



Motion Dynamics of Foragers in Honey Bee Colonies

Fernando Wario^{1(✉)}, Benjamin Wild², David Dormagen², Tim Landgraf²,
and Vito Trianni¹

¹ ISTC, National Research Council, Rome, Italy
{fernando.wario,vito.trianni}@istc.cnr.it

² Department of Mathematics and Computer Science, Freie Universität Berlin,
Berlin, Germany
{b.w,david.dormagen,tim.landgraf}@fu-berlin.de

Abstract. Information transfer among foragers is key for efficient allocation of work and adaptive responses within a honey bee colony. For information to spread quickly, foragers trying to recruit nestmates via the waggle dance (dancers) must reach as many other non-dancing foragers (followers) as possible. Forager bees may have different drives that influence their motion patterns. For instance, dancer bees need to widely cover the dance floor to recruit nestmates, the more broadly, the higher the food source profitability. Followers may instead move more erratically in the hope of meeting a dance. Overall, a good mixing of individuals is necessary to have flexibility at the level of the colony behavior and optimally respond to changing environmental conditions. We aim to determine the motion pattern that precedes communication events, exploiting a data-driven computational model. To this end, real observation data are used to define nest features such as the dance floor location, shape and size, as well as the foragers' population size and density distribution. All these characteristics highly correlate with the bees walking pattern and determine the efficiency of information transfer among bees. A simulation environment is deployed to test different mobility patterns and evaluate the adherence with available real-world data. Additionally, we determine under what conditions information transfer is most efficient and effective. Owing to the simulation results, we identify the most plausible mobility pattern to represent the available observations.

1 Introduction

Honey bee colonies, along with ant and termite colonies, are the best-known examples of superorganisms, social groups made up of members of the same species which display signs of self-organization and collective intelligence [16, 22]. The honey bee foraging behavior has been intensely studied by the scientific community. Nevertheless, despite the general mechanisms underlying self-organization during foraging activities being well understood [11, 17], there is still much to learn about the effects of individual differences among bees and how

such differences impact the overall behaviors. In particular, information transfer among foragers is a key aspect, as it determines how the colony flexibly modulates the workload and adapts to external contingencies and internal demands. For information transfer, a good mixing of individuals is necessary, and this is supported by the ability of workers to move and meet other workers carrying valuable information.

The goal of this study is to understand how the motion patterns of foragers influence information exchanges. More specifically, we focus on waggle dances, whereby foragers recruit nestmates to valuable food patches. We aim at identifying the features of the motion pattern followed by bees before dancing and following behaviors. To this end, real observational data are used to define fundamental environmental properties (comb surface characteristics) such as dance floor location, shape and size, as well as colony features such as forager population size and density distribution, all characteristics that highly correlate with the bees motion pattern [14]. Then, a simulation environment is deployed to test different mobility patterns for forager bees within the hive. To determine the mobility pattern of simulated bees, we assume that foragers may or may not take into account the detailed characteristics of the dance floor. A correlated random walk model [1,6] follows the assumption that only an approximate location for the dance floor is known to the bees, which is modelled as a location bias toward which bees turn with a fixed probability. Conversely, a random waypoint model [2]) follows the assumption that the location and dimensions of the dance floor are known, as the model postulates that displacements are determined by randomly sampling target locations within the relevant areas. From simulations, we also obtain the interaction rate among foragers, which shows under what conditions information transfer is most effective and efficient. On such a basis, can we shed light on the most plausible assumptions by matching real-world observations with the simulations resulting from different mobility patterns? Answering this question will provide interesting hypotheses for further studying the information transfer abilities among forager bees, and will also suggest design principles for the efficient implementation of swarm robotic systems.

In the following, we describe the methodology used to model the environmental properties of the hive and to test the selected mobility patterns in our simulation environment (see Sect. 2). Then, we present and evaluate the results obtained from simulations in Sect. 3. Finally, in Sect. 4 we discuss the plausibility of the different mobility patterns being presented, and propose as a follow up to this work a detailed comparison between our simulation results and real-world data at the single trajectory level.

2 Methodology

As mentioned above, this study is grounded on real-world data, which were obtained using the BeesBook System [18], an experimental system that allows tracking marked bees within an observation hive during weeks. The system is highly reliable, localizing markers with a 98% recall at 99% precision and decoding more than 98% of the markers correctly [3,21]. A BeesBook dataset consists

of a list of registers detailing the position and identity of each marked bee—once detected—for each video frame during the full extension of the experimental season. Additionally, through the Waggle Dance Detector module [19], the Bees-Book system provides a record of dance activity that enumerates all detected dances, including duration and location on the honeycomb surface.

