

Collective Decision-Making in Honey Bee Foraging Dynamics

Valery Tereshko and Andreas Loengarov

School of Computing, University of Paisley, Paisley PA1 2BE, Scotland

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Abstract

We consider a bee colony as dynamical system gathering information from an environment and adjusting its behaviour in accordance to it. Intelligent decision-making emerges from enhancing the level of communication among the individuals. Since the foragers communicate information about the environment to the nest, the latter means enhancing the coupling level of colony and environment. When individuals are only informed at a local level, colony's decisions are thus also made locally. In other words, the choice is not a collective but individualistic one - trails to every profitable nectar source coexist, and the colony fails to select the most profitable source. Unlike, a colony of globally informed individuals exhibits collective intelligence, i.e. it is able to select the most profitable food source in an explored environment.

1 Introduction

Social insect societies consist of simple cognitive units that are only locally informed or uninformed yet are able to collectively make globally intelligent decisions in the selection of food sources. Even more impressive is the fact that these globally intelligent decisions are made about an environment of food sources which is varying both widely and rapidly. It is therefore important for the survival of insect societies that they be able to search large regions for food sources and act quickly to exploit any rich discoveries. In adapting to perform these tasks, social insects have developed many ways of communicating information between individuals, pheromone trail laying, stridu-

lation, and the celebrated waggle dance to name a few examples.

We are interested in seeing how the synergistic information exchanging interactions between the individuals leads to globally intelligent selection of food sources in an unpredictable environment. To achieve the latter, we develop a simple model of these interactions which will be able to quickly select the "best" food source in a changing environment of food sources. Although these models may be generalized to all social insect societies, we will focus for concreteness on the behaviors of the honeybee. Honeybees are also special among social insects for the importance of the nest as a center of information and recruitment. In social insects such as ants, recruitment also occurs at the nest, but a more important form of communication and recruitment may be pheromone laying in the field. We are interested not only for applications to human endeavors, but also the evolution of communication in a society.

We consider a bee colony as dynamical system gathering information from an environment and adjusting its behaviour in accordance to it. Intelligent decision-making emerges from enhancing the level of communication among the individuals. Since the foragers communicate information about the environment to the nest, the latter means enhancing the coupling level of colony and environment. This approach is in line with dynamical theory of cognition, when an agent's nervous system, its body and its environment are each described as coupled dynamical systems. An agent's behaviour arises, thus, from the interaction between its brain, body and environment, and a trajectory of the complete dynamical system

formed by their coupling [1].

2 Description of System and Background

Previous mathematical models have been put forth of the collective selection of food sources by social insects which show very good quantitative agreement to experimental results [2]. This model grouped bee activity into four compartments, unloading nectar from a source, dancing for a source, feeding at a source, or following a dancer, and corresponding probability functions were developed for changing between these activities.

The minimal model of forage selection that lead to the emergence of collective intelligence has been developed [3, 4]. It consists of three essential components: food sources, employed foragers, and unemployed foragers, and defines two leading modes of the behaviour: recruitment to a nectar source and abandonment of a source.

Food Sources: The value of a food source to an insect depends on many factors including its proximity to the nest, richness or concentration of energy, and the ease of extracting this energy. For the simplicity of our model, however, we wish to describe the “profitability” of a food source with a single quantity. Experimental research gives us an idea of how these factors are ranked in an insects evaluation of the profitability of a source. It has been shown that a richer source that is further from the nest elicits the same profitability rating (as measured by number of waggle dances) as a source that is closer but not as rich, when they have the same net energetic efficiency [5]. That is, when the energy gain minus the energy cost divided by the energy cost is the same. It is this number, therefore, that we will use to describe our food sources. In our model, we wish to see how insects react to food sources with different values of this quantity, if they always are able to select the “best” food source in a changing environment.

Employed Foragers: Employed foragers are associated with a particular food source which they are currently exploiting or are “employed” at. They

carry with them information about this particular source, its distance and direction from the nest, and the profitability of the source. Employed foragers will share this information with a certain probability. The greater the profitability of a food source, the higher the probability the honeybee will do a waggle dance and share her information with her nestmates. Note, however, that employed foragers are only locally informed — they know only of the food source they are currently exploiting and continue frequenting this food source until it is depleted, at which point they become unemployed foragers.

