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How Information-Mapping Patterns Determine Foraging Behaviour of a Honey Bee Colony

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Abstract. We have developed a model of foraging behaviour of a honeybee colony based on reaction-diffusion equations and have studied how mapping the information about the explored environment to the hive determines this behaviour. The model utilizes two dominant components of colony's foraging behaviour — the recruitment to the located nectar sources and the abandonment of them. The recruitment is based upon positive feedback, i.e autocatalytic replication of information about the located source. If every potential forager in the hive, the onlooker, acquires information about all located sources, a common information niche is formed, which leads to the rapid selection of the most profitable nectar source. If the onlookers acquire information about some parts of the environment and slowly learn about the other parts, different information niches where individuals are associated mainly with a particular food source are formed, and the correspondent foraging trails coexist for longer periods. When selected nectar source becomes depleted, the foragers switch over to another, more profitable source. The faster the onlookers learn about the entire environment, the faster that switching occurs.

1. Introduction

Social insect societies can be viewed as a complex system of interacting individuals. These societies perform decision-making without symbolic representation; they exploit the physical constraints of the system as well as communication among individuals. Unlike conventional information processing, these systems are highly flexible and fault tolerant. Despite the fact that each individual follows only a few simple rules, interactions between individuals can lead to the emergence of a collective behaviour, which enables the colony to make intelligent decisions in a complicated and changing environment. Behaviour of insect societies has proved highly effective in a range of different situations, such as building activities [1], formation of trail networks and foraging patterns [2, 3], synchronisation of activities [4], sorting [5], and dynamical division of labour [6].

One of the main behavioural components of social insect societies featuring intelligent decision making in complex and unpredictable environments is foraging behaviour. We have developed a model elucidating the main features of a honey bee foraging dynamics. It is known that honeybee colonies choose between different patches of flowers, selectively exploiting the most profitable, i.e. the richest or closest to the nest, nectar sources [3, 7]. A mathematical model of the foraging behaviour of a honeybee colony was developed based on coupled nonlinear ODEs [3]. The model divided bee activity into four modes, namely unloading nectar from a source, dancing for a source, feeding at a source, and following a dancer. Corresponding probability functions were developed to describe alternation between these modes. The results tallied with experimental observations.

The model for forage selection of permanently replenishing nectar sources by a honeybee colony that takes the distribution of information about the explored environment into account has been developed [8]. The model is based on reaction-diffusion equations where the reaction terms describe direct communication of individuals (similarly to molecule collisions in a chemical reaction), and diffusion term describes indirect spreading of the information among the individuals [9]. In this paper, we generalizes this model considering the nectar concentration dynamics. This is the *minimal* model of a honeybee colony's foraging exhibits collective intelligence. It includes only two behavioural components — recruitment to the located food source and abandonment of it. The recruitment represents an active phase leading to autocatalytic replication of information about the located sources. Its mechanism is a positive feedback. The abandonmenti is a passive phase leading to dissipation of the information.

We focus on how communication among individuals leads to colony's collective behaviour. To study this issue, we look at mapping the information about the environment to the nest, and analyze the formed information-mapping patterns and their influence on the overall dynamics. If the information is uniformly distributed among all potential foragers in the nest, a common "labour market" is formed, which leads to rapid selection of the most profitable source. Otherwise, different "labour niches" can be formed, which leads to long-term coexistence of corresponding foraging trails.

We consider the nectar dynamics during the exploitation and its influence on the colony's dynamics. Initially, more profitable source attracts the majority of foragers. As a result, this source is depleted faster and eventually becomes less attractive than others. Such switching in profitability leads, with some delay, to switching in majority of foragers associated with correspondent sources.

