



# Gone With the Wind: Honey Bee Collective Scenting in the Presence of External Wind

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## ABSTRACT

Wind is a common environmental factor in the behavior of animals, such as the honey bees (*Apis mellifera* L.). Volatile pheromones are one of the main communication signals in honey bees that can be sensed and further propagated via the scenting behavior, in which bees release pheromones and fan their wings to direct the signals. While studies have correlated the effect of wind and the foraging behavior of bees, we aim to study how wind, interacting with the pheromone signals, can impact the resulting collective behavior of the bees in the context of a swarm localizing their queen and aggregating around her. We experimentally show that strong external wind interferes with the aggregation around the queen by reducing the number of scenting bees in the communication network and disrupting the directionality of the scenting signals. To further understand the behavioral mechanisms that change with different wind conditions (direction and magnitude), we use an agent-based model that simulates pheromone flow with the diffusion equation and simple rules of behaviors for virtual bees. We use the Covariance Matrix Adaptation-Evolutionary Strategy (CMA-ES) algorithm to search over the behavioral parameter space for the optimal parameters in different environmental wind conditions. We find that, turbulent wind flowing in random directions shows minimal effect on the bees' collective scenting strategy and aggregation. However, in high unidirectional wind (e.g., flowing towards the right side of the arena), the bees must spatially align a shorter scenting network along the wind's direction to localize the queen and aggregate.

## CCS CONCEPTS

• Applied computing → Biological networks.



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CI '23, November 06–09, 2023, Delft, Netherlands

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ACM ISBN 979-8-4007-0113-9/23/11.

<https://doi.org/10.1145/3582269.3615594>

## KEYWORDS

honey bees, agent-based model, collective scenting, cma-es, computer vision

### ACM Reference Format:

Dieu My T. Nguyen, Golnar Gharooni Fard, Michael L. Iuzzolino, and Orit Peleg. 2023. Gone With the Wind: Honey Bee Collective Scenting in the Presence of External Wind. In *Collective Intelligence Conference (CI '23)*, November 06–09, 2023, Delft, Netherlands. ACM, New York, NY, USA, 9 pages. <https://doi.org/10.1145/3582269.3615594>

## 1 INTRODUCTION

Social insects must effectively communicate to navigate environments with challenging variables, such as physical obstacles and wind. The honey bees have evolved the ability to form robust communication networks using volatile pheromone signals [3, 13]. One instance of honey bee pheromone communication is the collective scenting behavior in the context of a swarm localizing the queen and aggregating around her. The collective scenting behavior consists of bees sensing pheromones above a concentration threshold in their local environment and in turn releasing pheromones from the Nasonov gland, directionally fanning these chemical signals that decay rapidly in time and space to disperse the signals to other bees farther away [14, 16, 19]. Experimental and modeling works have shown that physical obstacles that partially block the flow of pheromones slow down the bees' localization and aggregation process to some extent, but do not entirely eliminate it. Furthermore, such obstructions can limit the range of behavioral parameters, including the bees' pheromone detection threshold and the magnitude of their wing-fanning [15, 17].

In this work, we investigate another common environmental or abiotic factor in the bees' pheromone communication for coordinating group processes: wind. Wind influences behavior of animals in general. For example, bald eagles (*Haliaeetus leucocephalus*) tend to rest from foraging in high wind conditions [6]. Strong winds can positively affect shearwaters (*Calonectris diomedea*) in aiding their travel to far food sources [4]. On the other hand, as wind magnitude increases, load size (i.e., size of vegetation collected)

decreases in leaf-cutting ants, reducing colony fitness and limiting the geographic distribution of foragers [1]. High wind conditions have been observed to cause a significant decrease in pollination activity, including a reduction in flower visiting rate, among honey bees, which leads to an increase in hesitancy to take off, as well as an increase in handling time [11, 12, 20, 22].

Although existing research has mostly examined the correlation between wind and foraging behavior in honey bees, our focus is on exploring how external wind interacts with pheromones (one of the primary spatio-temporal communication signals in bees), as well as with the internal wind generated by wing-fanning during collective scenting behavior. Specifically, we seek to understand how these factors impact the group process of searching for the queen and aggregating around her, which is a common behavior exhibited during reproductive swarming. To this end, we perform experiments in which bees search for the queen by following her pheromones and propagating chemical signals in environments with and without wind, by building on previous behavioral experimentation and image analysis tools in [16]. Further, we take inspiration from the experiments to build a queen-finding agent-based model that simulates pheromone diffusion using simple behavioral rules for individual bee agents [16, 17]. Previous applications of the model have successfully predicted the optimal ranges of behavioral parameters for honey bees, including the detection threshold and wing-fanning magnitude during scenting, in both simple and complex environments that include physical obstacles. In this work, we employ the Covariance Matrix Adaptation-Evolutionary Strategy (CMA-ES) algorithm [8] to automatically search for the optimal behavioral parameters that will allow the bees to successfully find the queen and aggregate around her in various wind conditions, such as unidirectional and turbulent (i.e., flowing in random directions) wind of various magnitudes. Insights from this work can illuminate how the bees modify their behavior in response to unpredictable environmental factors to achieve collective tasks that are important for colony survival.

