# Optimal balance of individual and collective in honeybee foraging

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**Abstract.** *Purpose.* Previously, we developed a minimal foraging model in a honey bee colony that is applicable to describe both the decision-making process and the phase transition between two behavioral modes of the colony, individual and collective. In this paper, we show that this model is also applicable to determine the optimal division of labor in the colony, namely, to determine the optimal proportions between different types of foragers, scouts and recruits. *Model.* We represent the steps in the foraging process as reactions of chemical kinetics, which leads to reaction–diffusion equations. The reaction part describes the dynamic modes of the foraging process: the recruitment of unemployed foragers to profitable food sources, that have become unprofitable as a result of their exploitation, and scouting. Diffusion describes the transfer of information in a honey bee colony. We assume almost perfect accuracy in the transmission and use of information about food sources in the colony, which is modeled by a very small diffusion coefficient of working foragers in the information space. On the contrary, the diffusion coefficient of unemployed foragers is chosen large to ensure their full mixing in the information space. This models the equal accessibility to transmitted information for all unemployed foragers in the hive. *Results.* We consider the profit of a colony on an exploited food source as the number of foragers working on that source, weighted by its value to the colony. It was found that with an increase in the intensity of scouting, the profit of the colony first grows, and then begins to fall, thus illustrating that there is an optimal balance of scouts and recruits, which ensures the greatest influx of food resources into the colony. *Conclusion.* An optimal division of labor in a honey bee colony, defining a dynamic balance between exploration and exploitation in a constantly changing environment, is essential to the survival of the colony. Considering that scouts use exclusively personal information, and recruits take advantage of social information, we can say that our model describes the optimal balance between the individual and the collective in the colony.

*Keywords*: honey bee colony, foraging, scouting, recruitment to the source, individual behaviour, collective behaviour, colony profit, optimal ratio of foragers.

## Introduction

For a life, a colony of honey bees must effectively explore and exploit the surrounding space, that is, find and use attractive sources rich in nectar and pollen. It is believed that at the individual level, this behaviour is demonstrated by two types of foragers: scouts who search for food on their own, and recruits who are directed by nestmates to food sources using the so-called

waggle dance [1]. The former are mainly responsible for exploring the surrounding space and to a lesser extent for exploitation, while the latter focus exclusively on the exploitation of food sources.

There must be a certain (dynamic) balance between the exploitation of already known resources and the search for new ones. On the one hand, even with the exploitation of rich sources, there is always the possibility of the existence of sources that have not yet been explored, which are more abundant, more accessible (including difficulty of extracting nectar from a flower), superior in quality of food components, etc. The use of the latter can both increase the volume and improve the quality of the collected resource. Therefore, there should be a sufficient number of scouts among foragers who are able to find new sources.

The above is true for an arbitrary, including unchanging, environment. The latter, of course, is an idealization in the real world. During exploitation, the sources are depleted and become less attractive to bees. As a result, foragers refuse such sources, become temporarily unemployed and wait in the hive for information about other, more attractive sources. Such information is brought to the hive by both foragers working on currently profitable sources and scouts.

In reality, the picture is even more complicated due to the natural variability of the environment. On any given day, some plants bloom, while others are naturally depleted. The amount of nectar in a flower depends on the relative rate of secretion and reabsorption. In different flowers, secretion peaks are observed at different times of the day [2]. Also, the concentration of nectar is closely related to the relative humidity of the environment. After rain, some depleted plants can restore the ability to produce nectar [3]. It should also be borne in mind that adverse environmental conditions, such as hurricanes, heavy rains, hail, can damage plants and radically change the floral landscape.

Thus, the colony requires a sufficient number of scouts to find profitable (at the moment) sources in an ever-changing environment. However, their number should not be so large as to limit the number of recruits. Exploring the surrounding space, scouts find sources of different quality, both valuable for the colony and not so much. Recruits are always hired exclusively for profitable sources and fly to their source as long as the latter remains attractive in their eyes, which ensures a steady flow of food resources into the hive. Also, dancers, advertising their source, can recruit not one, but several recruits, which maximizes the food flow. It is the mechanism of recruiting recruits, that ensures the efficiency of exploitation.

