Collective Decision Making in Honey Bees: Selection of Nectar Sources and Distribution of Nectar Foragers Through Self-organization

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ABSTRACT

Among the various nectar sources in the field, honey bees are believed to selectively forage from the most profitable sources through a self-organizing process, wherein all bees eventually forage only at the most profitable source leaving not a single individual to forage at the less profitable site. We show that a self-organizing process not only selects sources, which are not necessarily the most profitable, but also distributes foragers among them. Each individual forager estimates a time-independent quantity for the nectar source she visits and follows a set of simple behavioral rules. The quantity is called the source 'value'. Once the source values are estimated by the foragers, self-organization takes over to manage the colony's decision making process. At steady state all foragers distribute themselves among a subset of sources whose 'values' are equal and higher than all sources not belonging to the subset. Through self-organization the colony collectively decides on selecting nectar sources and appropriately distributing its foragers.

1. Introduction

When flowers are in bloom the bees forage at the various nectar providing sources available in the field. The survival and prosperity of the colony depends on how they can choose among the available nectar sources, and how they can distribute the foragers among them. In the absence of a central authority, the bees have to collectively make this decision. Each bee is known to communicate the coordinates of her nectar source through the waggle dance (von Frisch 1967) to a few unemployed foragers that closely follow her dance. She does not visit each available source in the field to compare the profitability of the sources, nor do the dance followers compare all the dances to choose the best source (Seeley & Towne 1992). Each forager visits a source, collects nectar, returns to her hive and advertises her source to a few follower bees. Each unemployed forager follows just one dance, chosen more or less at random, before she leaves the hive in search of the forage site she was informed about. With this limited communication, the colony is faced with a challenge of deciding which sources should be foraged and how best to distribute its foragers between the selected sources.

The process by which the bees deploy the foragers is believed to be self-organization, wherein a set of simple behavioral rules could describe the colony's decision making process (Seeley et al. 1991, Camazine & Sneyd 1991). This model, hereafter called the SCS model, is based essentially on the following three simple rules: (1) On return from the source, after foraging, the bee unloads the nectar. Then, she either immediately resumes foraging, or resumes foraging after dancing, or simply abandons the source. Each of these different choices is made with a probability $f_d(1-f_x), f_d$, and f_x respectively; where f_d is the probability with which the bee would dance for the source, and f_x is the probability with which she would abandon the source. (2) The duration τ for which the dancer dances for her source is determined by a gauge of source profitability P carried by each forager (Seeley 1994). (3) The deserters assemble on the following floor f, to follow the dancers. Here each unemployed forager chooses the next source that she would forage. The probability of an individual to choose a source among the various advertised sources f_f^i depends on the duration each dancer dances for her source, and the number of dancers on the dance floor d_i.

These rules when expressed mathematically show how the number of foragers at each nectar source evolves with time depending on a set of parameters like the aforementioned three probabilities (f_d, f_x, f_f) and the time each forager spends (i) at the source, or foraging floor $(T_a = 1/p_a)$, (ii) on the dancing floor $(T_d = 1/p_d)$, and (iii) on the following floor $(T_f = 1/p_f)$. The choosing probability f_f is a function of the dance duration τ and the instantaneous number of dancers d_i. All other parameters are time-independent and are believed to be either determined by some internal gauge by each individual bee, or is measured by each bee. Knowing these $6m+1$ input-parameters $(f_x^i, f_d^i, \tau_i, p_{ai}, p_{di}, p_{hi}, p_f)$, where $i = 1, 2, ..., m$, for the m sources in the field and $3m+1$ initial values (a_i, d_i, h_i, f), the system of equations in the SCS model describe how an initial distribution of foragers $(a_{10}, a_{20}, ..., a_{m0})$ evolves over time. At steady state the equations allow an 'all or none' distribution, wherein all foragers abandon the less profitable source among the two available ones in the field and congregate at the more profitable one.