## 2 METHODS

### 2.1 Experimental setup & computer vision image analysis

We followed the experimental methods originally described in [16]. Here, we briefly summarize the methods and describe the inclusion of wind in the setup. We use a 2-D back-lit arena (50x50x1.5 cm) to prevent flying for ease of handling and recording, as bees have been shown to scent while standing [14]. We record the experiments aerially with a video camera (4k resolution, 30 fps). A caged queen bee is fixed at the top right corner of the arena. Worker bees are placed at the bottom left corner. A plexiglass sheet is placed on top of the arena to enclose it. To generate external wind, we cut the left and right edges of the arena, cover the edges with thin mesh roles, and place a fan (B-Air Vent VP-25 Compact, on high speed) on the left side to impose wind flowing towards the right side of the arena. To create a smooth and uniform wind flow across the arena, the output air channels are also covered with a couple of layers of mesh. For each of the two environmental conditions (i.e., in the presence and absence of external wind), we perform nine experiments with varying number of bees. The approximate number of bees for the

no wind experiments are: 250, 310, 320, 370, 400, 420, 590, and 650 [16]. The approximate number of bees for the wind experiments are: 220, 230, 280, 300, 360, 370, 430, 490, and 500.

We use the computer vision and deep learning approaches presented in [16] to automatically detect scenting bees and estimate their orientations in frames or images extracted from the experimental videos. Individual bees (i.e.,  $x, y$  centroids) are detected by applying a combination of the Otsu's method of adaptive thresholding, morphological transformations, and the connected components algorithm [2, 5, 18]. To classify a bee as scenting or non-scenting based on the visual indicators (i.e., wide wing angles of the fanning behavior while scenting), we process the images with the trained ResNet-18 convolutional neural network (CNN) model that achieved 95.17% test accuracy on classifying the scenting behavior in bees, as described in [16]. To obtain the scenting direction, we use the trained regression CNN model that achieved 96.71% test accuracy with 15° of error tolerance on estimating bee orientation [16].

Extracting the position, classification, and orientation data for individual bees using image analysis enables us to reconstruct attractive surfaces to correlate the scenting events with the spatiotemporal density of bees. For each scenting bee  $i$  at time  $t$ , its position is defined as  $s_{i,t}^p$ , and its direction of scenting as  $s_{i,t}^d$  (unit vector). Assuming the scenting bees provide directional information to non-scenting bees,  $s_{i,t}^p$  and  $s_{i,t}^d$  are treated as a set of gradients that define a minimal surface of height  $f(x, y, t)$ , which corresponds to the probability that a randomly moving non-scenting bee will end up at position  $(x, y)$  by following the scenting directions of scenting bees:  $f(x, y) = \sum_{\nabla f} \int \nabla f dx dy$ , where  $\nabla f = s_{i,t}^p + s_{i,t}^d$ . Tikhonov regularization is used to regularize the least squares solution of surface reconstruction from its gradient field [9, 10].

Lastly, we obtain several time-series properties of the experiments including the number of scenting bees over time (rolling mean with window size of 100 frames) which is averaged over the nine experiments with varying number of bees for each experimental condition. Similarly, we obtain the average bee distance to the queen, computed as the the average distance of all black pixels to the queen's location, as the bee detection method cannot detect every single individual bee when they touch or overlap. Since the queen's cage is stationary, the remaining black pixels in the arena can be used as a proxy for the moving bees.

### 2.2 Modeling pheromone advection-diffusion

In a 2-D virtual arena, we treat a single scenting bee as a point source of localized and instantaneous pheromone emission. The 2-D advection-diffusion equation is used to describe pheromone concentration,  $C(x, y, t)$ , at a position and time [16]:

$$C(x, y, t) = \frac{C_0}{\sqrt{t}} \exp \left( -\frac{(x - w_x w_x t)^2 + (y - w_y w_y t)^2}{4Dt} - \gamma t \right) \quad (1)$$

where  $C(x, y, t)$  is the concentration at position  $[x, y]$  at time  $t$ ,  $C_0 = 0.0575$  is the constant initial concentration,  $w_x$  and  $w_y$  are the  $x$  and  $y$  components of emission vector respectively,  $D = 0.6$  is the constant diffusion coefficient, and  $\gamma = 108$  is the decay constant. The behavioral parameter representing the directional bias,  $w_b$ , is

the magnitude of the advection–diffusion of pheromone released by a bee. To account for external wind, we modify the equation as such:

$$C(x, y, t) = \frac{C_0}{\sqrt{t}} \exp\left(-\frac{A^2 + B^2}{4Dt} - \gamma t\right) \quad (2)$$

where  $A = x - w_b w_x t - w_w w_{wx} t$  and  $B = y - w_b w_y t - w_w w_{wy} t$ ,  $w_w$  is the magnitude of the wind, and  $w_{wx}$  and  $w_{wy}$  are the  $x$  and  $y$  components of the wind direction vector. The constant environmental parameters of the model are: the size of the 2-D arena ( $X_{min} = -3$  and  $X_{max} = 3$ ) and the size of a grid cell ( $\delta_X = 0.01$ ), the start and final time of the simulation ( $t_i = 0$  and  $t_f = 50$ ) and the time integration constant ( $\delta_t = 0.005$ ).

### 2.3 Modeling behavioral rules

The behavioral rules of virtual bees in a simulated environment in an agent-based model have been described in detail in [16] and [17]. We summarize the rules here for brevity. The queen bee is stationary and frequently releases pheromone isotropically or axisymmetrically (i.e.,  $w_b = 0$ ). Worker bees follow the rules: (1) A worker bee randomly walks around the arena. (2) If she detects the queen’s pheromone above the concentration threshold ( $T$ ), the bee adjusts her orientation ( $w_x$  and  $w_y$ ) towards the direction uphill the gradient. With probability of 0.5, she will either walk up the gradient or scent, i.e., stand still to emit and fan her own pheromones for a given period of time. (3) These secondary signals propagate pheromones to other bees, which follow the same rules to walk up the gradient or scent to further propagate the information.