Based on the above, the question naturally arises: how to find a compromise between exploration and exploitation? In other words, how does a colony of honey bees regulate the number of scouts and recruits under rapidly changing environmental conditions? As it turned out, this largely depends on the structure and distribution of feeding sites in the environment [4, 5], but it is still a matter of debate [6].

Obviously, dancing is useful if the probability of discovery of food sources is low, when, for example, flower patches are very small or very distant [7]. Under these conditions, dancing is useful, since a single forager is enough to involve others in the process [7]. In all cases where resources were low density, dancing colonies perform better than exploration colonies [8].

The technique of creating so-called disoriented dances helps to explore the importance of recruiting dances, when without light or only with scattered light, bees cannot convey the location of the food source during the dance [4, 9, 10]. Studies at the colony level with normal and disoriented dance show that waggle dance improves colony foraging in cases of difficulty finding food sources [9], their inconstancy or short-lived [5]. Also, information about the location of sources was useful when resources were unevenly distributed [4].

It is also necessary to take into account that bee colonies can gain weight in just a few weeks a year. For this reason, it is critically important that the colony can use the available high-quality resources under good foraging conditions, and dance is likely to play an important role in maximizing the efficiency of foraging during such periods [8].

However, at high resource densities, recruitment may be detrimental to foraging, because bees do not require social information to succeed in this case [10,11]. If the energy and time costs associated with the use of social information are high and do not bring significant benefits, then the strategy of waiting for social information becomes counterproductive [12].

There are two hypotheses about scout bees: (i) only some individuals have a tendency to scout [13] or (ii) all bees are prone to scout [14].

The first hypothesis assumes a genetically predetermined specialization of bees. C. Dreller suggested that the forager's propensity for exploration has a strong genetic basis, so that some foragers of the colony will mainly scout, and not follow the recruitment dances. With the help of destructive sampling, she determined that there is a genetic basis for being a scout or a recruit [13]. A similar effect of the genotype on an individual's propensity to perform certain tasks was previously found between pollen foragers and nectar foragers [15–19]. The above may suggest that scouts are genetically determined search specialists.

The second hypothesis assumes the universality of colony agents and its possible adaptability to changes in internal and external conditions. The first includes, for example, the level of food reserves in the hive, and the second changes in the environment. Within the framework of this concept, the role of an insect is determined by its response to various levels of stimuli, that is, the functional organization of the colony determines the role of the individual in it [20, 21]. In light of this understanding, it is considered that a strict separation between a scout and a recruit is unlikely [1]. The key task here is to study the mechanisms regulating the distribution of tasks and division of labour in insect communities [14, 22].

In environments where food availability changes rapidly and unpredictably, the adaptive distribution of foragers between scouting and recruitment is vital for the colony [23]. At the same time, the mechanisms determining adaptability do not exclude the influence of genetics, since the threshold of an individual's response may well be influenced by his genotype [24, 25].

There are several models that determine the optimal proportions of foragers [26–28]. All these models are specialized, that is, they were specially developed to solve the above problem.

In this paper, we show that our minimal model of honeybee foraging is able to demonstrate the optimal proportion of scouts. Unlike the above models, it is universal. Even in a truncated form (without taking into account scouting), this model demonstrates the basic principle of decision-making that ensures the success of the colony — the selection and exploitation of the best sources (from those known to the colony at the given time) [29–31]. And the full model already demonstrates both the selection of the best sources [32], and the phase transition from individual behaviour to combined, individual plus collective, where the latter plays a dominant role in resource collection [33].

## 1. The minimal model of foraging

Let us highlight the main components and stages of the process of foraging. All foragers are divided into *working* and *unemployed* [31, 33].

Working foragers are associated with their place of work (flower patch). Returning to the hive with the extracted nectar or pollen, foragers also carry information about the source of food

and convey it to their nestmates in the hive with the help of a waggle dance [20, 31, 33].