From this dataset, we obtained valuable information such as the spatial distribution of foragers and of the dances they performed, as well as the average speed of foragers. This information was used to define models for the dance floor and the density distribution of foragers on the honeycomb surface. This process is explained in the following section.

2.1 Data Preprocessing

The dataset used for the analysis was collected in 2016 during the months of July and August in Berlin, Germany. From this dataset, we considered 12 days between August the 8th and August the 19th, 2016. To focus our attention on the spatial distribution of foragers and dances, we first analyzed the local weather conditions—solar radiation, temperature and rainfall—during the experiment dates. These are known to impact foraging and, consequently, dancing activity [5,8]. From the analysis, we decided to limit the observation time window between 10:00 and 16:00 UTC+2, which covers the most favorable conditions for foraging and accordingly recorded the most relevant dance activity (see the top-left panel in Fig. 1). Overall, we considered a dataset with a total of 72 h, that shows fairly similar activity across all days and hours.

2.2 Foragers and Dances Distribution Models

Once obtained the dataset for the analysis, we extracted the information about the distribution of foragers and dances over the comb, in order to obtain an empirical model. In the case of the dance distribution, we observed that, within the considered time window, the dance rate was substantially homogeneous (see top-right panel in Fig. 1). Hence, we focused on the spatial distribution only. We began by dividing the surface of the comb in 21×37 cells of (1 cm^2) surface (the dimensions of the comb used during the recording season was $(21 \times 37 \text{ cm})$). Then, we computed the total number of dances for each cell during a day, as well as over the full temporal extension of the dataset. As the differences in the spatial distribution across days were negligible, we focused on the cumulative distribution over all days. This cumulative distribution was then normalized to represent the probability of a dance occurring in each of the defined cells. Finally, we fitted a 2D Gaussian function using non-linear least squares method to define a model for the dance floor (Gaussian centred at $\mu_d = (8.17, 12.42)$ with standard deviation $\sigma_d = (4.92, 3.96)$ and with standard deviation errors of $[5.28e-2, 4.25e-2, 7.53e-2, 6.02e-2]$, see the inset in the left panel of Fig. 2)

For the foragers' spatial distribution, first foragers were identified based on their social interaction patterns and spatial distributions in the nest [20], then

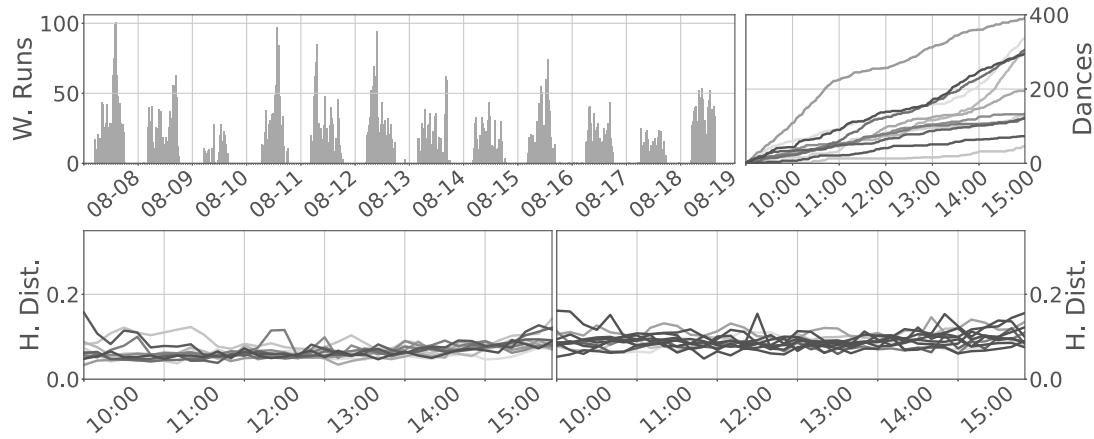


Fig. 1. Top left: Distribution of dances over multiple days. The number of waggle runs detected by the BeesBook system over a time interval of 1 min is displayed throughout the different days. Note that each dance consists of multiple waggle runs. Top right: Cumulative number of dances over different days. The cumulative distribution is approximately linear over the different days, indicating a constant rate of dances, although this rate differs from day to day. Bottom left: Hellinger distance between consecutive empirical density distributions during a day. Density distributions are computed over time intervals of 10 min, and compared to the previous time interval to show variations over time. Bottom right: Hellinger distance between empirical density distribution over 10-min intervals, and the overall model obtained from the whole dataset.

a grid over the image of the comb surface was defined. This grid, however, comprised of 46×70 cells, following the original structure of the BeesBook data-set. All the spatial parameters obtained for the model were later scaled properly. We then extracted the time series of the positions of all foragers, splitting the time series of each day into intervals of 10 min, and computing the cumulative distribution of foragers on the grid within each interval. These empirical distributions computed over these intervals were used to evaluate their homogeneity over time. To this end, we computed the similarity between distributions by means of the Hellinger distance [10]. The analysis shows that foragers density is fairly consistent during the selected window of time (see bottom-left panel in Fig. 1).