The self-organizing process very accurately describes the experimental results of Seeley et al. (1991) where all foragers converged onto the most profitable source, thus abandoning the less profitable one. However, a colony not only selects the most profitable foraging site, but is known to distribute foragers among nectar sources with different profitabilities (Bartholdi et al. 1993). How do the bees manage this difficult decision making process? Bartholdi et al. (1993) claim that each bee accumulates a quantity called the 'equal value' for each source. Through the equal value hypothesis they show that there exists no other allocation that can bring a value more than twice as quickly as the equal value rate allocation.

Here we modify the SCS model to achieve not only the selection of the nectar sources among the available ones in the field, but also the distribution of the foragers among the selected sources. The modification simplifies the set of equations to the bare essentials, reducing the number of input-parameters from $6m+1$ to $5m$ $(f_x^i, f_d^i, \tau_i, p_{ai}, p_{di})$, and the total number of differential equations from $3m+1$ to m. The modification is two fold: (i) any arbitrary variation of the total number of available foragers N is allowed. Hence, N is a function of time, and this variation is directly incorporated into the equations. (ii) A hypothesis called the 'no-accumulation hypothesis' is introduced, whereby it is assumed that there is no accumulation or depletion of foragers at the unloading, dancing and following compartments. Accumulation could reduce the foraging efficiency. Instead of accumulating, the foragers can as well look for other tasks in the colony. Looking for other tasks implies abandoning foraging which is conveniently incorporated in the temporal variation of N. Depletion of foragers at these three compartments can also affect the communication system between the dancers and followers, which in turn can affect the self-organizing process and thereby the foraging efficiency. For example, zero dancers makes the choosing probability indeterminate and all foraging is abandoned. Under the 'no-accumulation hypothesis' the total number of foragers available is equal to the total number of foragers at all the m nectar sources $N = \sum_{i=1,m}^{m} a_i$; where a_i is the number of foragers at the ith source. The SCS model is modified, and the notation changed, so as to make it easier to deal with any number of sources. The modified SCS equations are presented in section (2), with the first modification in sub-section (2.1). The no-accumulation hypothesis is then applied and the resulting equations described in sub-section (2.2).

The no-accumulation hypothesis allows the system of equations to be solved analytically even in a complicated evolving N scenario. This provides an insight into the mechanism of the self-organizing process. The equations provide a key quantity which we call the 'value' following the tradition set by Bartholdi et al. (1993). The value is somewhat similar to their value. This value is a function of a subset of the input-parameters that varies from source to source and is assigned or estimated by the forager for each source she visits; $v = v(f_x, f_d, \tau, p_d)$. Unlike the Bartholdi et al. (1993) assumption that the value for each source is accumulated by the foragers, the value here is determined by each forager and is time-independent. The analytic solutions (section 3) show that if two sources have unequal values then the steady state solutions is an 'all or none' distribution, with all the foragers eventually foraging at the source with the higher value, leaving no foragers at the lesser valued source. If the values are equal then the available foragers distribute themselves between the two sources. Hence the self-organizing process does not necessarily select the most profitable among two sources.

Analytical solutions are studied in one simple case for a three source model (section 4). The source with the highest value is shown to be selected through self-organization. If two of the three sources have a value equal to each other and higher than the third, then the third source is abandoned and the foragers distribute themselves between the two sources with equal value. The equations can be solved numerically for any number of sources if the initial values are provided. These initial values and distributions can be obtained from experiments.

We use the experimental data in section (5) from two specific experiments, Seeley et al. 1991 and Bartholdi et al. 1993, and show that the evolution of the distribution can be accurately explained in both cases. The bees abandon the lesser valued source for the highest valued in the experiment of Seeley et al. 1991, here the higher valued source is also the most profitable. In the Bartholdi et al. (1993) experiment, the bees distribute themselves between the two equal valued sources whose profitabilities are not identical. The two experiments can be explained not only under the assumption that there are only two available sources in the field, but also under the assumption that there are an arbitrary number of sources in the field, which is a realistic case.

