded to directions along the marker, perpendicular to the marker, and the vertical direction.

Frequency Response Analysis The periodic movement of the swarm in response to the marker motivated a frequency response based analysis. Specifically, we computed the Fourier transform of individual mosquito and swarm movement in each direction to calculate the contribution of different frequencies. We compute the Fourier transform of the movement data of the swarm X_ω^s , the marker X_ω^m , and individual mosquitoes using the fast fourier transform (*fft*) function in MATLAB. The absolute value and argument of the ratio of the Fourier transforms of swarm and marker denoted by $\hat{G}_c = X_\omega^s/X_\omega^m$ represents the relative gain and phase offset of the swarm to the marker at frequency ω .

A second aspect of our analysis aimed to characterize the coupling between the marker and the swarm. In classical control theory, the response $x(t)$ of a dynamical system to an input $u(t)$ can be described as a differential equation

$$a_0 \frac{d^n x}{dt^n} + a_1 \frac{d^{n-1} x}{dt^{n-1}} + \dots + a_n x(t) = b_0 \frac{d^m u}{dt^m} + b_1 \frac{d^{m-1} u}{dt^{m-1}} + \dots + b_m u(t), \quad (1)$$

where $\frac{d^n x}{dt^n}$, for example, denotes the n -th derivative of $x(t)$ and is also known as the order of the model. This time-domain relationship can be represented in the frequency domain in the form of a transfer function $\mathbf{G}(s) = \frac{X(s)}{U(s)}$, where $s = j\omega$, $j = \sqrt{-1}$ and ω is a value of frequency at which the transfer function is evaluated; $X(s)$ and $U(s)$ are the frequency domain representation of $x(t)$ and $u(t)$ respectively. The transfer function is a complex number whose magnitude represents the ratio of magnitudes of the two signals, and whose argument represents the phase shift between two signals. A characterization of this relationship is called system identification [22].

The process of system identification involved fitting the system response in frequency domain to experimental data. Prior to system identification, we conducted linearity tests to establish that the swarm response can indeed be represented by a linear dynamic relationship. Toward this we computed coherence at a frequency ω defined by $C(\omega) = \frac{|R_{MS}(\omega)|^2}{R_{MM}(\omega)R_{SS}(\omega)}$, where R_{MS} , is the cross power spectral density between the marker and the swarm, and R_{MM} , and R_{SS} are the power spectral density of the marker and swarm respectively. A high coherence value close to 1 indicates linear relationship [30].

We denote the swarm dynamics in the form of a transfer function with an internal time delay τ $G_o(s)e^{-s\tau}$. Since the swarm manages to follow the marker as it changes direction, we considered the existence of a feedback loop [8], where each mosquito tends to correct its motion based on how it senses the environment and other mosquitoes. Accordingly, the swarm response to the marker was modeled as a feedback loop as in Figure 2. Within this framework, the swarm responds to the marker as it processes social interactions within, giving rise to an internal time delay. The overall transfer function can therefore be written as [30]

$$G_c(s) = \frac{G_o(s)e^{-s\tau}}{1 + G_o(s)e^{-s\tau}}. \quad (2)$$

System identification was performed by minimizing the sum $\min_{G_o(s), \tau} \sum_{i=1, \dots, 5} |G_c(s_i) - \hat{G}_c(s_i)|$ over possible values of $G_o(s)$ and a single value of τ within

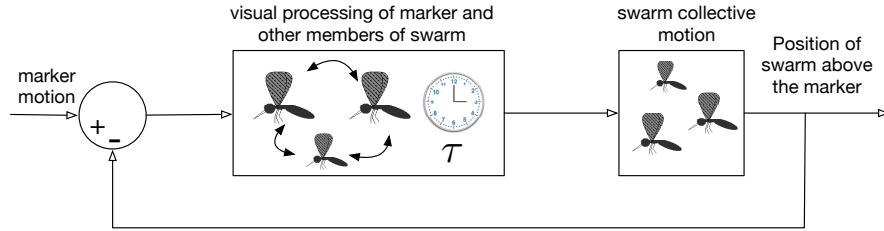


Fig. 2. We model the swarm response to the marker in the form of a feedback loop. Individual mosquitoes sense relative motion of the marker and members of the swarm and process it to give rise to collective behavior of following the marker. More mosquitoes in a swarm implies more social interactions which we model in the form of processing delay of the marker motion.