Unemployed foragers are not associated with any particular food source. We can say that they do not have a "work contract". Unemployed foragers are divided into *onlookers* and *scouts* [31, 33]. The first ones are the reserve workforce, which is waiting in the hive for information about food sources, and, having received this information, can follow to the source and "get a job" there. The process of obtaining information itself takes place by observing dancing in a small area near the entrance to the hive, called the dance floor [20]. The latter independently search for food sources in the environment. If the scouts find a valuable source, they can join the ranks of those employed at this source.

Honey bees evaluate the source according to their internal scale, the main criteria of which are the proximity of the source to the hive, the ease of extracting nectar and its nutritional value, determined by the concentration of sugars, amino acids and vitamins [20]. Despite the fact that bees evaluate the quality of the source by a variety of factors, we describe the preference factor by the only parameter that can be called the value or profitability of the source [31, 33]. Experiments show that such a parameter can be the net energy efficiency of the nectar source [20].

Having denoted the working and unemployed foragers $X$ and $Y$ respectively, we present the stages of the foraging process in the form of chemical kinetics reactions.

Recruitment in the hive can be described by an autocatalytic reaction, when an onlooker hired for work, who then became a recruit, after working out his "shift", becomes an recruiter for other onlookers:

$$Y + X \rightarrow 2X. \tag{1}$$

A previously profitable source may lose its attractiveness for the colony, both due to its depletion during exploitation, and for environmental reasons, natural or catastrophic. Abandonment of an unprofitable source of nectar is inversely proportional to its current value. In this case, the working forager goes to the pool of unemployed:

$$X \xrightarrow{\frac{1}{f}} Y, \tag{2}$$

where $f$ is the profitability of the source.

Exploration of the surrounding space is an important component of the behaviour of a bee colony. Scouts can also collect nectar and pollen from a source they discover, adding to the hive's supply. In this case, they move into the category of working foragers, but they become them not as a result of recruitment, which has a collective nature, but in an independent way:

$$Y \xrightarrow{\varepsilon} X. \tag{3}$$

Since the number of scouts in the total amount of foragers of the colony is small (on average 10% [20]), we consider $\varepsilon$ small.

Scouts who use *personal* information about sources that they independently searched for in the environment form *individual* foraging regime. On the contrary, recruits who get jobs through recruitment, that is, using *social* information, form *collective* mode of foraging.

The stages (1)–(3) lead to the following reaction–diffusion equations:

$$
\begin{aligned}
\frac{\partial x(\mathbf{r}, t)}{\partial t} &= \left( y(\mathbf{r}, t) - \frac{1}{f(\mathbf{r}, t)} \right) x(\mathbf{r}, t) + \varepsilon y(\mathbf{r}, t) + D_x \frac{\partial^2 x(\mathbf{r}, t)}{\partial \mathbf{r}^2}, \\
\frac{\partial y(\mathbf{r}, t)}{\partial t} &= -\left( y(\mathbf{r}, t) - \frac{1}{f(\mathbf{r}, t)} \right) x(\mathbf{r}, t) - \varepsilon y(\mathbf{r}, t) + D_y \frac{\partial^2 y(\mathbf{r}, t)}{\partial \mathbf{r}^2},
\end{aligned}
\tag{4}
$$

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where $x$ and $y$ are densities, and $D_x$ and $D_y$ are the diffusion coefficients of working and unemployed foragers respectively, and $f(\mathbf{r}, t)$ is the *food landscape*, which assigns a profitability value each point of space $\mathbf{r}$.