2. Model

Consider foraging colony members as a system of interacting elements, involving "employed" and "unemployed" foragers [7]. Employed foragers are in the process of exploiting a food source; they carry information as to the location and profitability of this source. The information is communicated through the celebratory "waggle dance" on an area near the opening of the hive, the dance floor. It is thus that potential foragers are recruited.[1] The profitability of the nectar source is encoded in the number of waggle runs performed by the dancer. Onlookers, however, do not compare dances. Instead, such a bee follows only one dancer, chosen basically at random, before leaving the hive [10, 7, 11]. Since foragers from profitable sources dance for longer, and are also more likely to dance, the profitability of a food source is collectively communicated by proportions of dancers advertising different sources. Unemployed foragers have either never foraged before, or have abandoned an unrewarding nectar source and are seeking a new food source. Unemployed foragers become employed in one of two ways. Either they search the environment for a previously undiscovered patch of flowers ("scouting behaviour") or they remain in the hive, where they await information about nectar sources currently being exploited, and select an employed bee to follow ("following behaviour"). These bees are termed "scouts" and "onlookers" respectively. After locating a food source, scouts either become employed at that source, or abandon the source and rejoin unemployed foragers. It is thus that we determine the two dominant modes of foraging behaviour, namely *the recruitment phase* and *the abandonment phase*. As will be demonstrated, these two modes of behaviour govern foraging dynamics.

Taking Wright's idea of fitness landscape which assigns a fitness to each point in a genetic space [14], we introduce the profitability landscape $f(\boldsymbol{r})$ which assigns a food quality value (as judged by an insect) to each point in colony's "information space $\boldsymbol{r}$.[2] The latter represents the mapping of the explored physical space (performed by the dancers) onto the onlooker "perception space".

Let us formalise the foraging mechanism, using the chemical reaction analogy. Employed and unemployed foragers are denoted by X and Y, respectively; the nectar source by F. An employed forager recruits an unemployed bee to its food source at a rate proportional to that source's quality:

$$Y + X \xrightarrow{F} 2X\,. \tag{1}$$

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.

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[1] A number of bees, having relinquished their nectar to a food-storing bee, continue to forage without recruiting nestmates [3]. Since these bees "mind their own business" without affecting the forager-onlooker recruitment chain, they are not taken into account here.

[2] 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 [7].

Abandonment of food sources may also occur:[3]

$$X \longrightarrow Y \tag{2}$$

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

$$\begin{aligned}\frac{\partial x(\boldsymbol{r},t)}{\partial t} &= \Big(f(\boldsymbol{r},t)y(\boldsymbol{r},t)-1\Big)x(\boldsymbol{r},t)+D_x\frac{\partial^2 x(\boldsymbol{r},t)}{\partial \boldsymbol{r}^2}\,,\\ \frac{\partial y(\boldsymbol{r},t)}{\partial t} &= -\Big(f(\boldsymbol{r},t)y(\boldsymbol{r},t)-1\Big)x(\boldsymbol{r},t)+D_y\frac{\partial^2 y(\boldsymbol{r},t)}{\partial \boldsymbol{r}^2}\,,\end{aligned} \tag{3}$$

where x, y, and f are concentrations, and D_x and D_y are diffusion constants of employed and unemployed foragers respectively. For the sake of simplicity, it is assumed that characteristic rates of recruitment and abandonment reactions equal to 1.

Exploitation of the nectar source by the forager is described by the folowing reaction:

$$F + X \longrightarrow F' + N + X\,, \tag{4}$$

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

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

where β is the characteristic rate of depletion.

We consider the solution in a square domain Q. At its boundary ∂Q, no-flux conditions are imposed: $\partial x/\partial \boldsymbol{k} = 0$, $\partial y/\partial \boldsymbol{k} = 0$ where $\boldsymbol{k}$ is the outward normal to Q at $\boldsymbol{r} \in \partial Q$. 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 orthant $\mathbf{R}^2_+ = \{x, y, f \in \mathbb{R}^2; x, y, f \geq 0\}$. Let us suppose for simplicity that all foragers are initially distributed uniformly in space: $x(t_0, \boldsymbol{r}) = x_0$, $y(t_0, \boldsymbol{r}) = y_0$.