the *fmincon* routine in MATLAB. To test the dependence on swarm size, we additionally let the delay vary for each experiment so that the minimization is performed over possible values of $G_o(s)$ as well as a variable internal time delay as $\min_{G_o(s), \tau_i} \sum_{i=1, \dots, 5} |G_c(s_i) - \hat{G}_c(s_i)|$.

3 Results

3.1 Temporal dynamics of mosquito response to marker movement

Figures 3a,b,d, and e show the movements for the marker and the tracked mosquitoes in three-dimensions and then along the direction of marker movement for the lowest and highest frequency. The combined data for this study represents 16,241 three-dimensional position and velocity estimates from 63 trajectories.

We find that the primary movement of the swarm is along the direction of movement of the marker. In the case when the marker was moved at highest frequency a distinct back-and-forth movement was also present in the direction normal to the marker which the swarm also tended to follow.

3.2 Frequency response analysis of swarming over a moving marker

Figures 3c and f show the frequency response characteristics of the marker-swarm interaction along the direction of the marker. The dominant frequency (highest peak in each figure) denotes the frequency with which an entity (marker, swarm, or a mosquito) was primarily moving in the direction along the movement of the marker. We note that the dominant frequency for the swarm centroid aligns closely with that of the marker. The contribution of the dominant frequency to the swarm response is relatively low for when the marker is driven at high frequencies (0.52 and 0.64 Hz) compared to the low driving frequencies (0.14, 0.20, and 0.41 Hz).

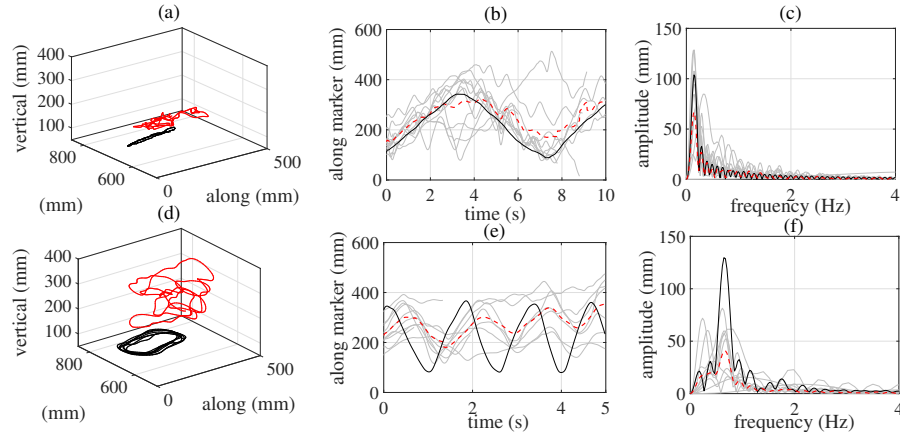


Fig. 3. Trajectory of a single mosquito (red) as the marker moved (black) at two different frequencies (a,d). Position of all mosquitoes (grey) and the swarm centroid (dashed red) along the direction of the marker; the marker position is shown in black (b,e). The frequency responses of the swarm centroid (dashed red), marker (black) and individual mosquitoes (grey) are shown in the direction along the movement of the marker (c,f).