Similar to the dance distribution, once we validated the temporal homogeneity of the foragers' density, we computed the normalized-cumulative distribution over the full temporal extension of the dataset. Finally, to obtain a parametric model of the forager density, we fitted a 2D Gaussian function to the cumulative distribution using non-linear least squares method (Gaussian centred at $\mu_p = (8.73, 11.07)$ cm, with standard deviation $\sigma_p = (9.99, 5.60)$ cm and with standard deviation errors of $[7.62e-2, 4.29e-2, 1.20e-2, 6.14e-2]$, see Fig. 2 left). We computed the Hellinger distance between model and distributions of foragers over time to verify that the model was providing a good representation over and across different days (see bottom-right panel in Fig. 1). This analysis revealed

that the model grasps sufficiently well the empirical density distribution of foragers extracted from the data across the full observation period.

Overall, the Gaussian models match reasonably well the real-world data, as shown in Fig. 2 left. In particular, the model for the density distribution of foragers matches visibly well to real-world data, also confirmed by the small Hellinger distance of $3.59\text{e}-2$. Conversely, the Gaussian model for dances has a worse match to the observation data, mainly due to the absence of parts of the dances, as the observation camera for detecting dances was covering only the bottom-left section of the honeycomb close to the entrance. It is interesting to notice that the distribution of dances is similar to the density distribution, but shifted towards the entrance to the honeycomb. We hypothesize that such a shift stems from the fact that dances are executed right after the forager has returned from a foraging trip. Hence, they could be performed closer to the entrance as the forager trajectory starts there.

2.3 Multi-agent Simulations

We have built a simulation environment prepared to progressively incorporate the features derived from the real-world observations, and to test the effect of different mobility patterns. The virtual arena is customized after the dimensions of the honeycombs used during the experimental seasons (21×37 cm). Since our study focuses on mobility patterns that precede and follow dance communication activity, we only simulate the behavior of forager agents. For each simulation, we consider a forager population of 200 agents, that corresponds to the average number of foragers observed during the experimental season. We divided the forager population into two groups, dancers and followers. According to the literature [7], between 5% and 10% of the colony population engage in foraging activities, depending on the colony size and the resources available in the vicinity of the hive. For the colony studied during the experimental season and for the days we consider to define our models, around 35% of the colony population was identified as being part of the forager class. For simplicity, we consider in our simulations 20% of the forager population (or 7% of the colony population) as dancers (hence, at any time, we count 40 dancers and 160 followers). While both dancers and followers adopt the same mobility pattern and move over the comb surface at the same average speed (fixed to 5 mm/s in compatibility to the observation data), they display different behaviors concerning dance communication. Dancer agents are the only ones that can switch from move to dance state, during which they stay still in place and broadcast their known foraging site. The foraging site is not relevant for the present study, hence it is fixed and identical for all dancers. In order to reproduce the uniform distribution of dances over time observed on the experimental data, dancer agents stop and dance with a fixed probability per unit time p_d , which can be tuned to reproduce the rate observed experimentally in a given day. Considering that the simulation is advanced by one step every 0.25 s, to obtain in average 400 dances in a day we set $p_d = 1.16\text{e}-4$. Each dance event lasts a fixed amount of time (3 s).

Followers, on the other hand, continuously patrol their vicinity in search of dancing agents (move state). When they come close enough to an agent actively dancing (within 1 body length, i.e., 2 cm), they switch to the follow state, also standing still in place until the dancer ends its broadcast. If the interaction between dancer and follower(s) lasts long enough (>0.25 s), the communication is considered successful and the follower acquires knowledge of the foraging location communicated by the dancer.

The simulations employ the Gaussian model for the density distribution of foragers to determine the mobility pattern of the bees. At initialization, dancers are positioned at the bottom-left corner of the arena, which corresponds to the entrance to the hive, while followers are initialized at random positions on the comb surface following the density distribution model. For each mobility pattern, dancer agents evaluate at each step whether to dance or not, while followers stop only when they perceive a dance in their proximity, as specified above. After performing a dance, the agent is removed from the arena and a new dancer is introduced at the entrance. In this way, we mimic the behavior of dancer bees that leave the hive after unloading and communicating the foraging source to their nestmates [4, 15]. Also, in this way we want to test the hypothesis that the dance distribution is shifted due to a bias in the starting position of the dancers' trajectories.