Each individual forager determines the value of the source. Once the value of the source is determined, the self-organizing process selects the sources and distributes the foragers among the highest equal valued sources. The value of the source $v = v(f_x, f_d, \tau, p_d)$, is time-independent if the input-parameters are time-independent. If the profitability of the source varies with time, which is bound to happen with finite resources and competition at the nectar source, then the value too can vary with time. Given a time-dependent value the hive is known to adjust the number of foragers in real time: the number of foragers at two equally profitable sources remains almost the same until the profitability of one of them is doubled, when the hive was shown to increase the foragers at the more profitable source while simultaneously decreasing its foragers at the other (Seeley 1995; section 5.13). Seeley called this phenomenon cross-inhibition. In section (6) we show that cross-inhibition between forager groups is simply a consequence of the change in value of the source when the profitability is changed. When the profitability was equal the values of the sources were equal, and the number of foragers remained more or less the same. When the profitability of one of the sources was doubled its value doubled. The immediate consequence of unequal values is to send all the foragers to the higher valued source while reducing the foragers at the lower valued one. Self-organization naturally explains cross-inhibition. Thus, the modified SCS model of self organization accurately describes how the hive collectively makes the decision of selection of the nectar sources and distribution of its foragers.

2. The Modified SCS model

We rewrite the Seeley-Camazine-Sneyd model in a "generalized" notation with two important modifications: (a) Evolution of the total number of available foragers is introduced in sub-section (2.1), (b) A 'No-accumulation hypothesis' is explained and introduced sub-section (2.2).

2.1. Non-conservation of N

The total number of available foragers N can change with time. The number of committed foragers can be increased via the shaking signal (von Frisch 1967, see Seeley 1995 section 6.2 for a list of other references). The shaken nonforagers and even the young 10 to 14 day old bees are known to be coaxed into entering the following floor to start foraging (Schneider et al. 1986). The effect of such shaking recruitment is to add to the number of followers f and effectively increase the total number of committed foragers N. The SCS model equations (A.1) become

$$\begin{aligned}
\frac{da_i}{dt} &= (1-f_x^i)(1-f_d^i)p_{hi}h_i + p_{di}d_i + f_f^i p_f f \quad (1) \\
&\qquad -p_{ai}a_i, \\
\frac{dd_i}{dt} &= f_d^i(1-f_x^i)p_{hi}h_i - p_{di}d_i, \qquad (2) \\
\frac{dh_i}{dt} &= p_{ai}a_i - p_{hi}h_i, \qquad (3) \\
\frac{df}{dt} &= \sum_{j=1}^{m} f_x^j p_{hj}h_j - p_f f + \frac{dN}{dt}, \qquad (4)
\end{aligned}$$

where 'i' refers to the ith nectar source, a, d, h and f refer to the four different compartments of the ith nectar source, dancing floor, unloading floor and following floor, respectively. The number of bees at the ith nectar source is a_i, the number dancing for source i is d_i, number unloading for source i is h_i and the number following the dancers is f. The average rate at which the foragers depart from the compartment y is p_y, whose inverse gives the time the forager spends in y; $T_y = 1/p_y$. The abandonment probability is f_x, the dancing probability is f_d and choosing probability is f_f which is defined as

$$f_f^i = \frac{\tau_i d_i}{\sum_{j=1}^{m} \tau_j d_j}, \qquad (5)$$

where τ_i is the duration of the dance, which is a fraction of the time spent by the dancer on the dancing floor $T_{di} = 1/p_{di}$ and is a linear function of profitability of the nectar source (Seeley 1994). The total number of foragers is N. The choice of f_f^i is not unique. If the followers sampled n different dancers, then the choosing probability for the ith source would be $(f_f^i)^n$ (Camazine & Sneyd 1991). However, it was conclusively shown (by Seeley & Towne 1992) that bees do not compare dances.

Equations (1)-(4) satisfy the relation

$$\frac{d}{dt}\left[\sum_{j=1}^{m}(a_j + d_j + h_j) + f\right] = \frac{dN}{dt}. \qquad (6)$$

The first modification from the original SCS model is in the last term dN/dt in equation (4) which allows any functional form for N, including the one (in Camazine & Sneyd 1991) which exponentially grows from an initial value of $N_\circ$ to an asymptotic value of N_{tot} with a time constant $1/k$ such that

$$\frac{dN}{dt} = k(N_{tot} - N), \qquad (7)$$

where the solution for N is

$$N = N_{tot} + (N_\circ - N_{tot})\exp(-kt). \qquad (8)$$

It is emphasized that any functional form of N is equally valid for the analysis that follows.