This model provides a helpful analogy for information flows from employed foragers advertising their food sources to onlookers. By dancing, the employed foragers perform mapping of the environment to the nest. The onlookers acquire the above information by sampling (basically at random) a dance they encounter. Thus, information-mapping patterns are formed in the colony information space. We investigate how these patterns affect the system dynamics.

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[3] The expression (2) means the equal probability of abandonment for all nectar sources. It is reasonable to assume that the foragers are more likely to abandon the poorer sources than the richer ones. Dynamics of the developed model has not changed qualitatively when the abandonment rate is inversely proportional to the quality of the food source at a given point. However, the latest findings of the bee house hunting behaviour (that is equivalent to foraging in basic features) indicate that the dancers have a tendency to cease dancing independently of their housing preferences [12, 13]. This can be a programmed mechanism preventing the dancers to deadlock over two or more sites.

3. Analysis and Results

3.1. CONSTANT PROFITABILITY LANDSCAPE

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 in the space $\boldsymbol{r}$ determines their access to this information, thereby defining the pattern of information mapping over the onlooker pool.

In reality, most waggle dances occur on a small area, the dance floor, near the entrance to the hive and onlookers are able to obtain information about different nectar sources. To study how collective decision making emerges through communication between employed and unemployed foragers, we compare three cases: (i) locally informed onlookers possessing information about one local point of environment space without knowing of any other, (ii) globally informed onlookers possessing information on the entire environment space, and (iii) intermediate-range informed onlookers — the group of individuals quickly acquiring information about specific domain of the environment space (which corresponds to the intermediate situation between the above two cases) and slowly acquiring information about other parts of the environment (which, in the long term scale, reduces to the first case).

3.1.1. Theoretical Analysis

According to our model, the first case involves a situation where the diffusion of onlookers is so slow that they can acquire information only about local points of the environment. In the limit of vanishing diffusions, system (3) possesses an integral of motion

$$\frac{\partial x(\boldsymbol{r},t)}{\partial t} + \frac{\partial y(\boldsymbol{r},t)}{\partial t} \;=\; 0\,, \tag{6}$$

which yields a condition of constant *local* concentrations

$$x(\boldsymbol{r},t) + y(\boldsymbol{r},t) \;=\; x_0 + y_0 \;=\; C_0\,. \tag{7}$$

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

$$\frac{\partial x(\boldsymbol{r},t)}{\partial t} \;=\; \Big(\alpha(\boldsymbol{r}) - f(\boldsymbol{r})x(\boldsymbol{r},t)\Big)x(\boldsymbol{r},t)\,, \tag{8}$$

where $\alpha(\boldsymbol{r}) = C_0 f(\boldsymbol{r}) - 1$.

The profitability threshold, $1/C_0$, separates the patches of flowers which are attractive for foraging from the unrewarding sources. Bees begin to concentrate only on these patches whose value of profitability (that is reflection of the source abundance, distance to it from the hive, *etc.*) exceeds the threshold:

$$f(\boldsymbol{r}) \; > \; \frac{1}{C_0} \, . \tag{9}$$

Considering only n spatial modes which correspond to the local maxima of the profitability landscape, the infinite-dimensional system (8) reduces to a system of uncoupled equations describing logistic growth of employed foragers at a particular spatial point

$$\dot{x}_i(t) \; = \; \Big(\alpha_i - f_i x_i(t)\Big) x_i(t) \, , \tag{10}$$

where $\alpha_i = C_0 f_i - 1$ is the reproductive rate of i-th mode.