Special mention should be made about the space $\mathbf{r}$. We believe that bees are able to create an information map of physical space in their brains to navigate and search for the right sources. In general case, the space $\mathbf{r}$ is exactly the information space. Working foragers bring information about exploited sources to the hive and transmit it to onlookers through dance. The accuracy of the transmitted information can be modeled by the value $D_x$. We believe that this information is used by recruits almost perfectly, that is, they precisely find the right source and exploit it. This is modeled by a very small diffusion coefficient $D_x$ (information about the source does not spread out in the space $\mathbf{r}$, but is precisely localized at the required source). The reverse situation is with the diffusion coefficient $D_y$, which we choose to be large. This coefficient simulates the onlookers' access to information transmitted by dancers. We assume that the transmitted information is equally accessible to all onlookers in the hive, which can be simulated by completely mixing the latter in the information space. Thus, system (4) actually models the dynamics of information in a colony of honey bees.

However, for the food landscape and working foragers, namely the dynamics and distribution of the latter we are primarily interested in, this space can be considered as physical space. In this case, the food landscape represents the distribution of sources in real physical space, on which working foragers concentrate.

## 2. Dynamic balance

For simplicity of analysis, we assume that the nutritional value of sources does not change over time. At the same time, the structure of the landscape may change: new components may appear in it — new food sources discovered, which we also consider unchanged in their nutritional value. After the bees have discovered all the sources in the space they are exploring, they then operate in the "frozen" landscape when $f(\mathbf{r}, t) = f(\mathbf{r})$.

Let's carry out computer simulation by solving system (4) numerically. We use an explicit method of numerical integration of partial differential equations, where space and time are divided into discrete uniform subintervals, and the derivatives are replaced by their finite-difference approximations. Numerical integration is performed on a two-dimensional lattice of size 10 by 10, with a space and time step of 0.2 and 0.0002 respectively, which guarantees the stability and convergence of the explicit scheme. There are no flows at the boundaries of a given space, $\Omega$: $\frac{\partial x}{\partial \mathbf{r}}\big|_{\mathbf{r} \in \Omega} = 0, \frac{\partial y}{\partial \mathbf{r}}\big|_{\mathbf{r} \in \Omega} = 0$.

It is assumed that at the initial moment the overwhelming number of foragers are unemployed: the initial density of working and unemployed foragers in each of the cells is $x_0 = 0.001$ and $y_0 = 1$ respectively. In other words, at the initial moment, the colony has minimal information about available sources, but its information resource is large. The diffusion coefficient of working foragers is $D_x = 0.001$, which implies an almost perfect identification of food sources by recruits. On the other hand, the diffusion coefficient of unemployed foragers is $D_y = 10$, which ensures equal accessibility of onlookers to the information transmitted by the dancers.

Let us define the food landscape with a set of profitability values $q$: $f = f\big(q(\mathbf{r}, t)\big)$. Since we perform numerical integration on a two-dimensional lattice, this set is finite, and its size is determined accordingly by the size of the lattice and the step of integration over space. Consider a landscape with three spatially separated niches defined by distinct profitability values, beyond
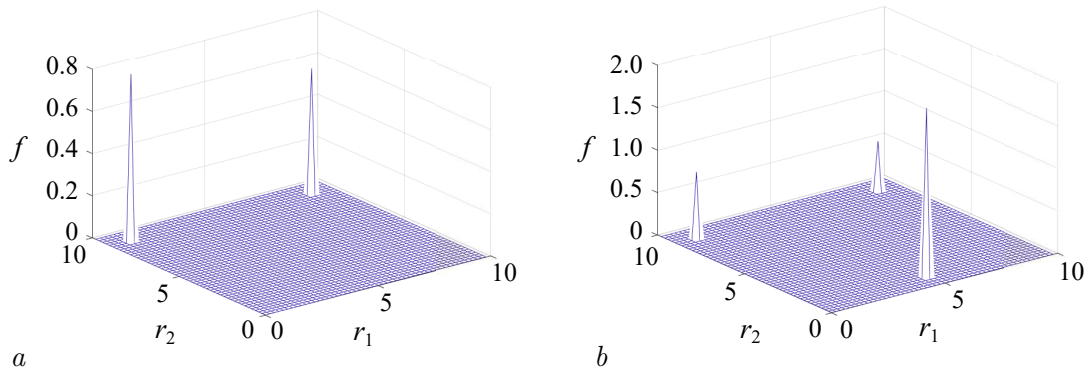
Fig. 1. Food landscape available to the colony before $t = 60$ ($a$) and so after $t = 60$ ($b$). The background source value for both figures is, from left to right, $f(\mathbf{r}) = 0.8$ and $0.6$ respectively, and the foreground source value in figure $b$ is $f(\mathbf{r}) = 2$