Unemployed Foragers: Unemployed foragers are looking for a food source to exploit. There are two types of unemployed foragers, scouts, who search the environment surrounding the nest (up to a 14 km radius) in search of new food sources, and onlookers who wait in the nest and find a food source through the information shared by employed foragers. Insect societies are quite sophisticated in their distribution of unemployed foragers. The percentage of unemployed foragers who are scouts varies from 5% to as much as 30% depending on the influx of information into the nest. The mean number of scouts averaged over conditions is about 10% [5].

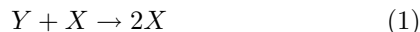
The model we developed elucidates the role of the nest as a reservoir of information, and the importance of information circulating freely throughout this reservoir. Each piece of information about the environment is able to circulate throughout the entire nest, but information about each region of the environment does not abound in equal quantities. The more insects who are recruiting for a different source, the more information there is circulating through the nest about this source, and this information carries more weight the greater the profitability of the source. So the value of a source is conveyed in the proportion of information about the source. Insects are recruited when information of a source reaches them, therefore they are recruited to each source in proportion to the amount of information circulating about that source.

Since information about all the current rich sources being exploited is available to an onlooker on the dance floor, presumably she could just watch numerous dances and choose to employ herself at the most

profitable source (as gleaned from number of waggle runs). Research has shown, however, that this is not what actually happens inside the nest [5]. Onlookers rarely watch an entire dance before alighting to the source indicated, therefore they cannot be taking into account the source profitability as this information is coded in the duration of the dance! How are bees preferentially recruited to more profitable sources? In the same manner as described above. There is a greater probability of onlookers choosing more profitable sources because at any given time more information is circulating about the more profitable sources. Employed foragers share their information with a probability which is proportional to the profitability of the food source, and the sharing of this information through waggle dancing is longer in duration. So at any given moment, the amount of information circulating about a food source will be proportional to the profitability of that source. In [3, 4], based on the above arguments, the recruitment is proportional to profitability of a food source. For simplicity, the abandonment is equally probable for all sources. In this paper, we make our model more biologically plausible taking into account the fact that onlookers pick up the dancer at random. Thus, the recruitment is now equally probable for any food source. Unlike, based on experimental data [5], the abandonment is inversely proportional to source's profitability.

3 Model

Let us formalize the foraging mechanism, the stages of which can be described in terms of chemical reactions. Employed and unemployed foragers are denoted by X and Y respectively; the nectar source by F :



Reaction (1) illustrates the autocatalytic nature of the recruitment process. If an employed forager recruits a nestmate by means of a waggle dance to a food source at which it is employed, the recruit will in

turn reinforce the trail and recruit other nestmates, and so forth.

An employed forager abandons an unrewarding food source at a rate inversely proportional to that source's quality:

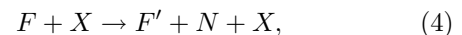


The kinetic equations corresponding to reactions (1-2) take the form

$$\begin{aligned} \frac{\partial x(\mathbf{r}, t)}{\partial t} &= \left(y(\mathbf{r}, t) - \frac{1}{f(\mathbf{r}, t)} \right) x(\mathbf{r}, t) + D_x \frac{\partial^2 x(\mathbf{r}, t)}{\partial \mathbf{r}^2} \\ \frac{\partial y(\mathbf{r}, t)}{\partial t} &= - \left(y(\mathbf{r}, t) - \frac{1}{f(\mathbf{r}, t)} \right) x(\mathbf{r}, t) + D_y \frac{\partial^2 y(\mathbf{r}, t)}{\partial \mathbf{r}^2}, \end{aligned} \quad (3)$$

where x and y are concentrations, and D_x and D_y are diffusion constants of employed and unemployed foragers respectively, and $f(\mathbf{r}, t)$ is *the food landscape*. Taking Wright's idea of fitness landscape which assigns a fitness to each point in a genetic space, the food landscape gives a food source quality value to each point in physical space. Numerous factors affect the assessment of food source quality as judged by an insect, such as proximity to the nest, richness (concentration of sucrose solution), ease of food extraction, predator risk. For the sake of simplicity, food sources are characterized by a single value proportional to the insects' characterization of the source, i.e. the larger the value, the "better" the source in the eyes of the insect. Experimental tests have confirmed that this single value may be the net energetic efficiency of the food source [5].