These behavioral rules are formalized as a probabilistic state machine (PSM) consisting of a set of finite states (shown in Table 1) that describes bee behavior and a transition matrix that describes how a bee may change from one state to another [16, 21]. We define the same state model  $SM_{worker} = (S, s_0, I, M)$  for each worker bee:

$$S = \{randomWalk, directedWalk, thresholdMet, emit, fan\}$$

is a set of finite states, where the variable *randomWalk* or abbreviated as *rWalk* is a random walk when the threshold is not met, *directedWalk* or *dWalk* is the walk up the concentration gradient, *thresholdMet* or *tMet* is when the threshold is met, *emit* is the instantaneous release of pheromone, and *fan* is the wing fanning at a constant position.  $s_0 = randomWalk$  is the initial state of all the bees.  $I = \{t_i, c_i\}$ , is a set of flags for the input conditions on state transitions, where for a given bee,  $t_i$  is a counter for the time that bee is in the *fan* state and  $c_i$  is the concentration at that bee’s position. The transition matrix  $M$  describes the conditions and probabilities for transitioning from the current state,  $s_c$ , to the next state,  $s_n$ .

### 2.4 CMA-ES Optimization

To search for optimal behavioral parameters ( $w_b$  and  $T$ ) in an environment with and without external wind, we employ the CMA-ES algorithm [8] available in the Python package “cma-es” (version 1.5.0). The algorithm generates sets of values for the two parameters within a search space. The CMA-ES algorithm then evaluates a cost function for each set of parameters, and updates the covariance matrix to expand in the direction of the optimal value for the next generation or iteration. The processes is repeated until the

**Table 1: Probabilistic state machine transition matrix for honey bee behavioral rules to transition from the current state,  $s_c$ , to the next state,  $s_n$ . Variables *randomWalk*, *thresholdMet*, and *directedWalk* abbreviated as *rWalk*, *tMet*, and *dWalk*, respectively.  $P_w$  and  $T$  represent the emission period made of the *emit* and the *fan* state and the threshold over which a bee can be activated from state *randomWalk*. Previously published in [16] and [17].**

$s_c \backslash s_n$	rWalk	tMet	emit	fan	dWalk
rWalk	$c_i < T$	$c_i \geq T$	0	0	0
dWalk	$c_i < T$	$c_i \geq T$	0	0	0
tMet	0	0	0.5	0	0.5
emit	0	0	0	1	0
fan	$t_i \geq P_w \wedge c_i < T$	$t_i \geq P_w \wedge c_i \geq T$	0	$t_i < P_w$	0

algorithm converges on a single parameter set with a cost function below a certain threshold.

For the honey bee aggregation model, we define the cost function for CMA-ES optimization using three properties previously used to delineate simulation outcomes into various phases which include the optimal outcome of aggregation around the queen via propagation of signals and a less optimal outcome of aggregation into small clusters [16]. The three properties are:  $N_{clusters}$  or the final number of clusters,  $N_{queen}$  or the final queen’s cluster size, and  $D_{active}$  or the distance of the farthest active bee (i.e., a bee whose threshold is met and is either scenting or walking up the gradient) to the queen to represent how far the signal propagation reaches. We use the density-based spatial clustering of applications with noise (DBSCAN) algorithm ( $\epsilon$ : 0.25, minimum number of bees to form a cluster: 5) to cluster bees at every time step [7], and obtain values for  $N_{clusters}$  and  $N_{queen}$ . For a simulation to be considered successful (i.e., aggregation around the queen via signal propagation or collective scenting),  $N_{clusters}$  should be minimal, and  $N_{queen}$  and  $D_{active}$  should be maximal. Thus, the cost function for CMA-ES optimization to minimize is given by:

$$Cost = 1 - [(1 - N_{clusters}) \times N_{queen} \times D_{active}]$$

Each simulation of a particular set of parameters  $w_b$  and  $T$  contains 50 virtual bees and runs for 10,000 time steps, which we have previously observed to be sufficient for the simulation to reach a final outcome (e.g., a single cluster around the queen or small clusters that are perpetually stuck in space). To configure some problem-specific settings of the CMA-ES algorithm, we constraint the parameter space, in which  $w_b$  is bounded between 0.001 to 1.0 and  $T$  is bounded between 0 and 60. These bounds were heuristically discovered in previous simulations of the bee aggregation phenomenon in a simple environment without external wind [16]. Thus, we use the same values in this algorithm to reduce computational time. The initial step size is 10, which is observed to be an appropriate measure between algorithm run time and optimal solution. The maximum number of generations is set to 50. By default, the search runs until the maximum number of generations or when an early termination criteria is met.

We use CMA-ES to search for the optimal set of behavioral parameters for the following environmental conditions: (1) Uni-directional wind flowing towards the right side of the arena. (2) Turbulent wind in which each scenting bee senses external wind from a random direction. In both conditions, we test various wind magnitudes,  $w_w$ : 0 (control), 50, 100, 200, and 300.

After finding the optimal simulations for the different conditions, we obtain various time-series properties: the average distance to the queen, the average queen's cluster size, the average number of scenting bees, and the average distance of the farthest active bee. Additionally, we characterize potential spatial bias of the scenting network and aggregation due to directional wind by measuring the difference between the number of scenting bees on the right and left side, normalized by the total number of scenting bees at each time step. This property shows whether there is any spatial bias towards the right side of the arena, where the wind is flowing in the uni-directional wind condition.