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

$$x_i^s \; = \; C_0 - \frac{1}{f_i} \, , \qquad i = 1, \ldots, n \, . \tag{11}$$

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

Consider now the opposite case when onlookers acquire all information available on the explored environment. This can be modelled by the diffusion mixing of onlookers in the space $\boldsymbol{r}$. The faster the diffusion, the more equal the access to all 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 equation

$$\begin{aligned} \frac{\partial x(\boldsymbol{r},t)}{\partial t} \; &= \; \Big(f(\boldsymbol{r}) y(t) - 1\Big) x(\boldsymbol{r},t) + D_x \frac{\partial^2 x(\boldsymbol{r},t)}{\partial \boldsymbol{r}^2} \, , \\ \frac{\partial y(t)}{\partial t} \; &= \; -y(t) \frac{1}{S} \int_Q f(\boldsymbol{r}) x(\boldsymbol{r},t) \, \mathrm{d}\boldsymbol{r} + \frac{1}{S} \int_Q x(\boldsymbol{r},t) \, \mathrm{d}\boldsymbol{r} \, , \end{aligned} \tag{12}$$

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

The integral of motion[1]

$$\frac{1}{S} \int_Q \frac{\partial x(\boldsymbol{r},t)}{\partial t} \, \mathrm{d}\boldsymbol{r} + \frac{\partial y(t)}{\partial t} \; = \; 0 \tag{13}$$

yields the condition of constant *total* concentration

$$\frac{1}{S} \int_Q x(\boldsymbol{r},t) \, \mathrm{d}\boldsymbol{r} + y(t) \; = \; x_0 + y_0 \; = \; C_0 \tag{14}$$

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

that allows us to eliminate variable y from system (12) which, in that case, reduces to a spatially extended Lotka-Volterra system with specific connection field

$$\frac{\partial x(\boldsymbol{r},t)}{\partial t} \;=\; \Big(\alpha(\boldsymbol{r}) - f(\boldsymbol{r})\frac{1}{S}\int_Q x(\boldsymbol{r},t)\,\mathrm{d}\boldsymbol{r}\Big)x(\boldsymbol{r},t) + D_x\frac{\partial^2 x(\boldsymbol{r},t)}{\partial \boldsymbol{r}^2}\,, \tag{15}$$

where $\alpha(\boldsymbol{r}) = C_0 f(\boldsymbol{r}) - 1$.

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

$$\dot{x}_i(t) \;=\; \Big(\alpha_i - f_i\sum_{i=1}^{n} x_i(t)\Big)x_i(t)\,. \tag{16}$$

Dividing i-th and j-th equations on $\alpha_i f_i$ and $\alpha_j f_j$, respectively and subtracting one equation from the another, one obtains

$$\frac{1}{f_i}\frac{\dot{x}_i(t)}{x_i(t)} - \frac{1}{f_j}\frac{\dot{x}_j(t)}{x_j(t)} \;=\; \frac{1}{f_j} - \frac{1}{f_i}\,. \tag{17}$$

The integration of (17) results in

$$\frac{x_i(t)}{x_j^\eta(t)} \;=\; \frac{x_i(0)}{x_j^\eta(0)}\exp[(\eta-1)t]\,, \tag{18}$$

where $\eta = f_i/f_j$.

Expression (18) provides an analytical proof of selection in the system. If the m-th mode is the fittest, i.e. corresponding to the maximum of the food landscape, then $\eta = f_m/f_j > 1$ for $\forall\ j \neq m$, $j = 1,\ldots,n$. Hence, it immediately follows that when $t \to \infty$, $x_m/x_j^\eta \to \infty$ for $\forall\ j \neq m$, $j = 1,\ldots,n$. However, the condition of constant total concentration (14) and positive definiteness of variables prevents the unlimited growth of the modes. This means that the amplitudes of all modes excluding the fittest one should tend to zero as time increases.

If the profitability value of at least one mode exceeds the replication threshold (9), then the trivial equilibrium

$$x_i^s \;=\; 0\,, \qquad i = 1,\ldots,n \tag{19}$$

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

$$x_m^s \;=\; C_0 - \frac{1}{f_m}\,, \qquad x_i^s \;=\; 0\,, \qquad i = 1,\ldots,n\,, \qquad i \neq m\,, \tag{20}$$

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.