2.2. The 'No-Accumulation Hypothesis'

The 'no-accumulation hypothesis' assumes that there is no accumulation or depletion of the number of bees in compartments d, h and f. Under this hypothesis the system of equations (1)-(5) yield analytical solutions. Mathematically, the hypothesis introduces the conditions that the time derivative of d_i, h_i and f are zero,

$$\frac{dd_i}{dt} = 0 = \frac{dh_i}{dt} = \frac{df}{dt}. \qquad (9)$$

In equations (2)-(4) we have,

$$\begin{aligned}
p_{di}d_i &= f_d^i(1-f_x^i)p_{hi}h_i, \\
p_{hi}h_i &= p_{ai}a_i, \\
p_f f &= \sum_{j=1}^{m} f_x^j p_{hj}h_j + \frac{dN}{dt}. \qquad (10)
\end{aligned}$$

Hence, equations (1) and (10) together give the modified SCS model equations

$$\frac{da_i}{dt} = f_f^i \left(\frac{dN}{dt} - \sum_{j=1}^{m} f_x^j p_{aj} a_j \right) - f_x^i p_{ai} a_i, \qquad (11)$$

and the choosing probability of equation (5) becomes

$$f_f^i = \frac{\tau_i f_d^i (1 - f_x^i)(p_{ai}/p_{di}) a_i}{\sum_{j=1}^{m} \tau_j f_d^j (1 - f_x^j)(p_{aj}/p_{dj}) a_j}. \qquad (12)$$

The input-parameters p_{hi} and p_f drop out. The effect of the rate at which the bees leave the following compartment would indirectly appear in the way the total number of bees evolve. However, its interesting to note that the self-organizing process must not be dependent on the rate at which the bees leave the unloading floor. Perhaps, the time spent on the unloading floor T_{hi}, on average, must be independent of the source. This could be because if the total search time, which is T_h, exceeds a certain level (roughly 50s) tremble dances are triggered (Seeley 1992, Kirchner & Lindauer 1994) through which the colony boosts its nectar processing rate by boosting the number of food storers.

The choosing probability could be defined differently than in equation (5), yet the general form of equation (12) will be

$$f_f^i = \frac{x_i a_i}{\sum_{j=1}^{m} x_j a_j}, \qquad (13)$$

where x_i is a function of the probabilities and mean rates of departures from the compartments. Equations (11) can be recast as

$$\frac{da_i}{dt} = \left[\frac{x_i}{\sum_{j=1}^{m} x_j a_j} \frac{dN}{dt} + x_i V - y_i \right] a_i, \qquad (14)$$

where $V = \sum_{j=1}^{m} y_j a_j / \sum_{j=1}^{m} x_j a_j$, and $y_i = f_x^i p_{ai}$. The set of m equations (14) describe the time evolution of an initial distribution of foragers $(a_1, a_2, ..., a_m)$ when the input-parameters x_i and y_i are given. The equations can be numerically solved for any number of sources, and analytically solved when the number of sources is limited; $m = 2, 3$. The two source model is solved analytically in the next section, and a specific case is solved for a three source model in section (4).