In this paper, we report the results for two different mobility patterns adapted to the density distribution model: a random waypoint model (RWM) and a biased correlated random walk (CRW). The former uses the foragers density model as a probability distribution function to draw intermediate location goals. The latter uses the estimated center of the dance floor as a bias for the random walk. The details are provided below. Other mobility patterns like Lévy walks [1] could be considered, which are however less suited for a constrained space like the beehive.

Random Waypoint Model (RWM). This mobility pattern allows agents to explore the whole arena by choosing a random destination and moving straight until the destination is reached. In our simulations, the choice of the new destination is proportional to the empirical density distribution of foragers. More specifically, each new destination is drawn randomly exploiting the 2D Gaussian model we obtained from real-world data. Whenever agents stop—to dance or to follow a dance—they lose memory of their previous destination, and a new one is drawn when motion is resumed. This mobility pattern assumes that foragers have some knowledge of their location over the honeycomb—i.e., a map—that they exploit to choose where to move next.

Biased Correlated Random Walk (CRW). A correlated random walk is the simplest mobility pattern that can be imagined for the bees, as well as for many biological and artificial systems [1, 6, 9]. With this model, agents alternate straight walks and random turns. In this simulations, the duration of the straight walks is sampled from a folded normal distribution $N(0, \sigma_w)$, with $\sigma_w = 0.75$ s.

The turning angle is instead drawn from a wrapped Cauchy distribution, characterized by the following probability density function:

$$f_C(\theta; \mu, \rho) = \frac{1 - \rho^2}{2\pi (1 + \rho^2 - 2\rho \cos(\theta - \mu))}. \quad (1)$$

where μ represents the average and ρ the skewness of the distribution. In our simulation, $\mu = 0$ implies that the turning angle is correlated with the current direction of motion, while the parameter ρ is varied to control the degree of correlation of the random walk, obtaining different levels of persistence in moving towards a given direction. Considering that $0 \leq \rho < 1$, smaller values lead to a more uniform distribution, hence less correlated walks, while higher values of ρ correspond to a skewed distribution, hence highly correlated walks.

The *location bias* parameter β is used to calibrate the agents' bias to move towards the center of the foragers' density distribution. At every turning event, the agent evaluates whether to draw a new random angle or to orientate towards the center of the foragers' density model, based on the probability β . In the latter case, a Gaussian noise $N(0, \sigma_\beta)$ is also added to the rotation angle, with $\sigma_\beta = 0.2\pi$. This value has been empirically tuned to account for imprecision in the rotation towards the center of the dance floor.

While moving, agents can reach the borders of the arena. Since only one side of the comb is simulated, the arena is considered to be bounded, and when agents come across one of the borders during their motion, they stop and change direction moving away from the border towards the center of the forager density distribution. Additionally, whenever agents stop to dance or to follow a dance, they lose memory of the previous direction of motion, and they chose a new orientation uniformly-random as soon as they resume motion.

3 Results

We performed extensive simulations to understand the effect of the mobility pattern on (i) the density distribution of agents during simulations, (ii) the distribution of dances by simulated agents and (iii) the ability to transfer information between dancers and followers. In all simulations, dancers and followers employ the same mobility pattern. We implemented a total of thirteen different scenarios: one with RWM calibrated with the empirical density distribution of foragers, and 12 with the CRW by varying the parameters $\rho \in \{0, 0.3, 0.6, 0.9\}$ and $\beta \in \{0.01, 0.05, 0.1\}$. For each scenario, we ran 100 simulations, each one for $T = 28800$ time steps, equivalent to 2 h of colony activity. Similar to what was done with the real-world observation data, we divide the arena in a grid to compute the spatial distribution of foragers and dances. We also record which dancers and followers interact during dance communication events (dance partners) to analyze the information transfer and the level of mixing in the population.

The density distribution of all forager agents under the RWM mobility pattern is shown in Fig. 2 right. The correspondence with the Gaussian model calibrated on the empirical density distribution of foragers is remarkable, as also testified by the small Hellinger distance between the empirical density distribution and the simulations, which averages to 0.028 (see Fig. 4). This is somewhat expected given that the RWM exploits the full Gaussian model of the empirical density distribution to determine target destinations; hence movements are constrained within the areas with higher observed density. The distribution of dances shows a pattern similar to the forager density, with a negligible shift towards the entrance. This is because the RWM is characterized by a quick diffusion towards the area in which target destinations are sampled, hence it is not impacted significantly by the initial position of the (dancer) agents.