### 3 RESULTS

#### 3.1 Experimental Results

We first compare the dynamics of the queen localization and aggregation behavior in bees in the presence and absence of wind. In Fig. 1A, we show snapshots of an example experiment ( $N=320$  bees) without wind over time [16]. Here, we observe a collective scenting network forming early on as bees spatially spread out and create cascades of scenting events. Consequently, by approximately 1800 seconds or 30 minutes, most bees have aggregated at the queen's cluster. The average attractive surface over all time frames show that the collective scenting events correlate to the spatial-temporal density of the bees (i.e., the region around the queen shows the highest  $f$  values). Similar snapshots are shown for an example experiment ( $N=360$  bees) with wind flowing towards the right of the arena (Fig. 1B). In general, we observe less scenting bees over time, and by approximately 30 minutes, only a small fraction of the bees have clustered around the queen. The average surface is relatively flat and does not indicate the collective scenting events pointing towards the queen's direction.

Quantification of time-series properties further support the qualitative observations. On average, there are less scenting bees over time when wind is present (Fig. 1C). However, the average bee distance to the queen quickly decreases and then plateaus in the absence of wind, indicating quick clustering around the queen (Fig. 1D). With wind, the distance begins to decrease later (approximately 500 seconds) and reaches a higher final distance compared to the distance in experiments without wind.

#### 3.2 Model optimization results

Using the experimental results as an inspiration for modeling, we use CMA-ES to search for the optimal values for the behavioral parameters of bee agents in unidirectional and turbulent wind of varying magnitude as above-mentioned. For unidirectional wind flowing towards the right of the virtual arena, the optimal parameters are  $w_b = 22.85$  and  $T = 0.001$  for  $w_w = 0$  (control),  $w_b = 22.13$  and  $T = 0.001$  for  $w_w = 50$ ,  $w_b = 19.76$  and  $T = 0.002$  for  $w_w = 100$ ,  $w_b = 9.13$  and  $T = 0.001$  for  $w_w = 200$ , and  $w_b = 7.77$  and  $T = 0.002$  for  $w_w = 300$ . Snapshots of these simulations show aggregation

into a single cluster around the queen for all five simulations (Fig. 2). Simulations with  $w_w = 0$  and  $w_w = 50$  show similar signal propagation events in which scenting bees form long percolation chains homogeneously (Fig. 2A-B). From  $w_w = 100$ , the scenting chains spatially shift to the right side of the arena toward the direction of the wind (Fig. 2C). Increasing wind magnitude further to  $w_w = 200$  and  $w_w = 300$ , results in shorter scenting chains and a more pronounced effect of the wind direction on the spatial arrangement of the final cluster (Fig. 2D-E). We also quantify several properties of the simulations over time. The average distance to the queen for all five simulations shows sharp decrease at the beginning and plateau afterwards, but these dynamics are slower and plateau at higher distance with higher wind magnitude (Fig. 4A). The average queen's cluster size and number of scenting bees show similar dynamics of a quick increase and a following plateau, with temporal delays in higher wind (Fig. 4B-C). The average distance of the farthest active bee, which is a proxy for how far the signal propagates, show maximal values early on and sharply decreases to a plateau (Fig. 4D) as inversely correlating to the number of scenting bees over time. Lastly, as the unidirectional wind becomes stronger (i.e., higher  $w_w$ ), the scenting network is spatially biased towards the right side of the arena along the wind's direction (Fig. 5A).

With turbulent wind, the optimal parameters are  $w_b = 21.16$  and  $T = 0.001$  for  $w_w = 0$  (control),  $w_b = 21.50$  and  $T = 0.002$  for  $w_w = 50$ ,  $w_b = 24.04$  and  $T = 0.001$  for  $w_w = 100$ ,  $w_b = 24.55$  and  $T = 0.001$  for  $w_w = 200$ , and  $w_b = 21.21$  and  $T = 0.005$  for  $w_w = 300$ . Snapshots of these simulations show fairly similar scenting percolation chains that are spread throughout the arena and a single cluster of similar shape around the queen by the end of the simulations (Fig. 3). Likewise, the time-series data of the average distance to the queen, queen's cluster size, number of scenting bees, and farthest active distance for these simulations show closely similar dynamics, insensitive to  $w_w$  (Fig. 4E-H). However, unlike in unidirectional wind, in turbulent wind,  $w_w$  has less of a stark effect on the spatial bias of the scenting network of bees (Fig. 5B).