which profitability is minimal. Everywhere outside the niches, the level of profitability can be arbitrarily small, but not equal to zero, in order to prevent the coefficient of abandonment of unprofitable sources, which is inversely proportional to profitability, from going to infinity (Eq. (2)). It is assumed that at first, namely up to the time $t = 60$, bees know information about only two food sources:

$$q(r_1, r_2, t < 60) = \begin{cases} 0.8 & \text{for } r_1 = 1, \ r_2 = 9, \\ 0.6 & \text{for } r_1 = 9, \ r_2 = 9, \\ 0.001 & \text{for everyone else } r_1, \ r_2, \end{cases} \quad (5a)$$

and with the onset of this moment, they discover the third source, and the whole landscape opens up to them:

$$q(r_1, r_2, t \geqslant 60) = \begin{cases} 0.8 & \text{for } r_1 = 1, \ r_2 = 9, \\ 0.6 & \text{for } r_1 = 9, \ r_2 = 9, \\ 2 & \text{for } r_1 = 5, \ r_2 = 1, \\ 0.001 & \text{for everyone else } r_1, \ r_2. \end{cases} \quad (5b)$$

The above landscapes are presented in Fig. 1, $a$ and $b$, respectively.

Note that to verify the experiment, we performed numerical integration of two landscape options. The first option is described in this article. Alternatively, we "smoothed" the above landscape with a diffusion operator. The coefficient of such diffusion and the time of its action were small, which prevented any significant spreading of the sources, but at the same time, he action of the diffusion was sufficient to ensure the smoothness of the function. As a result, Gaussian peaks were obtained, as should be the case with diffusion. The integration of these two options led to qualitatively identical results.

Bees consider a source profitable if its profitability exceeds a level called the profitability threshold [29–31, 33]. In our system, this threshold is $T_p = \frac{1}{x_0 + y_0 - \varepsilon}$. Bees start dancing only for those sources whose profitability exceeds this threshold. In this case, recruits are attracted, that is, the collective mode of foraging is activated. For sources whose profitability is below this threshold, foraging occurs only individually, without transmitting information to hivemates. In our case, the profitability of the initially available sources (see Fig. 1, $a$) is below the threshold, and therefore, when $t < 60$, the system is in the individual phase of foraging. Next, the colony finds an attractive source, the profitability of which is above the threshold (see Fig. 1, $b$), and

proceed to the combined phase, which includes both individual and collective components of behaviour. In the combined phase, the collective component plays a dominant role, since it is it that generates (through recruitment) the majority of foragers [33]. Therefore, it would not be an exaggeration to call the combined phase collective, which reflects its essence.

Let us consider the distribution of the density of working foragers in a given food landscape for a colony with the intensity of scouting $\varepsilon = 0.1$. Fig. 2, $a$ demonstrates the distribution at $t = 59.8$, that is, in the individual phase. As can be seen, foragers concentrate on two sources known by this time (densities 293.3 and 201.9 respectively). If we imagine that only these two sources will be known to bees further, then the above densities will not change, that is, these are stationary densities for the specified conditions. Fig. 2, $b$ demonstrates the distribution at $t = 200$, that is, already in the collective phase of foraging. It immediately catches the eye that the bulk of working foragers concentrates on a profitable source, where the density reaches 598.8. At the same time, the density of foragers on two unprofitable sources decreases compared to the individual phase (187.4 and 134 respectively). These values do not change over time, which indicates their stationarity. With other values of the intensity of scouting, only the stationary densities of foragers change, but the picture remains qualitatively the same.

