Data-Driven Modeling of Distributed Resource Sharing in Honeybee Swarms

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1. INTRODUCTION

Autonomous, adaptive and robust interaction networks allow super-organisms to exchange information and resources between their individual building blocks. These networks play critical roles in the function of these entities. In honeybees [Seeley 2009], for instance, communication networks allow sensing and reproduction of tactile signals, thus serving as "signal amplifiers" for information about the location of food sources. And bees do not just share information about the location of food; they also share food itself via regurgitation, essentially "charging" nestmates who do not have access to that resource. This process, termed Trophallaxis and shown in Fig. 1A, allows fast and efficient dissemination of nutrients through the colony and is crucial for its survival [Farina 1996]. There are subtleties in this process, though. Among other things, a bee that just finished feeding a nestmate faces a dilemma that is depicted in Fig. 1B: should it feed another nearby nestmate or move to feed a nestmate at a new spot? To answer that question, and to identify efficient set of local rules of behavior that guide food distribution, we constructed an agent-based model of interactions via trophallaxis in honeybees (*Apis Mellifera* L.), using a set of behavioral experiments to design and validate that model.

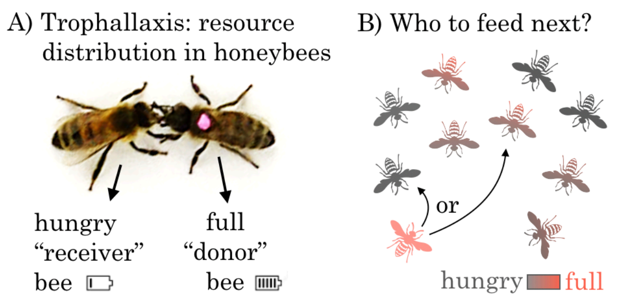

Fig. 1: Distributed resource sharing in honeybee swarms. A) Two bees performing Trophallaxis – exchange of regurgitated food in an assay for automatically monitoring of interactions [4]. B) Forager bees come back with full stomachs and share their food with hungrier nestmates.

2. BEHAVIORAL EXPERIMENTS

Four different colonies of honeybees *Apis mellifera* L. were used to conduct four sets of behavioral experiments. Fig. 2A shows a sketch of our experimental setup. The arena is a $33 \times 33cm$ square, covered with non-glare plexiglass to keep the bees contained and limit their motion to 2D. We recorded a top view of the arena (see Fig 2B) using a Video Camcorder (29.97 fps), for about 30 minutes in each experiment. The subject bees were collected one day in advance and divided into two separate groups totalling about 120 individuals. One group was *deprived* of food for 24 hours before each experiment; the others had constant access to food. These *fed* bees, which comprised 5-10% of the whole population in each experiment, were carefully marked with a pink circle on their thorax. We started each experiment by introducing the deprived bees into the arena and allowing them 15 minutes of equilibration time before introducing the fed bees. Trophallaxis encounters began shortly thereafter (Fig. 2B).

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Our main observation from these video recordings of the experiments was that the bees start to aggregate as the fed bees are introduced to the group, as opposed to the more scattered arrangement at the start of the experiments; see the two snapshots from the experiments in fig. 2B. To quantify this observation, we used the notion of *connected components*, to study how the presence of full bees would affect the arrangement of the group. In particular we measured and tracked how the size of these bee clusters change as time passes. We found that the number of bees that join the clusters increases after the introduction of the fed bees; see the increasing trend of the red line in fig. 2D.

3. THE DATA-DRIVEN AGENT-BASED MODEL

Previous theoretical and computational approaches in modeling collective trophallactic systems made significant progress using tools from network theory and statistical physics to describe the food intake in a colony at the limits of infinite colony size and long time scales [Gräwer et al. 2017; Greenwald et al. 2018]. Here, we extend these models to account for the spatial inhomogeneity observed in our experiments. We design an agent-based model of honeybee interaction which helps us understand how simple, local rules regarding trophallaxis, followed by all members of a bee colony, can lead to efficient, global food distribution across the group. The simulations proceed on a 33×33 gridded square box with periodic boundaries. The amount of food that agent i carries in the n^{th} time step, denoted as $f_i(n)$, is shown with gradations of red in Fig. 2C. Agents are categorized into two different sets according to their initial food level: $f_i(0) = 1$ and $f_i(0) = 0$, respectively, to match the fed and deprived bees in the experiments. In the beginning of each simulation, both sets of bee-agents are dispersed randomly across the simulation arena, with random initial headings. Agents move via a correlated random walk: at each step, they modify their previous heading by an angle increment $\Delta\theta$, drawn from a uniform distribution with mean $\theta = 0$ and standard deviation θ^*, and then take one step in the new direction to the next neighborhood cell. This random walk is biased to model attraction between individuals:

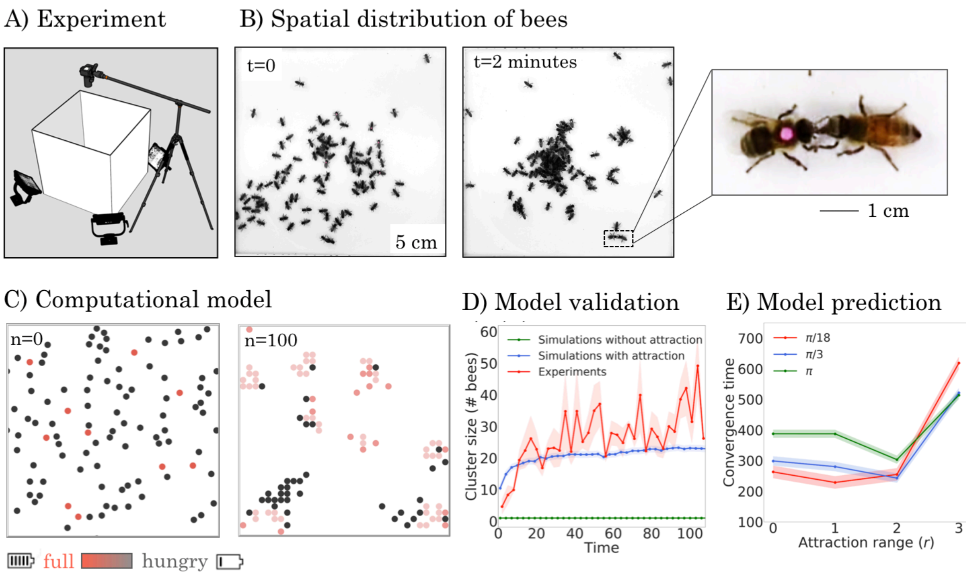

Fig. 2: A) Experimental setup. B) Spatial distribution of bees in the experiments. C) Evolution of our computational model with attraction D) Cluster size compared in experiments and simulations with and without attraction. E) Convergence time of the model with attraction for different θ^* values.

bee-agents that are within an *attraction range* of radius (r) move to the next neighborhood cell toward each other in the next time step. Trophallaxis exchanges happen when agents with different food levels encounter one another: if two available agents i and j are in the immediate neighborhood of one another, and $\Delta f(n) =\mid f_i(n) - f_j(n) \mid > 0$, then they initiate an exchange process in which the food is divided evenly between them. Both members of an encounter pair remain stationary until the exchange is complete. Previous studies have shown that the time required for the exchange is proportional to the amount of food involved [Greenwald et al. 2015]. To estimate realistic values for trophallaxis duration, we performed a separate set of experiments with the same honeybee species focusing on measuring all trophallaxis duration. We took the longest measured trophallaxis duration in those experiments (50 seconds) as an estimate of how long it takes to transfer the largest amount of food in the model. The simulation stops when the food is distributed evenly across all agents, as measured with a two-part metric that assesses both its variance across individual agents at each time step and the variation of that variance in successive time steps.

To validate our model, we compared the clusters formed by agents in the simulations with those of the natural bees in our experiments. As shown in Fig. 2D, the model with attraction is a good match to the natural behavior of the honeybees. Using this validated model, we then explored the effect of attraction range (r), width of the turning angle of the random-walk (θ^*), and density (ρ) on the efficiency of food distribution among the agents. This involved running the model with different values of these parameters and measuring the convergence time. As shown in Fig. 2E, that time generally increased with θ^*, for a particular density. *That is, a more-tightly constrained random walk leads to more-efficient food distribution.* Unsurprisingly, convergence is more rapid at higher densities, probably because of the associated increase in the encounter likelihood at each time step. Interestingly, the convergence time increased sharply when non-local or larger attraction ranges were allowed. That is, *short-range attractions can increase the efficiency of food distribution among the agents.* Our model is currently guiding another set of experiments, with the goal to study the effects of short-range attraction on honeybees' interactions.

4. DISCUSSION AND CONCLUSION

Social insects and their collective intelligence have always been a reliable source of inspiration for the design of artificial multi-agent systems, optimization algorithms, and mostly swarm robotics [Bonabeau et al. 1999]. Beyond its importance for understanding distributed feeding in biological systems, this study can inspire engineering applications, such as electrical power sharing in swarms of search and rescue robots [Schioler 2007]. A well-known problem in autonomous swarm robotics, for instance, is re-charging of robots that are far away from a charging station [Schmickl and Crailsheim 2006; Rubenstein et al. 2012]. To prosper, a honeybee colony has to solve a similar problem; their solution involves forager bees collecting resources (food) and sharing it via trophallaxis, essentially charging nestmates who do not have direct access to those resources.

To explore this behavior, we presented an agent-based model that is not only inspired by trophallaxis behavior, but also designed and validated using laboratory experiments on honeybees. The rules in the model, and the values of the free parameters in those rules, were chosen via targeted experiments; the overall model was validated via comparisons between the movement patterns in the real and simulated bees. A comprehensive set of simulation results, performed with the validated model, suggest that the movement patterns of the individual agents, as well as their density and the range over which they are attracted to one another, affect the food-distribution efficiency. In particular, a combination of small turning angles, higher densities, and shorter-range attraction leads to the most efficient food distribution among the agents. The results of this study could potentially be used in designing a local rule set for efficient, self-organizing resource-distribution systems.

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