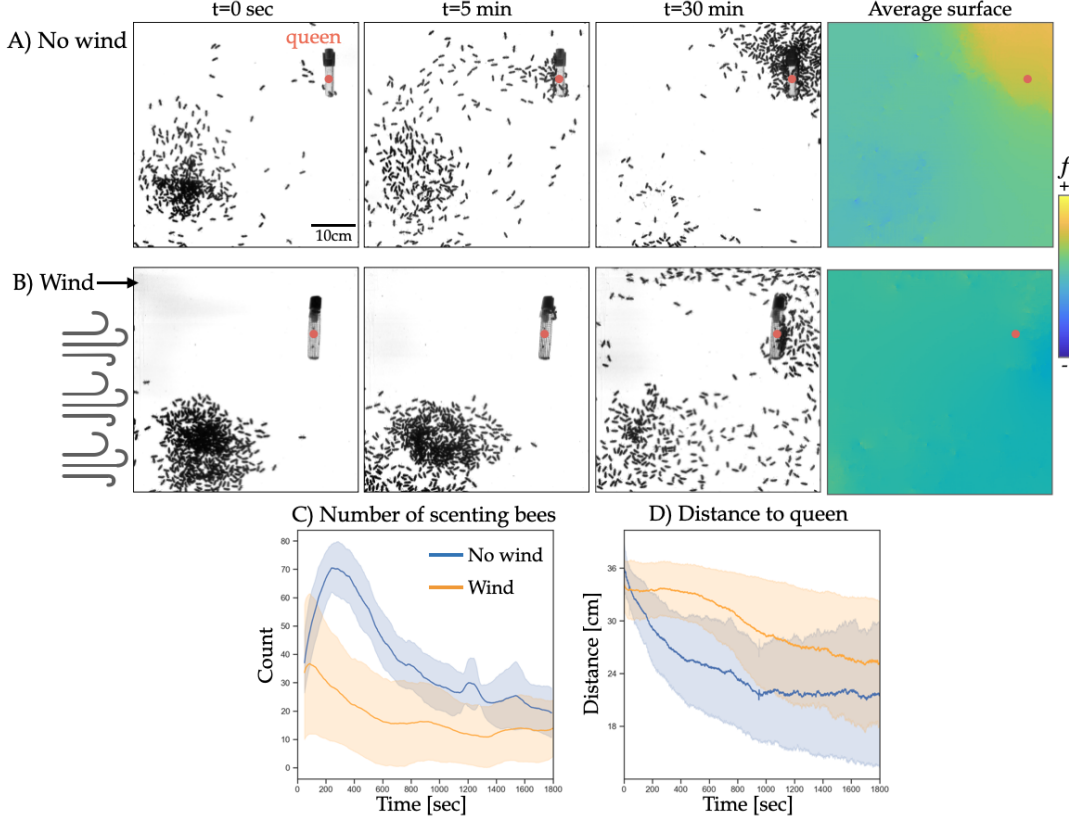
Lastly, we show the progression of the CMA-ES algorithm over iterations of the optimization process for both wind conditions with various values of  $w_w$ . For all conditions, the average cost decreases over time, and converges to relatively lower costs in lower  $w_w$  conditions. In other words, the algorithm converges in fewer number of iterations with lower  $w_w$ , and progresses all the way to the user-defined maximum of 50 iterations in  $w_w = 300$ .

### 4 DISCUSSION

In this study, we explore the impact of external wind on the pheromone communication of honey bees, particularly when searching for and aggregating around the queen. Our experimental findings indicate that wind entering the square arena from one side reduces the number of bees detecting the scent. Our data suggests that wind introduced from one side of a square arena diminishes the bee's ability to detect and follow the local scent gradients. This disruption in scent directionality can negatively impact group behaviors, such as swarming, where precise pheromone communication is pivotal.

We take inspiration from the experimental results of a single wind condition to further explore the impacts of external wind on the behavioral parameters (detection threshold,  $T$ , and magnitude