3.3 System identification of swarm-marker relationship

The coherence between swarm and marker movement was found to be more than 0.8 for the range of frequencies with which the marker was moved (Fig. 4a). Identification of the linear dynamical system that best represents the relationship between the marker and the swarm revealed that the error reduced as we increased the order of the system from 0 (a proportional gain) to 4. The reduction in error is little beyond a second order system (h1) which has a non-zero delay of 0.354 s (h2, Fig. 4b). A variable delay model produces less error than a constant delay model (See Appendix A for the open-loop transfer functions with constant and variable delay). Figure 4c shows the relative magnitude and phase of the response along with the best fit second order model with constant delay and variable delay. Table 1 lists the five trials with the average number of positions tracked and the amount of variable delay. The amount of delay correlates to the average number of positions tracked (h3, linear regression model, $p = 0.0494$, $F = 10.2$, $R^2 = 0.773$). No correlation existed between the amount of delay and driving frequency (linear regression model, $p = 0.525$, $F = 0.513$, $R^2 = 0.145$).

4 Discussion

Swarming in insects is a complex collective behavior governed by multiple internal and external stimuli. In some insects that fly, a visual marker forms a crucial external stimulus for initiating and maintaining the swarming behavior in the wild [12]. Here, we conducted laboratory experiments with a *An. stephensi*

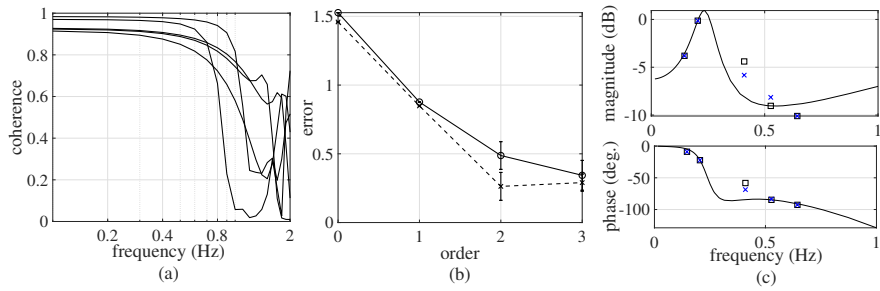


Fig. 4. (a) Coherence of all five datasets with respect to frequency. (b) Error \pm standard deviation in frequency response fit as a function the order of model for a model with constant delay (solid) and variable delay (dashed). The different values correspond to the different number of zeros that are possible for a given number of poles in the transfer function. (c) Ratio of magnitude and phase shift of the frequency response of the swarm to the marker (squares), best fit second order model with constant delay (solid line) and separate variable delay model for each line (crosses).

| Date & time | Driving freq. (Hz) | Swarm size | Internal time delay (s) |
|---------------------|--------------------|-----------------|-------------------------|
| 2016-03-26 19:17:07 | 0.14 | 5.27 ± 0.44 | 0.0654 |
| 2016-03-26 19:14:54 | 0.20 | 5.74 ± 1.86 | 0.0402 |
| 2016-03-26 19:07:55 | 0.40 | 9.57 ± 2.24 | 0.6783 |
| 2016-03-25 19:17:17 | 0.52 | 9.42 ± 2.28 | 0.7891 |
| 2016-03-26 19:20:11 | 0.64 | 7.80 ± 1.12 | 0.0718 |

Table 1. Details of the trials that were analyzed for this study in the order of increasing marker frequency. Swarm size denotes the average number of positions tracked per video frame. The internal time delay represents the intra-swarm processing of external cues in the linear system representation of the swarm-marker relationship.

mosquito swarm responding to a moving marker. The swarm followed the marker as it moved to-and-fro with different frequencies. A mathematical representation of a feedback loop with delay was fit to the frequency response data of the swarm.

Marker following behavior In following the marker, the swarm demonstrated a distinct repetitive movement pattern along the direction of movement of the marker. It is unlikely that this movement is due to any external influence other than the marker. This is because at the highest frequency of 0.64 Hz in our experiments, the hand movement was not entirely parallel to the camera plane and in that case, we simultaneously find that the swarm follows the marker in a direction normal to the camera plane. It is also unlikely that the hand holding the marker stick created a looming stimulus, which would constitute a repelling influence only, and would not have attracted the swarm towards itself when moving away from the cage.