Once exploited for nectar, the food source F is depleted by the forager:



where F' is the depleted source, and N is the consumed nectar. This leads to a kinetic equation of the source depletion:

$$\frac{\partial f(\mathbf{r}, t)}{\partial t} = -\beta f(\mathbf{r}, t) x(\mathbf{r}, t), \quad (5)$$

where β is the characteristic rate of depletion. So the profitability of the i th food source decreases with

the number of foragers who are exploiting it. We also made $f_i(t)$ decrease in proportion to its own profitability based on the qualitative relation that a highly profitable source takes less time to exploit than a less profitable one. This evolution of f_i in time does not take into account what may in actuality be more important factors in changing the profitability of a source, that is, changing weather conditions, seasonal variations, and replenishing of nectar stores. These elements can be added in a later model, the essential behavior we wished to observe in this model was how insects would respond when a selected food source decayed in profitability below that of other sources.

We consider the solution in a square domain Q . At its boundary ∂Q , no-flux conditions are imposed: $\partial x/\partial \mathbf{k} = 0$, $\partial y/\partial \mathbf{k} = 0$ where \mathbf{k} is the outward normal to Q at $\mathbf{r} \in \partial Q$. In accordance with the physical nature of the system, the forager concentrations, their diffusion constants, and food landscape values are assumed to be non-negative, i.e. $D_x, D_y \geq 0$, and x, y and f belong to positive subspace $\mathbb{R}_+^2 = \{x, y, f \in \mathbb{R}^2; x, y, f \geq 0\}$. Let us suppose for simplicity that all foragers are initially distributed uniformly in space: $x(t_0, \mathbf{r}) = x_0$, $y(t_0, \mathbf{r}) = y_0$.

4 Analysis

Firstly, in order to study collective selection of the most profitable food source, we "freeze" the food landscape, i.e. we study system (3) where food sources are constantly being replenished. Employed foragers are assumed to diffuse very slowly, which corresponds to localization of information about every point of the explored environment space. The diffusion of unemployed foragers inside the nest determines their access to this information, thereby defining the pattern of information mapping over the nest.

In reality, most waggle dances occur on a small area, 4 – 18 cm from the entrance to the hive, the "dance floor", and onlookers are able to obtain information about different nectar sources. To study how collective intelligent choice emerges through communication between employed and unemployed foragers, we compare two cases: (i) locally informed onlookers, individually possessing information about one local

point of environment space without knowing of any other, and (ii) globally informed onlookers possessing information on the entire environment space.

According to our model, the first case involves a situation where the diffusion of onlookers is so slow that information about every point of environment is localized within the nest. In the limit of vanishing diffusions, system (3) possesses an integral of motion

$$\frac{\partial x(\mathbf{r}, t)}{\partial t} + \frac{\partial y(\mathbf{r}, t)}{\partial t} = 0, \quad (6)$$

which yields a condition of constant *local* concentrations

$$x(\mathbf{r}, t) + y(\mathbf{r}, t) = x_0 + y_0 = C_0 \quad (7)$$

This allows elimination of the variable y from system (3) which, in that case, reduces to a spatially extended logistic equation

$$\frac{\partial x(\mathbf{r}, t)}{\partial t} = (\alpha(\mathbf{r}) - x(\mathbf{r}, t))x(\mathbf{r}, t), \quad (8)$$

$$\text{where } \alpha(\mathbf{r}) = C_0 - \frac{1}{f(\mathbf{r})}. \quad (9)$$

Food quality threshold, $1/C_0$, indicates the patches of flowers which are attractive for foraging. Bees begin to concentrate only on those patches which amount of nectar exceeds the threshold:

$$f(\mathbf{r}) > 1/C_0 \quad (10)$$

The nature of the problem allows us to take into account a countable set of n spatial modes which correspond to the local maxima of the food landscape. Considering only these modes, the infinite-dimensional system (8) reduces to a system of uncoupled equations describing logistic growth of employed foragers at a particular spatial point

$$\dot{x}_i(t) = (\alpha_i - x_i(t))x_i(t), \quad (11)$$

$$\text{with } \alpha_i = C_0 - \frac{1}{f_i} \quad (12)$$

to be the reproductive rate of i -th mode.