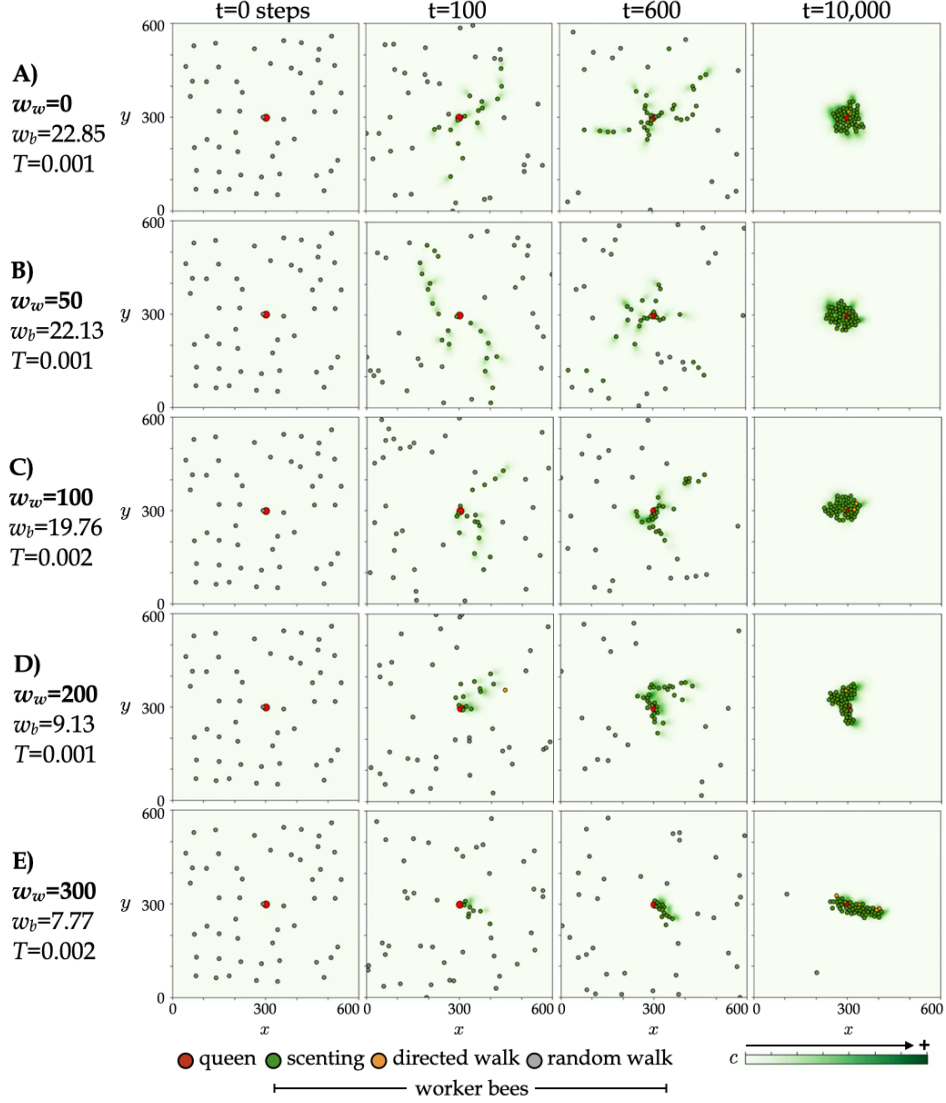


**Figure 1: Experiments in the presence and absence of external wind. A)** Snapshots of an example experiment ( $N = 320$  bees) in a relatively simple environment without external wind. The queen bee is caged and placed at the top right corner. Worker bees are placed at the bottom left corner. Over time, the bees form a collective scenting network and aggregate around the queen after approximately 30 minutes. The average attractive surface correlating scenting events and the density of bees over all time frames show that the most “attractive” area (high  $f$  values) is the area around the queen. **B)** Snapshots of an example experiment ( $N = 360$  bees) in an environment with external wind flowing toward the right side of the arena. Only a fraction of bees aggregate around the queen by the end of our 30-minute experiment. The average surface is relatively flat and does not indicate a particular area of highest attraction. **C)** The average number of scenting bees over time for experiments with (orange curve) and without (blue curve) wind. **D)** The average distance to the queen over time for experiments with (orange curve) and without (blue curve) wind.

of biased emission or wing-fanning,  $w_b$ ) and collective mechanism of localization and aggregation in an agent-based model of honey bee behavior in a more complex environment with unidirectional and turbulent wind of various magnitudes. We find that, in unidirectional wind, at lower wind magnitudes ( $w_w \leq 100$ ), the bees employ the normal collective scenting strategy with low  $T$  (e.g.,  $T \approx 0.001$ ) and intermediate  $w_b$  (e.g.,  $w_b \approx 22$ ) values to form a network of signal receivers and senders, spatially spread throughout the arena. Similarly, at higher wind magnitudes ( $w_w \geq 200$ ), the optimal parameters maintain low  $T$  values, but the bees lower their  $w_b$  or wing-fanning magnitude to achieve aggregation around the queen into a single cluster. Additionally, at higher unidirectional wind, bees spatially align more along the wind’s direction (towards the right of the arena) to scent and follow the pheromone signals. As this necessary alignment limits the arena’s space for signals to spread and be received by bees, the optimal simulations at

high wind show less pronounced scenting percolation (i.e., shorter scenting chains) as bees rely more on approaching the queen and the right-biased scenting chains via random walk to sense local pheromone signals. While an environmental factor’s magnitude may surpass the bees’ ability to adapt and survive, there may be a range of wind magnitudes in which the insects’ communication networks remain robust. Our modeling results show that individual agents with simple rules of behavior can collectively adapt to some wind conditions. The individual bees’ ability to scent directionally and thus collectively aligning a scenting network along the wind’s direction may contribute to the robustness of their communication network.

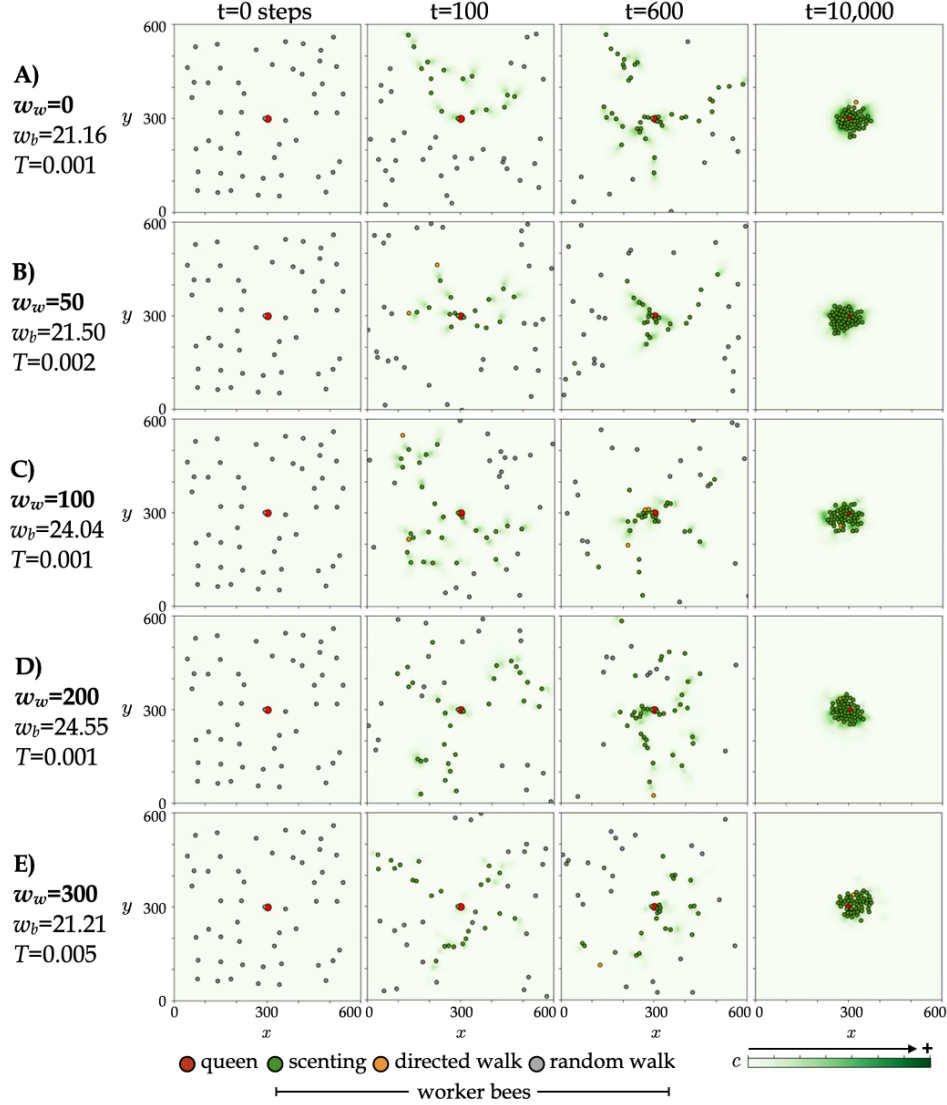
While our model shows that unidirectional wind affects the mechanism of localization and aggregation, turbulent wind flowing in random directions does not interfere with the directional scenting signals produced by bees. If the bees were placed in a