Hypotheses related to system identification A second order description of swarm dynamics within a feedback loop serves well to represent the swarm response to the marker. This agrees with similar findings in midges [23, 32] and mosquitoes [5]. The amplitude ratio and phase difference between the marker and the swarm movement show that the swarm is best able to keep up at a frequency of 0.2 Hz where it has nearly the same amplitude and a low phase difference. Interestingly, this is not the lowest frequency at which the marker was moved indicating the presence of an ideal optic flow from the environment. At 0.64 Hz, the highest frequency at which we moved the marker, the magnitude ratio was close to 0.4 showing that the swarm was only able to keep up 40% of the way and lagged behind at nearly half a cycle.

Dependence of delay on swarm size The existence of a non-zero internal time delay confirm our hypotheses about how the swarm interacts with the marker. The existence of correlation between time delay and swarm size further confirms that the interactions within the swarm need to be balanced against external cues, much like in other animal groups. Compared to [32], where midge swarms were shown to respond viscoelastically to external perturbations, with social interactions likely manifesting in the form of elasticity of the swarm, the modeling framework here imparts a single description (transfer function) to the swarm over varying frequencies and seeks to model social interactions in the form of an internal delay. We did not find a frequency dependence of the internal delay; finding such a dependence would imply that the internal dynamics of the swarm vary with driving frequencies—a result that may have been expected in light of the dependence of storage and loss moduli on driving frequencies in midge swarms [32]. However, a direct relationship between an internal time delay as modeled here and viscosity of a swarm is not obvious. At the same time, the experiments described here are preliminary with a much smaller dataset and relatively smaller swarms, and should therefore only serve to motivate future hypotheses.

The value of the delay is much higher at 0.678 s for swarms that have nine or more mosquitoes tracked per time step (the actual number of mosquitoes in the swarm are possibly more because we do not track mosquitoes that enter the swarm during the time we tracked) than 0.071 s for swarms where less than 8 mosquitoes per time step. This is a large difference in the delay with a small increase in the number of mosquitoes and suggests a nonlinear relationship warranting further investigation in terms of more experiments and larger swarms. Does the existence of a delay imply that a single mosquito would have followed the marker without delay? It is difficult to answer this question because the social interactions may also serve to reinforce the response to an external stimulus. Isolating environmental versus social cues in collective behavior is an open question in collective animal behavior [18], and methods in information theory have been particularly effective in separating causal influences across space and time [15, 6]. Future experiments with swarming insects that can help tease out the effects of external versus internal information will require controlling the environment at a higher detail with multiple perspectives and modalities. With respect to

mosquitoes, acoustics have been found to play a critical role in species and sex recognition [29], and therefore isolating environmental and social effects entails an accurate reproduction of sound within the swarm. In this context, an accurate sound propagation and perception model must be developed for implementation on top of three-dimensional position data. Such a model can be used to reconstruct the visual and acoustic cues perceived by individual mosquitoes within a swarm. Finally, the robustness properties of the marker following behavior can inform target tracking algorithms for robotic swarms [27].

Vector control From the perspective of vector control, results in this study provide a quantifiable description for evaluating landmarks which in the form of markers act as consistent mating sites [26]. For example, field observations of the *An. gambiae ss.* have indicated that swarms generally form over high contrast regions that interrupt the regularity of the landscape [9] over certain times of the day [33]. The results here imply that in the wild a swarm of *An. stephensi* mosquitoes would be able to follow moving markers (e.g. head of a human or an animal) at speeds of up to 50 cm/s. A long-term experimental study analyzing how long such following behavior can last may provide possible mechanisms by which mosquitoes may travel long distances. The mathematical description of swarming over a marker described here can also be used to numerically compare different species of mosquitoes [24] or for evaluating the swarming behavior of transgenic mosquitoes for use in sterile insect techniques [16].