Every mode associated with a food value exceeding the food quality threshold converges to the attractor

$$x_i^s = C_0 - \frac{1}{f_i}, \quad i = 1, \dots, n. \quad (13)$$

When individuals are only informed at a local level, colony's decisions are thus also made locally. In other words, the choice is not a collective but individualistic one - trails to every profitable nectar source, i.e. source which food value satisfies condition (9), coexist, and the colony fails to select the most profitable source.

Let us consider now the opposite case when onlookers have access to all information available on the explored environment. Distribution of this information through the nest can be modelled by diffusional mixing of onlookers. The faster the diffusion, the more equal the accessibility to information by each individual in the nest. In the limit of onlooker's full mixing (uniform distribution of input information) system (3) reduces to the system of integro-differential equations:

$$\begin{aligned} \frac{\partial x(\mathbf{r}, t)}{\partial t} &= \left(y(t) - \frac{1}{f(\mathbf{r})} \right) x(\mathbf{r}, t) + D_x \frac{\partial^2 x(\mathbf{r}, t)}{\partial \mathbf{r}^2} \\ \frac{\partial y(t)}{\partial t} &= -y(t) \frac{1}{S} \int_Q x(\mathbf{r}, t) \, d\mathbf{r} + \frac{1}{S} \int_Q \frac{1}{f(\mathbf{r})} x(\mathbf{r}, t) \, d\mathbf{r} \end{aligned} \quad (14)$$

where $y(t) = (1/S) \int_Q y(\mathbf{r}, t) \, d\mathbf{r}$ is the spatially-averaged concentration of onlookers over domain Q with area $S = \int_Q d\mathbf{r}$.

The integral of motion¹

$$\frac{1}{S} \int_Q \frac{\partial x(\mathbf{r}, t)}{\partial t} \, d\mathbf{r} + \frac{\partial y(t)}{\partial t} = 0 \quad (15)$$

yields the condition of constant *total* concentration

$$\frac{1}{S} \int_Q x(\mathbf{r}, t) \, d\mathbf{r} + y(t) = x_0 + y_0 = C_0 \quad (16)$$

that allows us to eliminate variable y from system (12) which, in that case, reduces to a spatially ex-

¹Integration over the space eliminates the diffusional term in the first equation of system (12) due to boundary conditions.

tended Lotka-Volterra system with a special connection matrix

$$\frac{\partial x(\mathbf{r}, t)}{\partial t} = [\alpha(\mathbf{r}) - \frac{1}{S} \int_Q x(\mathbf{r}, t) \, d\mathbf{r}] x(\mathbf{r}, t) + D_x \frac{\partial^2 x(\mathbf{r}, t)}{\partial \mathbf{r}^2}. \quad (17)$$

In the limit of vanishing D_x if only modes corresponding to local maxima of the food landscape are taken into account, the infinite-dimensional system (15) reduces to the system of coupled equations for spatial mode amplitudes

$$\dot{x}_i(t) = \left(\alpha_i - \sum_{i=1}^n x_i(t) \right) x_i(t). \quad (18)$$

Dividing i -th and j -th equations on x_i and x_j respectively and subtracting one equation from the another, one obtains

$$\frac{\dot{x}_i(t)}{x_i(t)} - \frac{\dot{x}_j(t)}{x_j(t)} = \frac{1}{f_j} - \frac{1}{f_i} \quad (19)$$

The integration of equation (17) results in

$$\frac{x_i(t)}{x_j(t)} = \frac{x_i(0)}{x_j(0)} \exp \left(\left(\frac{1}{f_j} - \frac{1}{f_i} \right) t \right). \quad (20)$$

Expression (20) provides an analytical proof of selection in the system. If the m -th mode is fittest and unique, then $f_m > f_j$ for $\forall j \neq m, j = 1, \dots, n$. Hence, it immediately follows that when $t \rightarrow \infty, x_m/x_j \rightarrow \infty$ for $\forall j \neq m, j = 1, \dots, n$. However, a condition of constant total concentration (14) and positive definiteness of variables prevents unlimited growth of modes. This means that the amplitudes of all modes excluding the fittest should tend to zero as time increases. If more than one mode are fittest, then they both survive.