3.1.2. Numerical analysis

Let us consider the case when the information about an explored environment is not uniformly distributed among the onlookers — namely, there are groups of onlookers that quickly acquire information about some patch of flowers and slowly acquire information about other patches. This case can be modelled by the intermediate values of onlooker's diffusion in the space $\boldsymbol{r}$. To model this situation, consider a profitability landscape with three separate niches (Fig. 1). The diffusional length $l_{d(k)}$ of onlookers in the k-th niche can be evaluated as [15]

$$l_{d(k)} \; = \; \sqrt{D_y \tau_{d(k)}} \, , \tag{21}$$

where $\tau_{d(k)}$ is the characteristic time of diffusion in the k-th niche.

Everywhere outside the niches, the reproductive rate is kept equal to the profitability threshold, so as the foragers are neither attracted to nor repelled from there. The characteristic diffusion times $\tau_{d(k)}$ can be approximated then as

$$\tau_{d(k)} \; \sim \; \frac{1}{\alpha_{m(k)}} \; = \; \left(C_0 f_{m(k)} \frac{1}{S} - 1 \right)^{-1}, \tag{22}$$

where $\alpha_{m(k)}$ and $f_{m(k)}$ are, respectively, the maximal reproductive rate and the maximal profitability value in the k-th niche.

If $D_y \sim 11$, diffusion length of onlookers is comparable to the niche size. Then, the three clusters of onlookers are formed in the space $\boldsymbol{r}$. Each cluster is well informed about its "own" nectar source, and there is slow diffusion exchange of information between clusters. To observe the dynamics, we performed computer simulations. We use the explicit method of numerical integration of PDEs when space and time are divided into discrete uniform subintervals, and derivatives are replaced by their finite-difference approximations. The numerical integration is performed on a 2D lattice with the space step $\Delta_r = 0.25$. The time steps are chosen to guarantee the stability and convergence of the explicit method. Firstly, we considered a food landscape with a "neutral" base that neither attracts nor repels employed foragers. On this base one distinguishes three separate niches which are attractive to bees — in the first and second niches, there are two peaks of value 2.25 and 2.6, and 1.9 and 2.25 respectively, and in the third niche, there is one peak of value 1.9 (Fig. 1). Throughout, the initial concentrations of foragers is taken to be $x_0 = 0.01$, and their diffusion is taken to be $D_x = 0.001$ respectively. Initially, the concentration of employed foragers begins to grow proportionally to the food landscape distribution. At $t \simeq 100$ then, foragers abandon the less profitable nectar source in the second niche and switch over completely to the more profitable neighbouring source. For this reason, the concentration of foragers at this source becomes even higher than at the most profitable source in the first niche. Concentration of bees at the third niches is markedly reduced (Fig. 2a). At $t \simeq 150$, foragers abandon the third niche (Fig. 2b). At $t \simeq 300$, all foragers in the first niche switch over to the more profitable nectar source. The concentration of bees at the second niche becomes very low (Fig. 2c). At $t \simeq 370$, all bees select the

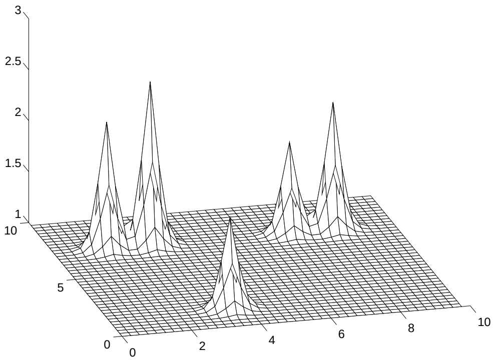

Fig. 1: Profitability landscape.

most profitable food source only (Fig. 2d). We considered the same food landscape but with a "zero" base which repels employed foragers. The results were similar — sequential abandonment of less profitable sources and eventual selection of the most profitable source at approximately the same time.