3. Analytic Solutions for a Two Nectar Source Model

In the presence of 2 nectar sources the SCS model shows that the only choice of forager distribution in the steady state is an 'all or none' distribution. The evolution of the forager distribution to the steady state can be traced for the modified SCS model described by equation (14) by obtaining analytic solutions. The 'all or none' steady state distribution is shown to be the consequence of unequal values assigned by the individual forager to the nectar sources, and all the foragers eventually forage at the source with the highest value, thus abandoning the source with a lesser value. The value of a source is defined by a quantity $v_i = x_i/y_i$, where $y_i = f_x^i p_{ai}$ and x_i depends on the choice of the choosing probability f_f^i. The value is made up of parameters which are evaluated by each individual forager. The choosing probability in equation (12) gives the value expression to be of the form

$$v_i = \frac{\tau_i f_d^i (1 - f_x^i)(p_{ai}/p_{di})}{f_x^i p_{ai}}. \qquad (15)$$

In a two nectar source model, equations (14) become

$$\frac{da_1}{dt} = \frac{x_1 a_1}{x_1 a_1 + x_2 a_2} \left(\frac{dN}{dt} + y_1 a_1 + y_2 a_2 \right) - y_1 a_1, \qquad (16)$$

$$\frac{da_2}{dt} = \frac{x_2 a_2}{x_1 a_1 + x_2 a_2} \left(\frac{dN}{dt} + y_1 a_1 + y_2 a_2 \right) - y_2 a_2. \qquad (17)$$

Take $x_2 = \beta x_1$ and $y_2 = \alpha y_1$ to represent $v_1 = (\alpha/\beta) v_2$; α and β are constants. The total number of available foragers at any time $N = a_1 + a_2$. So, its sufficient to solve for either a_1 or a_2. For a_1, equation (16) becomes

$$\frac{da_1}{dt} = \frac{a_1}{(1-\beta) a_1 + \beta N} \left(\frac{dN}{dt} + y_1 (\alpha - \beta)(N - a_1) \right), \qquad (18)$$

whose solution can be shown to satisfy the equation

$$a_1^\beta (N_\circ - a_{10}) \exp[(\beta - \alpha) y_1 t] + a_1 a_{10}^\beta - N a_{10}^\beta = 0, \qquad (19)$$

where a_{10} is the initial value of a_1.

The solution can be studied for different conditions. (a) If $a_{10} = N_\circ$ then equation (19) admits the only solution $a_1 = N$, provided $a_{10} \neq 0$, leaving the forager distribution to be $(a_1, a_2) \equiv (N, 0)$. On the other hand if $a_{10} = 0$ then the only solution is $a_1 = 0$, with the forager distribution $(0, N)$. This merely points out the fact that the forager distribution cannot increase from a value of zero. Atleast one forager has to visit the nectar source before its foragability is placed on the decision making floor.

(b) When the values are equal $v_1 = v_2$, that is when $\alpha = \beta$. The equation (19) simplifies to

$$a_1^{\beta}(N_\circ - a_{10}) + a_1 a_{10}^{\beta} - N a_{10}^{\beta} = 0, \qquad (20)$$

showing that, a_1 evolves with time if N does. However, if N does not evolve with time ($N = N_\circ$), then $a_1 = a_{10}$ is the only solution. When the values are equal, the initial distribution does not evolve with time unless N itself is time dependent.

Equation (20) can be solved numerically for any value of β. In atleast three special cases ($\beta = 0, 1$ and 2) the solutions of equation (20) are

$$\beta = 0 \quad \Rightarrow \quad a_1 = N - (N_\circ - a_{10}), \qquad (21)$$

$$\beta = 1 \quad \Rightarrow \quad a_1 = \frac{N}{N_\circ} a_{10}, \qquad (22)$$

$$\begin{aligned} \beta = 2 \quad \Rightarrow \quad a_1 &= \frac{a_{10}^2}{2(N_\circ - a_{10})} \qquad (23) \\ &\times \left[-1 + \sqrt{1 + \frac{4N}{a_{10}^2}(N_\circ - a_{10})} \right]. \end{aligned}$$

The steady state solutions in these special cases are obtained by taking limits as $t \to \infty$ and the other time varying quantity N asymptotically goes to N_{tot}.