Thus, in the collective phase, a redistribution of foragers occurs: some of the scouts switch to watching the dances and eventually become recruits. This is how the system adapts to changing conditions (a profitable source found in our case), and a dynamic balance arises between scouts and recruits, or, more generally, between exploration and exploitation.

### 3. Profit dynamics and its optimum

In a stationary, time-independent food landscape, consider the colony's profit $P$ as the total spatial density of working foragers, weighted by the profitability (in the eyes of bees) of that space:

$$P = \int_{\mathbf{r}} f(\mathbf{r})x(\mathbf{r})\, d\mathbf{r}. \tag{6}$$

Let us simplify the problem by considering a corresponding discrete set of food sources with a discrete set of forager densities. In this case, we define the profit $P_d$ as a weighted (by the profitability of sources) sum of such densities:

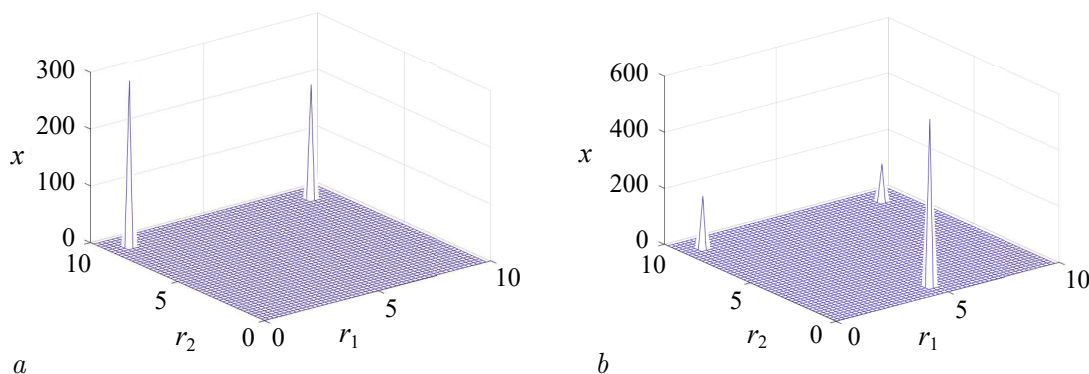$$P_d = \sum_{i=1}^{n} f_i x_i, \tag{7}$$