When the diffusion length of onlookers is compared to the distance between discovered food niches, a common information niche is formed in the nest. The faster the onlookers diffuse, the more the uniformly input information is distributed among them, and, hence, the more rapidly every onlooker obtains all information available. As a result, in the considered food landscape the same scenario to the above develops but in a shorter timescale. Fig. 3 illustrates selection of the most profitable nectar source at two different constants of onlooker diffusion. One can see that the colony needs less time to select the "best" source and to abandon all others when the diffusion of onlookers is more rapid.

3.2. DEPLETING NECTAR SOURCES: ANALYSIS OF SWITCHING BEHAVIOUR

Let us take into account the depletion of the nectar sources during their exploitation, i.e. consider the system of equations (3) and (5). It is assumed that the depletion is a slow process and, hence, its characteristic rate β is small. We consider a simple food landscape with two patches of nectar concentration of the maxima 3.7 and 3.2 respectively (Fig. 4). At $D_y = 0.5$, the difference in number of forager concentrated at the two patches changes slowly when time increases.[2] The depletion intensities of both patches are not differ too much, i.e. exploitation of both nectar sources is commensurable. The majority of employed foragers, thus, remains on the initially reacher patch of flowers, not switching to another one (Fig. 5a). Increasing D_y means faster acquisition of the information about the entire environment. As a result, more foragers begin to concentrate at the most profitable source, which leads to its rapid depletion. Eventually, another patch of flowers becomes more preferable for bees, and their majority switches over to

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[2] Throughout, we assume extremely weak diffusion of the nectar ($D_f = 10^{-9}$), which guarantees smoothness of its distribution over the space.

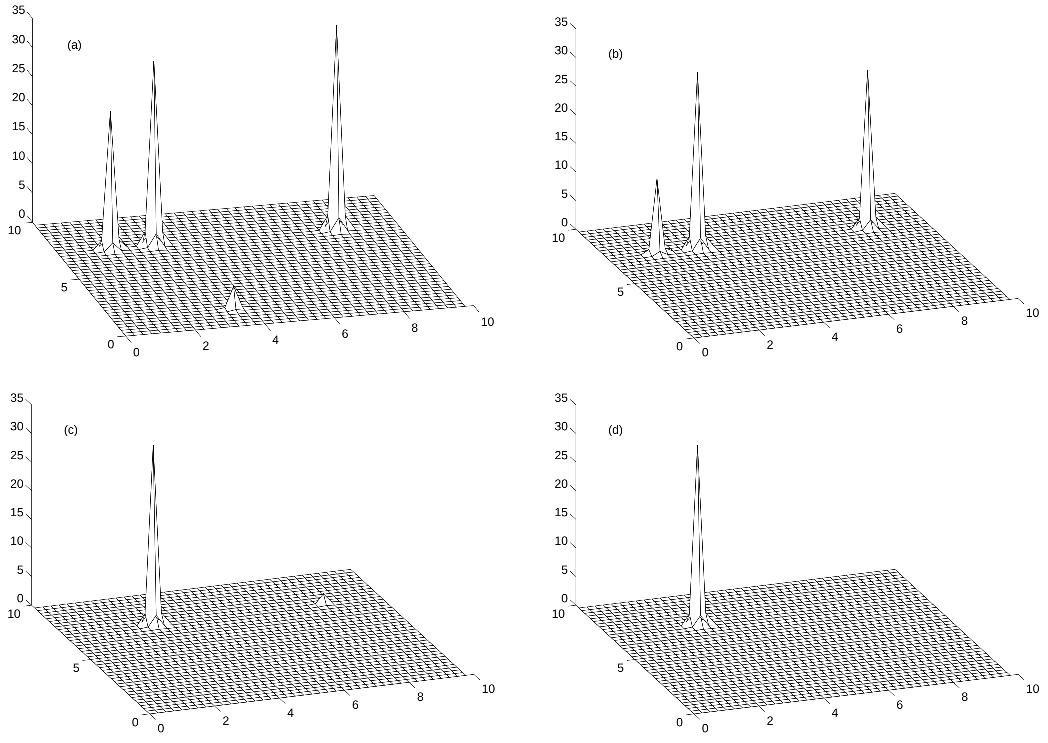


Fig. 2: Concentration of the employed foragers at the following parameter values: $x_0 = 0.01$, $y_0 = 1$, $D_x = 0.001$, $D_y = 1$, and (a) $t = 102$, (b) $t = 150$, (c) $t = 300$, (d) $t = 367$.