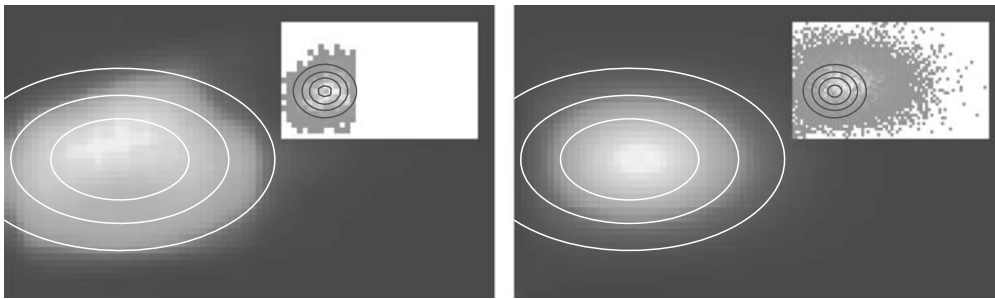


Fig. 2. Left: Overall empirical density distribution of foragers computed on the whole dataset. The background heatmap represents the empirical density distribution obtained from data. The white isolines represent the Gaussian model fitted on the data (centred at $\mu_p = (8.73, 11.07)$ cm, with standard deviation $\sigma_p = (9.99, 5.60)$ cm). Inset: overall dance distribution obtained from data. The black isolines correspond to the Gaussian model fitted on these data (center at $\mu_d = (8.17, 12.42)$ with standard deviation $\sigma_d = (4.92, 3.96)$). Note that the observation camera for dance events covers only the bottom-left part of the honeycomb, hence data points on the right part are missing. Right: density distribution of foragers obtained from simulations using the RWM. The heatmap corresponds to the distribution, while the white isolines correspond to the Gaussian model estimated from the real-world data. Inset: distribution of dances obtained from simulations. The black isolines correspond to the Gaussian model estimated from the data.

When the CRW mobility pattern is employed for dancers and followers, the interplay between persistence in motion and bias to return to the dance floor strongly determines the spatial distribution of the agents, as shown in Fig. 3. Specifically, the larger the location bias β , the narrower the dispersion of agents around the center of the density distribution model. Indeed, when the agents orientate towards the dance floor center with higher probability, they remain clustered and do not diffuse much across the honeycomb. The correlation coefficient ρ instead determines how much an agent would persist in a chosen direction. Generally speaking, higher values of ρ correspond to larger diffusion. This is particularly visible when the location bias β is small (left column in Fig. 3), but

has the opposite effect with a strong location bias. Indeed, if an agent frequently reorients towards the center, a high persistence will contribute to move to it even during the subsequent walks, while a small persistence would make agents quickly bend in a completely different direction, hence reducing the impact of the location bias. By comparing the Hellinger distance obtained over the 100 runs shown in Fig. 4, we observe that the best values are for an intermediate level of β , while we observe that ρ has smaller effects, with opposite trends for small or high values of β . Compared to the RWM, the CRW density distributions are slightly worse, but not much difference is observable for $\beta = 0.05$.