For $\beta = 2$ and an initial distribution $(a_{10}, a_{20}) \equiv (0.5N_\circ, 0.5N_\circ)$ the steady state solution is

$$\lim_{t\to\infty} a_1 = \frac{a_{10}}{2} \left[-1 + \sqrt{1 + \frac{4N_{tot}}{a_{10}}} \right], \qquad (24)$$

where $\lim_{t\to\infty} N = N_{tot}$. If $N_{tot} = 0$, $(a_1, a_2) \to (0, 0)$. If $N_{tot} = 2a_{10}$, $(a_1, a_2) \to (a_{10}, a_{20})$. However, it should be noted that $N_{tot} = 2a_{10}$ does not necessarily imply that N is independent of time, N could evolve with time giving an asymptotic value equal to the initial value $N_\circ$.

An interesting situation is $N_{tot} = 6a_{10}$. Equation (24) shows that $(a_1, a_2) \to (2a_{10}, 4a_{10})$. With $a_{10} = 10$ the initial distribution $(10, 10)$ evolves to the non-zero steady state distribution of $(20, 40)$. This closely matches the experimental result in Bartholdi et al. (1993), where a mean initial distribution of $(10, 10)$ evolves to $(20.9 \pm 0.8, 39.0 \pm 2.2)$. Later we shall solve equation (18) with the experimentally observed parameters of α and β and trace the evolution of the distribution with time.

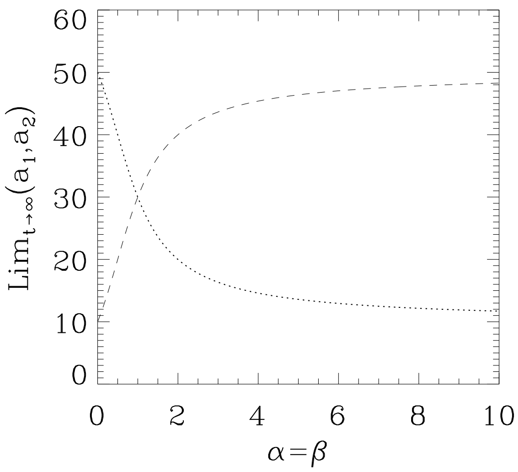

Fig. 1.— An initial distribution of $(a_{10}, a_{20}) \equiv (10, 10)$ foragers are evolved upto 4 hr for two nectar sources with equal values $v_1 = v_2$, for different values of $\alpha = \beta$, where $x_2 = \beta x_1$, and $y_2 = \alpha y_1$; $v_i = x_i / y_i$. The steady state distribution $\lim_{t\to\infty}(a_1, a_2)$ is plotted against $\alpha = \beta$, dotted line represents $\lim_{t\to\infty} a_1$ and dashed line, $\lim_{t\to\infty} a_2$. The source whose x_i is larger (equivalently, whose y_i is larger) gets the larger share of foragers.

The steady state solution can be computed numerically for any $\alpha = \beta$. For an initial distribution of $(10, 10)$ with $N_\circ = 20$ which evolves to a steady state asymptotic total value of $N_{tot} = 60$ equations (14) can be solved numerically until the initial distribution reaches an asymptotic value $\lim_{t\to\infty}(a_1, a_2)$. The total number of foragers N reaches its asymptotic value $N_{tot} = 60$ in roughly 3 hours when $k = 2$. The steady state distribution $\lim_{t\to\infty}(a_1, a_2)$ is plotted in figure (1) for the different values of $\alpha = \beta$. The dotted line traces $\lim_{t\to\infty} a_1$ and dashed line traces $\lim_{t\to\infty} a_2$. The steady state distribution depends on the value of $\alpha = \beta$. When $\alpha = \beta = 2$ the steady state values are $(20, 40)$. The source with the larger of the two x_i, or equivalently y_i, is the source that has the larger number of foragers among the two sources.

(c) When the values are not equal; $v_1 > v_2$, i.e. $\alpha > \beta$. At the limit of $t \to \infty$ equation (19) yields $a_1 = N$ as the solution if $a_{10} \neq 0$. Any non-zero initial distribution $(a_{10}, a_{20}) \to (N, 0)$. Similarly, for $v_1 < v_2$, or $\alpha < \beta$, at the limit of $t \to \infty$ equation (19) admits the only solution $a_1 = 0$. That is, $(a_{10}, a_{20}) \to (0, N)$. Hence, when $v_1 \neq v_2$ the only solutions admitted are $(N, 0)$ or $(0, N)$, depending on whether $v_1 > v_2$ or $v_1 < v_2$. The source with the higher value is selected.