Appendix A

The transfer function for open-loop dynamics with constant delay that best fit data from all five trials was

$$\begin{aligned} G_o(s) &= \frac{0.3481s^2 + 0.7023s + 1.379}{1.023s^2 + 0.3121s + 1.452} e^{-0.354s} \\ &= \frac{(s + 1 - 1.715j)(s + 1 + 1.715j)}{(s + 0.1525 - 1.1813j)(s + 0.1525 + 1.1813j)} e^{-0.354s}, \end{aligned}$$

where $j = \sqrt{-1}$. The open-loop transfer function with variable delay was

$$\begin{aligned} G_o(s) &= \frac{1.185s + 0.8562}{1.1s^2 + 0.4979s + 1.596} e^{-\tau_i s} \\ &= \frac{(s + 0.7224)}{(s + 0.2262 - 1.1827j)(s + 0.2262 + 1.1827j)} e^{-\tau_i s}, \end{aligned}$$

where τ_i corresponds to the best fit delay for trial i .

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References

1. Attanasi, A., Cavagna, A., Del Castello, L., Giardina, I., Melillo, S., Parisi, L., Pohl, O., Rossaro, B., Shen, E., Silvestri, E., Viale, M.: Collective Behaviour without Collective Order in Wild Swarms of Midges. *PLoS Computational Biology* **10**(7), e1003697 (2014)
2. Benelli, G., Mehlhorn, H.: Declining malaria, rising of dengue and zika virus: insights for mosquito vector control. *Parasitology Research* **115**(5), 1747–1754 (2016)
3. Bouguet, J.Y.: Camera Calibration Toolbox for Matlab (2010). URL http://www.vision.caltech.edu/bouguetj/calib_doc/index.html
4. Butail, S., Manoukis, N.C., Diallo, M., Ribeiro, J.M.C., Lehmann, T., Paley, D.A.: Reconstructing the flight kinematics of swarming and mating in wild mosquitoes. *Journal of the Royal Society Interface* **9**(75), 2624–2638 (2012)
5. Butail, S., Manoukis, N.C., Diallo, M., Ribeiro, J.M.C., Paley, D.A.: The dance of male *Anopheles gambiae* in wild mating swarms. *Journal of Medical Entomology* **50**(3), 552–559 (2013)
6. Butail, S., Porfiri, M.: Detecting switching leadership in collective motion. *Chaos: An Interdisciplinary Journal of Nonlinear Science* **29**(1), 011,102 (2019)
7. Charlwood, J.D., Jones, M.D.R.: Mating in the mosquito, *Anopheles gambiae* sl. *Physiological Entomology* **5**(4), 315–320 (1980)
8. Cowan, N.J., Ankarali, M.M., Dyhr, J.P., Madhav, M.S., Roth, E., Sefati, S., Sponberg, S., Stamper, S.A., Fortune, E.S., Daniel, T.L.: Feedback control as a framework for understanding tradeoffs in biology. *Integrative and Comparative Biology* **54**(2), 223–237 (2014)
9. Diabate, A., Tripet, F.: Targeting male mosquito mating behaviour for malaria control. *Parasites & Vectors* **8**(1), 347 (2015)
10. Diabate, A., Yaro, A.S., Dao, A., Diallo, M., Huestis, D.L., Lehmann, T.: Spatial distribution and male mating success of *Anopheles gambiae* swarms. *BMC Evolutionary Biology* **11**(1), 184 (2011)
11. Downes, J.A.: The Swarming and Mating Flight of Diptera. *Annual Review of Entomology* **14**(1), 271–298 (1969)
12. Dublon, I.A.N., Sumpter, D.J.T.: Flying insect swarms. *Current Biology* **24**(18), R828–R830 (2014)
13. Gibson, G.: Swarming behaviour of the mosquito *Culex pipiens quinquefasciatus*: a quantitative analysis. *Physiological Entomology* **10**(3), 283–296 (1985)
14. Jones, J.C.: Are mosquitoes monogamous? *Nature* **242**(5396), 343–344 (1973)
15. Lord, W.M., Sun, J., Ouellette, N.T., Bollt, E.M.: Inference of causal information flow in collective animal behavior. *IEEE Transactions on Molecular, Biological and Multi-Scale Communications* **2**(1), 107–116 (2016)
16. Manoukis, N.C.: Drivers of mosquito mating. *Science* **371**(6527), 340–341 (2021)
17. Manoukis, N.C., Diabate, A., Abdoulaye, A., Diallo, M., Dao, A., Yaro, A.S., Ribeiro, J.M.C., Lehmann, T.: Structure and Dynamics of Male Swarms of *Anopheles gambiae*. *Journal of Medical Entomology* **46**(2), 227–235 (2009)
18. Miller, N., Garnier, S., Hartnett, A.T., Couzin, I.D.: Both information and social cohesion determine collective decisions in animal groups. *Proceedings of the National Academy of Sciences* **110**(13), 5263–5268 (2013)
19. Mohan, B.N.: Sexual Behaviour of *Anopheles fluviatilis* in Captivity. *Nature* **169**(4294), 280–280 (1952)
20. Ni, R., Puckett, J.G., Dufresne, E.R., Ouellette, N.T.: Intrinsic fluctuations and driven response of insect swarms. *Physical Review Letters* **115**(11), 118,104 (2015)