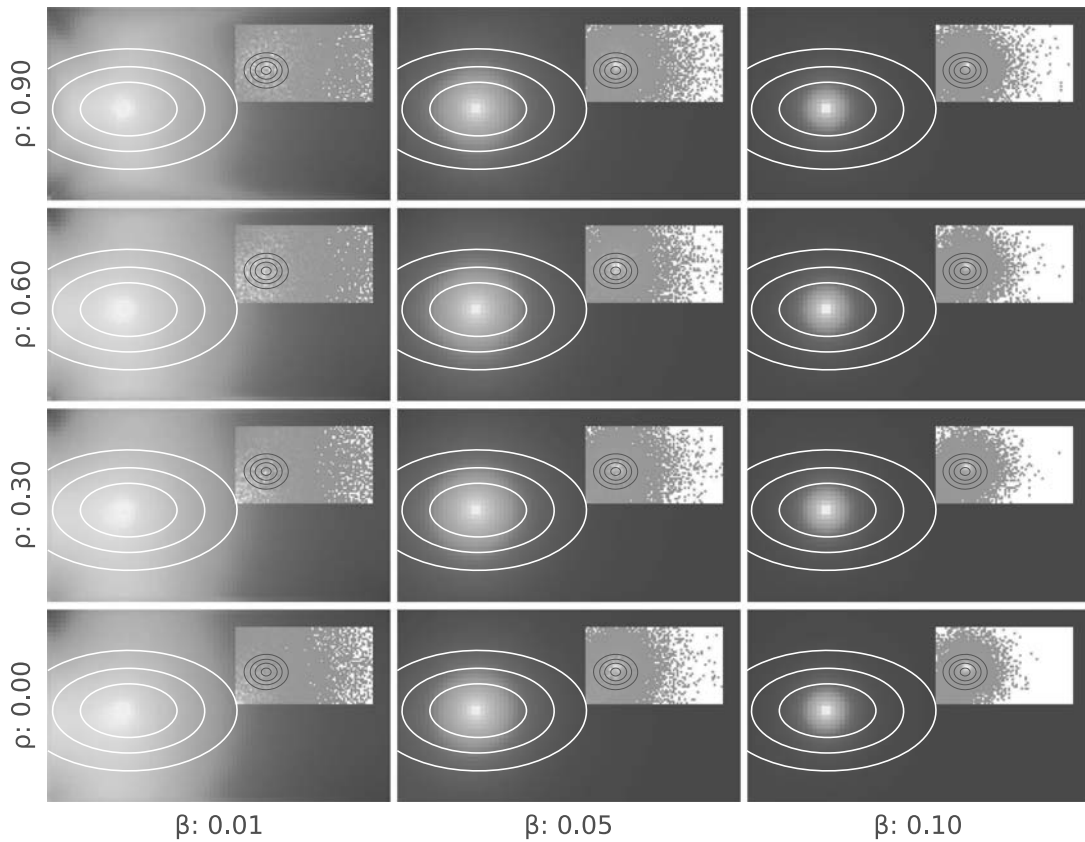


Fig. 3. Density distribution of foragers for each combination of β and ρ tested with simulations. The insets represent the distribution of dances for the same combination of parameters.

The insets in Fig. 3 show the dance distribution obtained with simulations when the CRW mobility pattern is employed, and compare to the Gaussian fit obtained from real-world data (black). The shift towards the entrance is remarkable especially for low location bias ($\beta = 0.01$) and for small CRW persistence ($\rho = 0$). The former entails that movements are not frequently oriented toward the center, the latter entails a small diffusion of the agents. Hence, dancers do not reach the dance floor quickly and dances are mostly performed close to the entrance. Conversely, when β is high, dancers quickly stabilize their motion

around the final distribution, and the shift towards the entrance is less visible, in a similar way to what observed with the RWM. Intermediate values of the location bias correspond to the best qualitative match between the dance distribution observed in simulation and the model obtained from real data.

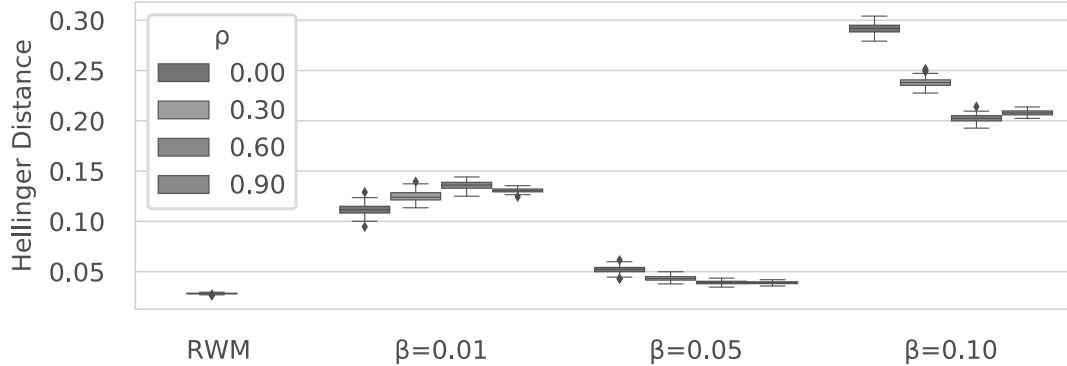


Fig. 4. The Hellinger distance computed between the density distribution obtained in each of the 100 simulation runs, compared to the Gaussian model obtained from the empirical density distribution.

Finally, we analyze the information transfer efficiency for all the studied scenarios (see Fig. 5). To this end, we compute the convergence time as the time required for all followers to obtain information about the foraging site by attending to one dance, at least. We compute the cumulative distribution function of the convergence times across the 100 runs using the Kaplan-Meier estimation [12], censoring those runs that do not converge within the allotted time. We fit a Weibull distribution on the estimated function and use the fitted function to compute average and standard deviation of the convergence times. The average values are shown in the left panel of Fig. 5. Additionally, we show the average number of followers for each dance event (middle panel) and the redundancy of information received by a forager, computed as the number of different dance partners encountered during the simulation (right panel). The RWM leads to rather fast convergence, with a moderate number of interactions and mild redundancy (see the red arrow on the colorbars in Fig. 5). Concerning the CRW, it is possible to note that, the higher the location bias β , the faster the transfer of information between dancers and followers. This is because the foragers are compact around the center of the dance floor, and interactions are numerous (higher number of followers per dance event) but also very redundant (higher number of partners per follower). Also in this case, the CRW persistence ρ has opposite effects depending on the location bias β , as the two parameters concur in determining the diffusion of agents away from the dance floor.