There are two general analytic solutions of equation (19) for arbitrary α that are of interest. That is, when $\beta = 1$

$$a_1 = \frac{N a_{10}}{a_{10} + (N_\circ - a_{10}) \exp[(1-\alpha) y_1 t]}, \tag{25}$$

and when $\beta = 2$,

$$\begin{aligned} a_1 &= \frac{a_{10}^2}{2(N_\circ - a_{10}) \exp[(2-\alpha) y_1 t]} \\ &\quad \times \left[-1 + \sqrt{1 + \frac{4N}{a_{10}^2} (N_\circ - a_{10}) \exp[(2-\alpha) y_1 t]} \right]. \end{aligned} \tag{26}$$

We have thus shown that in the case of two nectar sources the self-organizing process chooses the one whose value is the highest, so that at steady state all the foragers forage only at the source with the highest value. How does the hive distribute the foragers among a large number of nectar sources available in the field? The self-organizing process converges on sending all the foragers to the sources with the maximum value. If m_1 out of the m available sources have an equal value higher than the rest of $m - m_1$ sources, then at steady state all the foragers distribute themselves between the m_1 sources, thus abandoning the $m - m_1$ sources with a lower value. In the next section we demonstrate it by deriving analytic solutions when $m = 3$ and $m_1 = 2$, and in the subsequent section we numerically solve the differential equations for $m = 10$ and $m_1 = 4$.

4. Analytic Solutions for a Three Nectar Source Model

In the presence of three nectar sources, two of which have the same value $v_2 = v_3$, foragers will choose either the first source with value v_1, or the two equal valued sources, depending on which of them has a higher value. If $v_2 = v_3 > v_1$, then the foragers will abandon source 1, and all of them will distribute themselves between source 2 and source 3. On the other hand, if $v_2 = v_3 < v_1$, then the foragers will abandon the sources 2 and 3, and converge onto the first source.

We choose a case where $v_1 = (\alpha/\beta) v_2 = (\alpha/\beta) v_3$, with $x_2 = x_3 = \beta x_1$ and $y_2 = y_3 = \alpha y_1$. For $i = 1$ equation (14) takes a form identical to equation (18) yielding solutions satisfying an equation identical to equation (19). For $v_1 > v_2$ (i.e. $\alpha > \beta$), $\lim_{t\to\infty} a_1 = N$ and $\lim_{t\to\infty}(a_2 + a_3) = 0$, or, $(a_{10}, a_{20}, a_{30}) \to (N, 0, 0)$; sources 2 and 3 are abandoned. For $v_1 < v_2$, on the other hand, $\lim_{t\to\infty} a_1 = 0$ and $\lim_{t\to\infty}(a_2 + a_3) = N$. In the general case, to get the distribution (a_2, a_3) we solve for a_2. For $i = 2$, equation (14) takes the form

$$\frac{da_2}{dt} = \frac{a_2}{(1-\beta) a_1 + \beta N} \left\{ \beta \frac{dN}{dt} + y_1 (\beta - \alpha) a_1 \right\}, \tag{27}$$

where a_1 is given by equation (19); the equation is identical in form for $i = 3$. Solving equation (27) gives

$$a_2 = a_{20} \exp \left\{ \int_0^t A(t) dt \right\}, \tag{28}$$

where

$$A(t) = \frac{1}{(1-\beta) a_1 + \beta N} \left\{ \beta \frac{dN}{dt} + y_1 (\beta - \alpha) a_1 \right\}. \tag{29}$$