Fig. 2. Density distribution of working foragers at $t = 59.8$ ($a$); $t = 200$ ($b$)
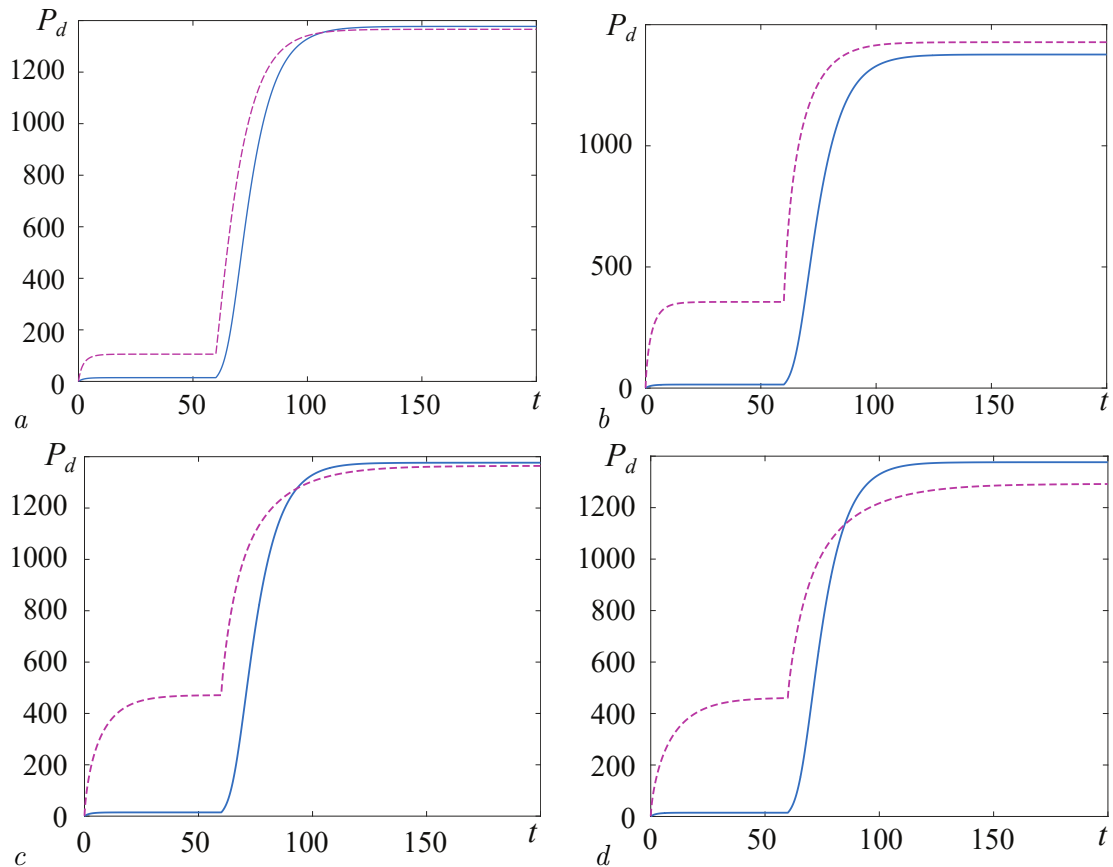
Fig. 3. Colony profit dynamics for different levels of scouting intensity. Everywhere the solid line shows the dynamics for $\varepsilon = 0.001$. The dashed line shows the dynamics for: $\varepsilon = 0.01$ ($a$); 0.1 ($b$); 0.7 ($c$); 1.0 ($d$)

where $n$ is the number of food sources.

In principle, it is possible to consider a simple (unweighted) integral or sum, and this will also reflect the profit of the colony. However, if we take into account that the profitability of a food source is a complex indicator, including, for example, such a component as the difficulty of extracting nectar from a flower, we consider the definitions of profit presented above to be more reasoned.

Let us now consider the dynamics of the colony's profit, $P_d$ at different levels of scouting intensity $\varepsilon$. As a sample, we will choose a colony with a very low intensity of scouting, $\varepsilon = 0.001$, which can actually be considered a system without scouting. In Fig. 3, $a$–$d$ the profit of such a colony is shown as a solid line. As expected at such a low level of scouting, the colony's profit is minimal in the individual phase, that is, for $t < 60$. However, in the collective phase, there is an explosive increase in profit, stabilizing over time (see Fig. 3, $a$–$d$, $t \geqslant 60$). For simplicity, we will call the considered dynamics basic.

Let us compare the above colony with colonies in which scouting plays a more significant role, namely, consider colonies with $\varepsilon = 0.01, 0.1, 0.7$ and 1.0 (see Fig. 3, $a$–$d$, dashed line for each variant of scouting intensity respectively). In all cases, the profit dynamics of such colonies resembles the basic dynamics, but with different stationary levels in the individual and collective phases. As we can see, in the individual phase, the profit for such colonies is everywhere higher than the base one, and the increase in profit is proportional to the increase in the intensity of scouting. For the collective phase, namely, this phase is the leading one in the foraging of a colony