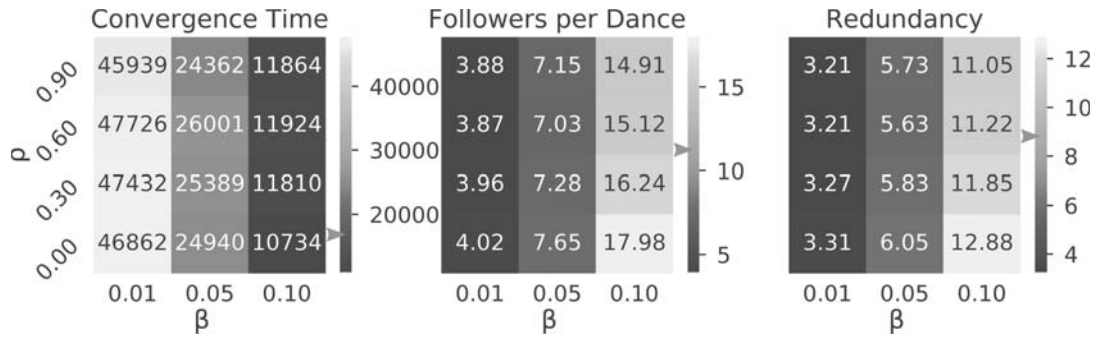


Fig. 5. Information transfer efficiency and effectiveness with different mobility patterns. Each panel represents the average over 100 runs. The matrices show the results for CRW. The results for the RWM are indicated by a red triangle on the colorbar. Left: Average convergence time. Centre: Average number of followers for each dance event. Right: Redundancy of information received, computed as the average number of different partners recorded for each follower agent.

4 Discussion and Conclusions

The comparison made between the empirical density distribution and the simulated one allows us to speculate about the plausibility of the mobility pattern we have implemented. The RWM is clearly the one that produces the best match. However, its implementation would entail that bees are precisely aware of their location over the honeycomb, relying on a kind of map to choose the next location to move to. Additionally, the negligible shift towards the entrance observed in the distribution of dances also makes less plausible the RWM. In fact, to obtain a better match, dancer bees should employ a different map than follower bees, but as each forager can take both roles, it would be difficult to imagine that the employed map changes according to the role. On the contrary, the CRW model is based on much more parsimonious assumptions. Here, we assume only that bees can re-orient towards the dance floor—with noise—with a certain probability. Having a sense of the direction of the dance floor is a much less cognitively-demanding ability than a complete map of the honeycomb. Additionally, the CRW provides a better match for the distribution of dances, for the same parameters that minimize the difference between empirical and simulated density distribution of foragers (i.e., $\beta = 0.05$). Finally, the ability to transfer information among foragers—as observed with the CRW—also suggests that intermediate levels of location bias allow to satisfactorily deal with the trade-off between convergence time and redundancy.

Future work will attempt to confirm the above discussion by looking at the detailed bees trajectories available from the BeesBook system. By looking at the real trajectories, a data-driven model can be made to determine what type of motion foragers perform, and how this is impacted by the local density of bees. Most importantly, we want to differentiate the trajectories that precede a dance communication event, to distinguish between dancers, followers and “idle” foragers, in order to understand how the behavioral state of foragers impacts

on its motion. We could actually observe differences between them that could support better techniques to spread information rapidly within the swarm. The gathered knowledge can be very useful to improve the design of artificial bee-inspired systems (e.g., swarm robotics systems [9,13]).

Acknowledgements. This work was partially supported by CONACYT, Mexico, through a grant for postdoctoral stay abroad, scholarship holder No. 272227.