**Figure 2: Simulations of the optimal behavioral parameters (bias magnitude,  $w_b$ , and concentration threshold,  $T$ ) in the presence of uni-directional wind of various magnitudes ( $w_w$ ). A) Snapshots of the optimal simulation of parameters  $w_b = 22.85$  and  $T = 0.001$  for  $w_w = 0$  or no wind. B) Snapshots of the optimal simulation of parameters  $w_b = 22.13$  and  $T = 0.001$  for  $w_w = 50$ . C) Snapshots of the optimal simulation of parameters  $w_b = 19.76$  and  $T = 0.002$  for  $w_w = 100$ . D) Snapshots of the optimal simulation of parameters  $w_b = 9.13$  and  $T = 0.001$  for  $w_w = 200$ . E) Snapshots of the optimal simulation of parameters and  $w_b = 7.77$  and  $T = 0.002$  for  $w_w = 300$ .**

different initial configuration, such as densely concentrated at one corner of the arena with the queen at the opposite corner as in the experiments, strong turbulent wind may have disrupted the scenting network produced by the bees as this network would be more directionally constrained and turbulent wind may lead to random signal directions. In our model's current initial configuration with bees homogeneously spread out in the arena and scenting percolation chains can form in any direction, turbulent wind has a minimal effect. Future modeling work will explore different initial configurations of bee positions.

In our study, we conduct wind experiments with actual bees, but we were limited to testing only one wind speed and direction. This is because of both experimental constraints and the fact that our subject animals are seasonal. Our future experiments should introduce wind of various magnitudes and directions to compare to our model results and observe whether the real bees will adjust the spatial arrangement of their scenting networks in some wind conditions as we observed in the simulations. The iterative comparisons between experiments and simulations will provide better insight



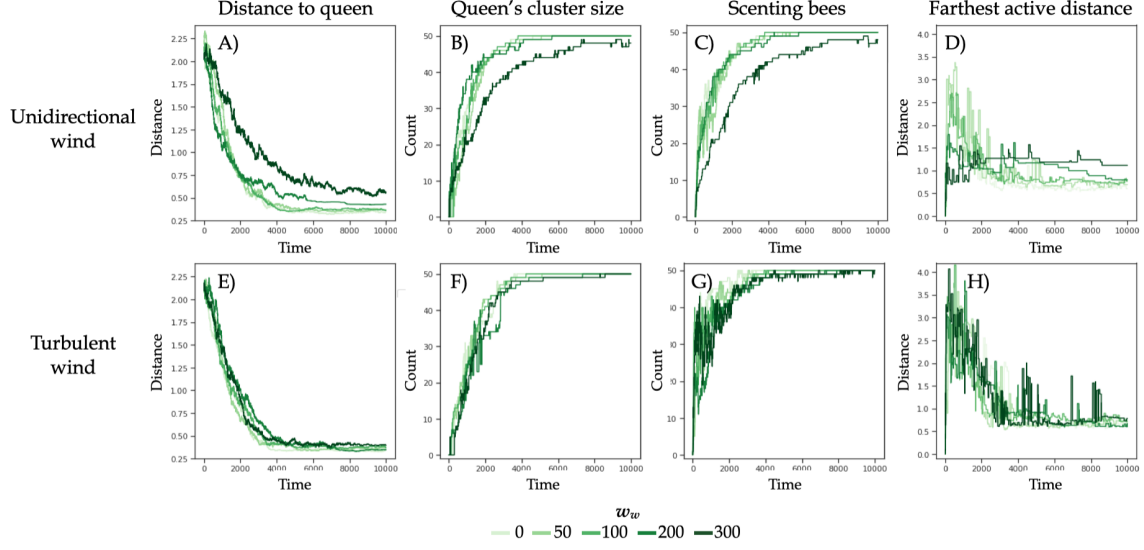
**Figure 3: Simulations of the optimal behavioral parameters (bias magnitude,  $w_b$ , and concentration threshold,  $T$ ) in the presence of turbulent wind of various magnitudes ( $w_w$ ). A) Snapshots of the optimal simulation of parameters  $w_b = 21.16$  and  $T = 0.001$  for  $w_w = 0$  or no wind. B) Snapshots of the optimal simulation of parameters  $w_b = 21.50$  and  $T = 0.002$  for  $w_w = 50$ . C) Snapshots of the optimal simulation of parameters  $w_b = 24.04$  and  $T = 0.001$  for  $w_w = 100$ . D) Snapshots of the optimal simulation of parameters  $w_b = 24.55$  and  $T = 0.001$  for  $w_w = 200$ . E) Snapshots of the optimal simulation of parameters and  $w_b = 21.21$  and  $T = 0.005$  for  $w_w = 300$ .**