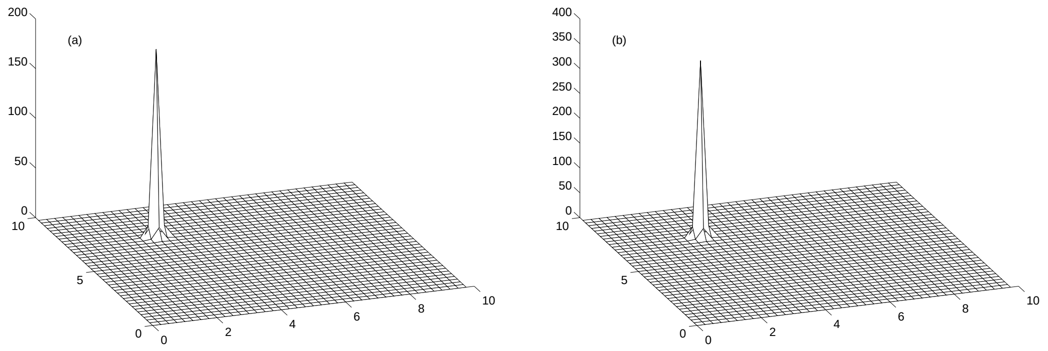


Fig. 3: Concentration of the employed foragers at the following parameter values: $x_0 = 0.01$, $y_0 = 1$, $D_x = 0.001$, and (a) $D_y = 6$, $t = 157$, (b) $D_y = 12$, $t = 97$.

that nectar source (Fig. 5b-c). One can see that the more equal access to all information is available, the faster that switching occurs.