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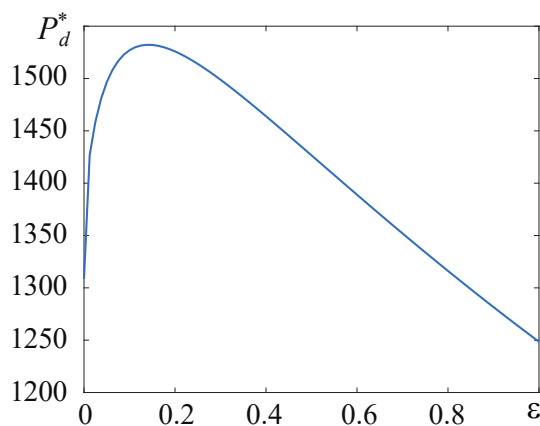
Fig. 4. Dependence of the stationary level of profit of the colony on the intensity of scouting

of honey bees, the situation is different. At $\varepsilon = 0.01$ in the stationary state, the colony's profit is almost equal to the profit of the base colony, remaining slightly lower (see Fig. 3, $a$). With an increase in the intensity of scouting, the profit becomes higher than the base one (Fig. 3, $b$, $\varepsilon = 0.1$). However, a further increase in the intensity of scouting leads to a decrease in profit, which falls below the base one (see Fig. 3, $c$, $\varepsilon = 0.7$ и рис. 3, $d$, $\varepsilon = 1.0$).

In accordance with the above, it can be assumed that there is a certain optimal value of the intensity of scouting that ensures the greatest influx of food resources into the colony. To confirm this, let's conduct a simple experiment. This time, for simplicity, let us assume that the food landscape consists of a single source, whose profitability is sufficient to recruit unemployed foragers from the hive (the source in the foreground, see Fig. 1, $b$). Let us also assume that this source is known to the bees immediately, and not after some time, as before. The latter will simply accelerate the output of the colony's profits to its stationary level, $P_d^*$. In our case, such as level is stably ensured at $t \geqslant 60$ for any values of $\varepsilon$ considered in this experiment. We calculated the stationary profit of the colony for the intensity of scouting from 0 to 1, and found that the optimal profit is achieved in the range $\varepsilon = 0.125...0.15$ (fig. 4).

## Conclusion

In fact, optimal division of labour is key to the survival of a honey bee colony. This is why the right balance between exploration and exploitation is so important. As we have seen, the system itself adapts to changes in the environment that are significant for the colony. Obviously, if scouts discover valuable sources rich in food resources, then it is rational to involve other foragers of the colony in their exploitation. This occurs by exchanging information about attractive sources with other inhabitants of the hive, using the universal language of bees — dance. In this case, the recruitment process begins, that is, the collective mode of foraging is activated. Our model demonstrates similar adaptability when, upon discovery of a profitable source, a behavioural shift occurs towards strengthening the collective component due to the reduction of individualist scouts.

Unlike scouts, recruits receive and use social information. The effectiveness of the latter is reflected by the explosive growth of the colony's profits in the collective phase (see Fig. 3, $a$–$d$). It begins exactly at the moment when the colony discovers a profitable source and begins recruiting

unemployed foragers to it. The recruitment mechanism is nothing but a positive feedback loop, that is, a self-reinforcing, autocatalytic process. Such growth is limited by the finiteness of the pool of unemployed foragers, and ends with the system reaching a stationary state. Comparing the steady-state profit levels of individual and collective behaviour clearly illustrates the power of the collective.

Given that the above explosive growth in the number of foragers corresponds to a change in the profitability of the food landscape, we can actually talk about a phase transition in this case. A dramatic change in the number of working foragers is associated with behavioral restructuring in the colony. Therefore, this phase transition can also be called a behavioural transition from individual to collective.

With an increase in the intensity of scouting, the colony's profit first increases sharply, quickly reaching a maximum, bypassing which it begins to slowly fall (see Fig. 4). This indirectly confirms experimental data that the number of scouts is on average 10% of the total number of foragers of the colony [20].

There is a hypothesis that scouts are failed recruits [25]. That is, these are the onlookers who were unable to identify the dance, and therefore the corresponding source, and decided to look for food on their own. There are also lost recruits — those who were able to identify the dance, but got lost on the way to the source, and accidentally discovered other, perhaps even new, food sources [1,14]. Both of them can be called reluctant scouts. Considering the above, the number of scouts correlates with the number of errors in the system, which, in turn, indicates a certain optimal (non-zero) level of errors that ensures maximal foraging efficiency. This is a topic for further research.

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