into the natural mechanisms the bees use to overcome such environmental challenges. Additionally, in the real world, animals may encounter multiple environmental perturbations at once. Therefore, studying the bees in a real or virtual environment with both wind and physical obstacles would be highly relevant and insightful. Lastly, the model so far only considers how wind affects pheromone signals. Future iterations of the agent-based model should take into account how wind, especially in higher magnitudes, can cause physical displacement of the bees, which may change the dynamics of

the scenting communication network and aggregation around the queen.

## ACKNOWLEDGMENTS

This work was supported by the National Science Foundation Graduate Research Fellowship Program under Grant No. DGE1650115 (D.M.T.N.) and Physics of Living Systems Grant No. 2014212 (O.P.).

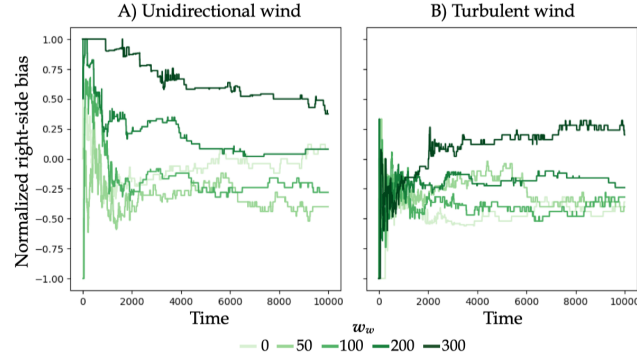


**Figure 4: Time series of simulations of the optimal behavioral parameters. A-D) Unidirectional wind of magnitudes  $w_w = 0, 50, 100, 200, 300$ . E-H) Turbulent wind of the same magnitudes. A,E) The average distance to the queen over time. B,F) The average queen's cluster size. C,G) The average number of scenting bees. D,H) The average distance of the farthest active bee to the queen.**

Any opinion, findings, and conclusions or recommendations expressed in this material are those of the authors(s) and do not reflect the views of the NSF.

## Supplementary Information

Open-source code for the computer vision pipeline and agent-based model are hosted at the following repositories: <https://github.com/peleg-lab/CollectiveScentingCV> and [https://github.com/peleg-lab/CollectiveScentingABM\\_Wind](https://github.com/peleg-lab/CollectiveScentingABM_Wind).

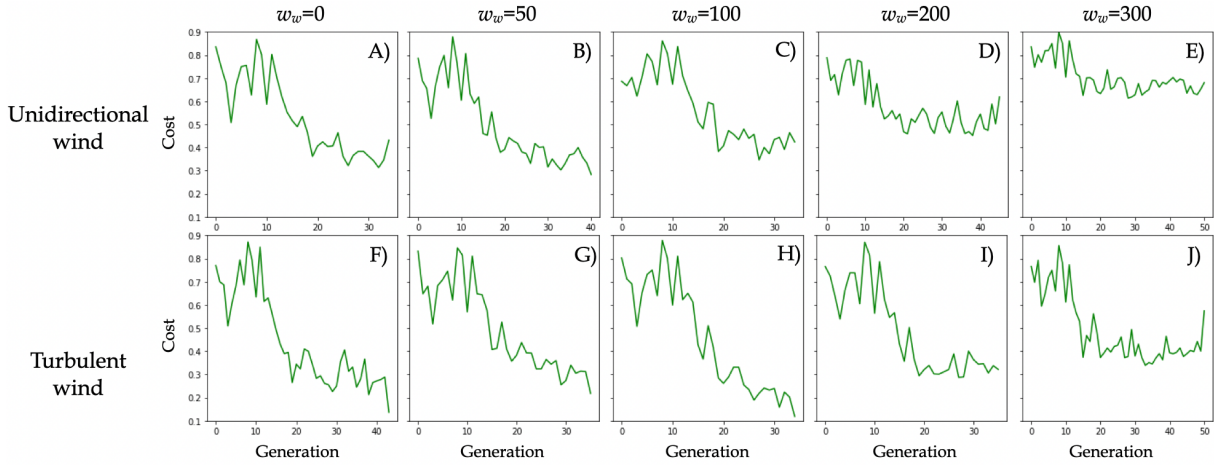


**Figure 5: Spatially biased percolation and aggregation. The difference between the number of scenting bees on the right side and on the left side of the arena over time. Each data point at a given time step is normalized by the total number of scenting bees at that time step. This normalized difference represents the spatial bias of scenting bees towards the right side of the arena; higher values indicate more bees scenting on the right or along the wind's direction in the case of uni-directional wind. A) The normalized right-side bias in optimal simulations with uni-directional wind flowing towards the right. B) The bias in optimal simulations with turbulent wind.**

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**Figure 6: CMA-ES optimization over iterations. A-E) The average cost of simulations in the iterations for unidirectional wind of magnitudes  $w_w = 0, 50, 100, 200, 300$ . F-J) The average cost of simulations in the iterations for turbulent wind of the same magnitudes.**

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