References

1. Bartumeus, F., Da Luz, M.G., Viswanathan, G.M., Catalan, J.: Animal search strategies: a quantitative random-walk analysis. *Ecology* **86**(11), 3078–3087 (2005). <https://doi.org/10.1890/04-1806>
2. Bettstetter, C., Hartenstein, H., Pérez-Costa, X.: Stochastic properties of the random waypoint mobility model. *Wirel. Netw.* **10**(5), 555–567 (2004). <https://doi.org/10.1023/B:WINE.0000036458.88990.e5>
3. Boenisch, F., Rosemann, B.M., Wild, B., Wario, F., Dormagen, D., Landgraf, T.: Tracking all members of a honey bee colony over their lifetime. *Front. Robot. AI* **5**, 1–10 (2018). <https://doi.org/10.3389/FROBT.2018.00035>. <https://arxiv.org/abs/1802.03192>
4. Camazine, S., Sneyd, J.: A model of collective nectar source selection by honey bees: self-organization through simple rules. *J. Theoret. Biol.* **149**(4), 547–571 (1991). [https://doi.org/10.1016/S0022-5193\(05\)80098-0](https://doi.org/10.1016/S0022-5193(05)80098-0)
5. Clarke, D., Robert, D.: Predictive modelling of honey bee foraging activity using local weather conditions. *Apidologie* **49**(3), 386–396 (2018). <https://doi.org/10.1007/s13592-018-0565-3>
6. Codling, E.A., Plank, M.J., Benhamou, S.: Random walk models in biology. *J. R. Soc. Interface* **5**(25), 813–834 (2008). <https://doi.org/10.1098/rsif.2008.0014>
7. Danka, R.G., Gary, N.E.: Estimating foraging populations of honey bees (Hymenoptera: Apidae) from individual colonies. *J. Econ. Entomol.* **80**(2), 544–547 (1987). <https://doi.org/10.1093/jee/80.2.544>
8. Devillers, J., Doré, J.C., Tisseur, M., Cluzeau, S., Maurin, G.: Modelling the flight activity of *Apis mellifera* at the hive entrance. *Comput. Electron. Agric.* **42**(2), 87–109 (2004). [https://doi.org/10.1016/S0168-1699\(03\)00102-9](https://doi.org/10.1016/S0168-1699(03)00102-9)
9. Dimidov, C., Oriolo, G., Trianni, V.: Random walks in swarm robotics: an experiment with kilobots. In: Dorigo, M., et al. (eds.) ANTS 2016. LNCS, vol. 9882, pp. 185–196. Springer, Cham (2016). https://doi.org/10.1007/978-3-319-44427-7_16
10. Hellinger, E.: Neue Begründung der Theorie quadratischer Formen von unendlichvielen Veränderlichen. *Journal für die reine und angewandte Mathematik* **136**, 210–271 (1909). <http://eudml.org/doc/149313>
11. Johnson, B.R.: Division of labor in honeybees: form, function, and proximate mechanisms, January 2010. <https://doi.org/10.1007/s00265-009-0874-7>
12. Kaplan, E.L., Meier, P.: Nonparametric estimation from incomplete observations. *J. Am. Stat. Assoc.* **53**(282), 457–481 (1958). <https://doi.org/10.1080/01621459.1958.10501452>
13. Miletitch, R., Dorigo, M., Trianni, V.: Balancing exploitation of renewable resources by a robot swarm. *Swarm Intell.* **12**(4), 307–326 (2018). <https://doi.org/10.1007/s11721-018-0159-8>

14. Ortis, G., Frizzera, D., Seffin, E., Annoscia, D., Nazzi, F.: Honeybees use various criteria to select the site for performing the waggle dances on the comb. *Behav. Ecol. Sociobiol.* **73**(5), 1–9 (2019). <https://doi.org/10.1007/s00265-019-2677-9>
15. Seeley, T.D.: Social foraging by honeybees: how colonies allocate foragers among patches of flowers. *Behav. Ecol. Sociobiol.* **19**(5), 343–354 (1986). <https://doi.org/10.1007/BF00295707>
16. Seeley, T.D.: The honey bee colony as a superorganism. *Am. Sci.* **77**(6), 546–553 (1989)
17. Seeley, T.D.: *Honeybee Democracy*. Princeton University Press, Princeton (2010)
18. Wario, F., Wild, B., Couvillon, M.J., Rojas, R., Landgraf, T.: Automatic methods for long-term tracking and the detection and decoding of communication dances in honeybees. *Front. Ecol. Evol.* **3**, 1–14 (2015). <https://doi.org/10.3389/fevo.2015.00103>
19. Wario, F., Wild, B., Rojas, R., Landgraf, T.: Automatic detection and decoding of honey bee waggle dances. *PLoS ONE* **12**(12), 1–16 (2017). <https://doi.org/10.1371/journal.pone.0188626>. <http://arxiv.org/abs/1708.06590>
20. Wild, B., et al.: Social networks predict the life and death of honey bees. *bioRxiv* (2020). <https://doi.org/10.1101/2020.05.06.076943>. <https://www.biorxiv.org/content/early/2020/05/06/2020.05.06.076943>
21. Wild, B., Sixt, L., Landgraf, T.: Automatic localization and decoding of honeybee markers using deep convolutional neural networks, February 2018. <http://arxiv.org/abs/1802.04557>
22. Wilson, D.S., Sober, E.: Reviving the superorganism. *J. Theoret. Biol.* **136**(3), 337–356 (1989). [https://doi.org/10.1016/S0022-5193\(89\)80169-9](https://doi.org/10.1016/S0022-5193(89)80169-9)