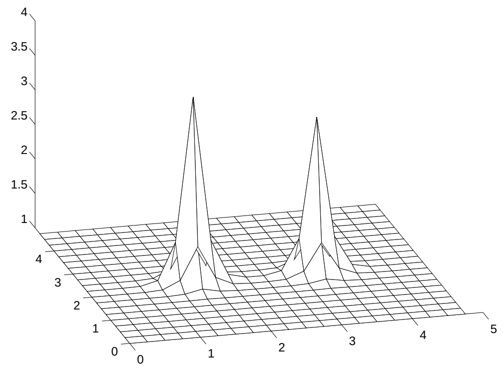


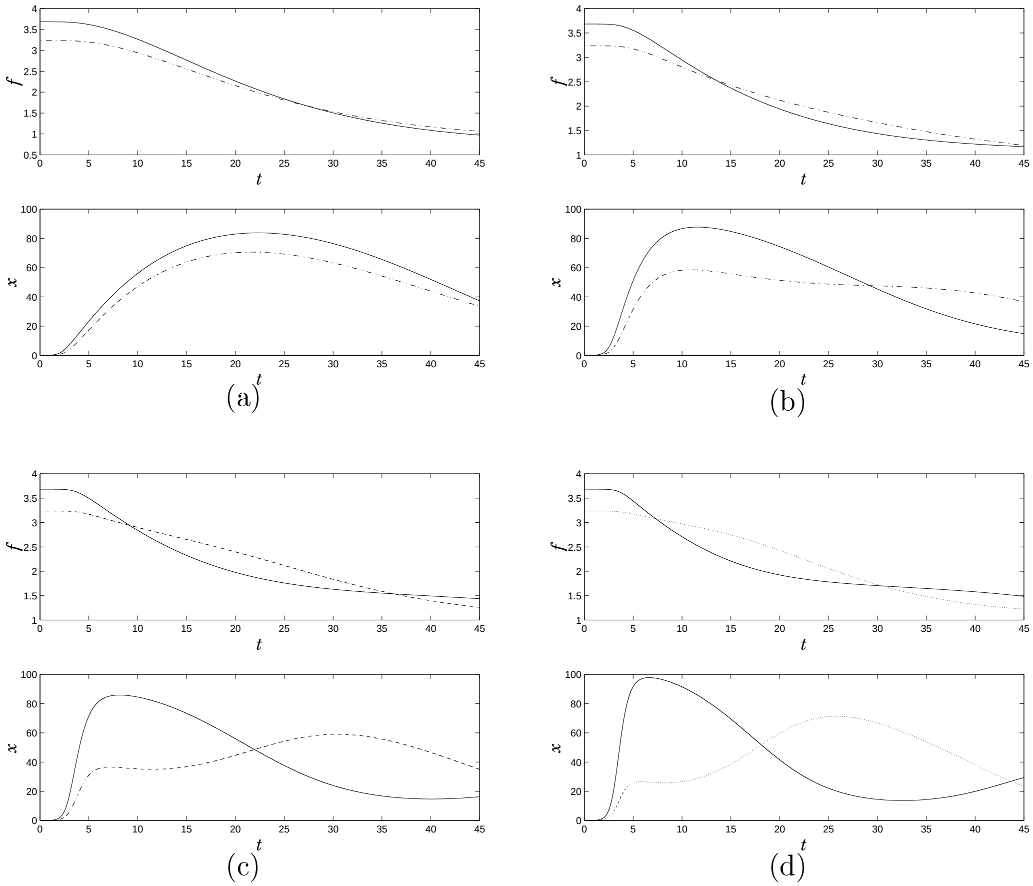
Fig. 4: Profitability landscape.

4. Discussion and Conclusions

We found that two dominant behavioural components govern the foraging dynamics, recruitment (when an unemployed bee follows one of the recruits and becomes employed at a food source) and abandonment (when a forager returns to the pool of unemployed bees). 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 [16]. 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, exploit 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.

Foraging leads to the formation of information-mapping pattern in the colony information space. We analysed how this pattern governs the colony behaviour. If it is a uniform pattern, i.e. all information are equally accessible to all individuals in the hive who are intended to forage, a common information niche is formed there. This leads to rapid selection of the most profitable nectar source. When the selected food source becomes depleted, foragers switch over to another source. If the pattern is not uniform, a number of informational niches are formed, and foraging trails to different food sources coexist for long periods. The model elucidates thus the role of the nest as *an information reservoir* and the dependence of dynamics from the information-mapping patterns.

From the point of view of complex system theory, the model shows how complex behaviour emerges from the interactions of individuals possessing very simple



(a) (b) (c) (d)

Fig. 5: Concentration of the nectar and the employed foragers at maxima of the food landscape. The solid and dash-dot lines correspond to initially the most and least profitable nectar sources and the foragers associated to these sources respectively. Calculation is made at the following parameter values: $x_0 = 0.01$, $y_0 = 1$, $\beta = 0.0005$, $D_x = 0.000001$, a) $D_y = 0.5$, b) $D_y = 2$, c) $D_y = 6$, and d) $D_y = 20$.

behavioural repertoire.

A model developed mimics, in principle, the main features of foraging and house-hunting behaviours of other insect societies. There are, however, the differencies. It is interesting to compare the foraging mechanism of bee and ant colonies. In an ant colony, foragers mark the route from the located food source to the nest by a special chemical agent, pheromone, which attracts other ants. Evaporation of pheromone takes a rather long period. An ant colony, therefore, can fail to select the most profitable food source, if it is presented after marking the less profitable source.[1] Unlike that, a bee colony is always capable of finding the optimal solution.

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[1] The experiments show that ants fail to choose if the longest branch is already marked [17].

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