21. Nielsen, H.T., Nielsen, E.T.: Swarming of mosquitoes: laboratory experiments under controlled conditions. *Entomologia Experimentalis et Applicata* **5**(1), 14–32 (1962)
22. Ogata, K.: *Modern Control Engineering*. Prentice Hall, New Jersey (1997)
23. Okubo, A.: Dynamical aspects of animal grouping: swarms, schools, flocks, and herds. *Advances in Biophysics* **22**(0), 1–94 (1986)
24. Poda, S.B., Nignan, C., Gnankiné, O., Dabiré, R.K., Diabaté, A., Roux, O.: Sex aggregation and species segregation cues in swarming mosquitoes: role of ground visual markers. *Parasites & Vectors* **12**(1), 589 (2019)
25. Puckett, J.G., Ni, R., Ouellette, N.T.: Time-frequency analysis reveals pairwise interactions in insect swarms. *Physical Review Letters* **114**(25), 258,103 (2015)
26. Sawadogo, S.P., Niang, A., Bilgo, E., Millogo, A., Maïga, H., Dabire, R.K., Tripet, F., Diabaté, A.: Targeting male mosquito swarms to control malaria vector density. *PloS One* **12**(3), e0173,273 (2017)
27. Senanayake, M., Senthooan, I., Barca, J.C., Chung, H., Kamruzzaman, J., Mursheed, M.: Search and tracking algorithms for swarms of robots: A survey. *Robotics and Autonomous Systems* **75**, 422–434 (2016)
28. Shishika, D., Manoukis, N.C., Butail, S., Paley, D.A.: Male motion coordination in anopheline mating swarms. *Scientific Reports* **4**(6318) (2014)
29. Simões, P.M.V., Ingham, R.A., Gibson, G., Russell, I.J.: A role for acoustic distortion in novel rapid frequency modulation behaviour in free-flying male mosquitoes. *Journal of Experimental Biology* **219**(13), 2039–2047 (2016)
30. Sponberg, S., Dyrh, J.P., Hall, R.W., Daniel, T.L.: Luminance-dependent visual processing enables moth flight in low light. *Science* **348**(6240), 1245–1248 (2015)
31. Sullivan, R.T.: Insect swarming and mating. *The Florida Entomologist* **64**(1), 44–65 (1981)
32. van der Vaart, K., Sinhuber, M., Reynolds, A.M., Ouellette, N.T.: Mechanical spectroscopy of insect swarms. *Science Advances* **5**(7), eaaw9305 (2019)
33. Wang, G., Vega-Rodríguez, J., Diabate, A., Liu, J., Cui, C., Nignan, C., Dong, L., Li, F., Ouedrago, C.O., Bandaogo, A.M., Simon Sawadogo, P., Maiga, H., Alves e Silva, T.L., Pascini, T.V., Wang, S., Jacobs-Lorena, M.: Clock genes and environmental cues coordinate *Anopheles* pheromone synthesis, swarming, and mating. *Science* **371**(6527), 411–415 (2021)