If the profitability value of at least one mode exceeds the replication threshold, then the trivial equilibrium

$$x_i^s = 0, \quad i = 1, \dots, n \quad (21)$$

loses stability and system (16) converges to a non-trivial attractor

$$x_m^s = C_0 - \frac{1}{f_m}, \quad x_i^s = 0, \quad i = 1, \dots, n; \quad i \neq m \quad (22)$$

where $f_m > f_i$, which corresponds to *selection* of the most profitable food source.

A colony of globally informed individuals thus exhibits collective intelligence, i.e. it is able to select the most profitable food source in an explored environment.

For depleting food sources, the model was able to qualitatively exhibit the behavior in response to a set of food sources we expect from social insect societies. We illustrate this with an example of environment with three food sources. Initially, $f_1(0) = 5$, $f_2(0) = 4$, and $f_3(0) = 3$. The insects first collectively choose the first food source, the largest numbers exploiting this source. At some $t = t_s$, $f_1(t) < f_2(t)$. At this time insects stop congregating at the first source and begin to move en masse to the second source. This cycle continues with the magnitude of the oscillations decaying as the sources become less profitable, and not worth the energy expenditure to exploit. Though individually informed about the profitability of one source, collectively the insects were able to choose the most profitable source, and were able to respond in switching to other sources when they became more profitable.

5 Discussion and conclusions

Although the nest is extended in physical space, it is localized in information space. Since there is no large correspondence between the location of a dance within the hive and the location of a food source in the environment [5], an onlooker is able to obtain information about any number of different sources.

When unemployed foragers are recruited, they then become recruiters themselves for a particular source — the information is able to reproduce itself. The ability of information to be reproduced by itself, or its fitness, is proportional to the quality of the food source. The mechanism is defined thus by a positive feedback, or by an autocatalytic reinforcement of useful information [6]. The dissipation of information occurs when foragers abandon unrewarding food sources. This ensures the mechanism of changing in the system and prevents its sticking in local optima. The carriers of information, employed foragers, ex-

plot an available “resource”, the pool of unemployed bees. The natural physical limitation of the hive, i.e. the condition for mass conservation, restricts the number of information carriers. The replication of information is thus naturally limited. All these factors lead to the competition of information and, as a result, only the most useful information, trail to the most profitable food source, survives in the system.

The advantages of this system are amazing. First, the individual units do not have to possess great cognitive powers to make individual decisions about which food source to choose, they simply respond to the information which they see. Second, the system makes the foragers very flexible, they do not put all their eggs in one basket and crowd at the current best source. It is important to keep information flowing about many different sources to be able to respond quickly to changes in the environment.

The natural selection which created this beautiful system of communication can also be seen within the system. Information about different parts of the environment are like species in competition. The fitness of the species is given by the profitability of the food source it describes. Information survives by continuing to circulate within the nest, and is able to reproduce itself by recruiting new foragers who become informed of the food source and come back to the nest and share their information.

Several things done by a social insect society allow them to effectively select food sources in a changing environment. Foragers are budgeted according to the amount of information about each source in the environment, which in turn is proportional to the profitability of each of these sources. Thus foragers are distributed widely and in numbers to best exploit the value of the food source. Even when highly profitable sources are found not all the foragers are employed. Scouts still search the environment for new sources, and a core of unemployed foragers is still left at the nest which allows for a quick response (increase in amount of information) if a new richer source is found.

The main principles of social insect foraging behaviour can find an application in a swarm of inexpensive insect-like robots [6, 7]. Usually, all these robots are physically and functionally identical, so

that any robot can replace any other robot. The swarm possesses a significant tolerance, the failure in a single agent doesn't stop performance of the whole system. Like insects, the robots individually have limited capabilities and limited knowledge of the environment. Nevertheless, the swarm develops collective intelligence. The experiments showed that insect-like robots are successful in real robotic tasks [7].

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