An example of the solution for $\beta = 1 \neq \alpha$ is

$$a_1 = \frac{N a_{10}}{a_{10} + (N_\circ - a_{10}) \exp[(1-\alpha) y_1 t]}, \tag{30}$$

$$a_2 = \frac{N a_{20}}{N_\circ + a_{10} \{ \exp[(\alpha - 1) y_1 t] - 1 \}}, \tag{31}$$

$$a_3 = \frac{N a_{30}}{N_\circ + a_{10} \{ \exp[(\alpha - 1) y_1 t] - 1 \}}, \tag{32}$$

where (a_{10}, a_{20}, a_{30}) is the initial forager distribution. The steady state distributions are

$$\alpha < \beta = 1 \quad \Rightarrow \quad \left(0, \frac{N_{tot} a_{20}}{N_\circ - a_{10}}, \frac{N_{tot} a_{30}}{N_\circ - a_{10}} \right), \tag{33}$$

$$\alpha > \beta = 1 \quad \Rightarrow \quad (N_{tot}, 0, 0). \tag{34}$$

The steady state values are given by $\lim_{t\to\infty}(a_1, a_2, a_3)$ of equations (30)-(32). In the presence of three sources the hive selects the source with the highest value and allocates all its foragers to it. If two of the three sources have the same higher value, the hive distributes its foragers among these two higher valued sources, completely abandoning the third.

5. Experimental Verification

The set of m equations (14) can be numerically integrated for any initial distribution $(a_{10}, a_{20}, ..., a_{m0})$, and any set of input-parameters x_i, y_i. The input-parameters and initial distribution are obtained from controlled experiments (Seeley 1995). In sub-section (5.1) we use the input-parameters measured in Seeley et. al (1991) and show that the initial distribution of $(11, 11)$ individuals between two sources with widely differing values evolves to a steady state distribution where the hive abandons the lesser valued source, which is also less profitable. In sub-section (5.2) we use the data from the experiment described in Bartholdi et. al. (1993), where the hive distributes its foragers between two equal valued sources with differing profitabilities. The evolution and steady state values are accurately described by the modified SCS model.

5.1. The Seeley et al. Experiment

In the Seeley et al. (1991) experiment two equidistant sucrose solution feeders are identical except for their sucrose concentrations; one contains a 2.5mol/L solution and the second a 0.75mol/L solution. The first source is more profitable. The initial distribution of foragers $(11, 11)$ is shown to evolve (figure 1 of Seeley et al. 1991; figure 5.34 of Seeley 1995) wherein the number of foragers at the first source increases rapidly and that at the second falls. At the end of 4 hours the concentrations are switched, making the first source less profitable. Immediately, the foragers at the first source drop and the foragers at the second source rise to a maximum value of roughly 125.

The input-parameters needed are given in table (5.3) of Seeley (1995). In our notation, in the first half of the experiment the input-parameters $(f_x^i, f_d^i, \tau_i, p_{ai}, p_{di})$ for the first source are $(0, 1, 0.38, 1/2.5, 1/1.5)$, and the second source are $(0.04, 0.15, 0.02, 1/3.5, 1/2)$; where the rates p are in min^{-1}. Since the initial total number of foragers $N_o = 22$ increases to about 130 at the end of the experiment in 8hr, we use an exponentially growing N with $N_{tot} = 225$ with a growth rate of $k = 0.095$ described by the equation (8). The parameters N_{tot} and k can be chosen differently as long as N_{tot} is equal to the experimental value at the end each phase of the experiment; $N_{tot}(t = 4\mathrm{hr}) = 86$ and $N_{tot}(t = 8\mathrm{hr}) = 130$. The time evolution of the distribution (a_1, a_2) can be obtained either by numerically solving the differential equation (14) with the input-parameters, or numerically solving for a_1 in equation (19) for the values of α and β obtained from the input parameters. The computed evolution of (a_1, a_2) is plotted in figure (2); dotted line denotes a_1, dashed line shows a_2, and solid line is N. From equation (15), the value of the first source is ∞. To avoid infinities in the numerical calculations we keep f_x^1 not exactly zero, but very close to zero, at 10^{-6}, and f_d^1 not at 1, but close to 1, at 0.999999. Hence, $v_1 = 158.2$ is very large compared to $v_2 = 4 \times 10^{-5}$. The values of $\alpha = 2.9 \times 10^4$ and $\beta = 7.2 \times 10^{-3}$. The hive selects the first source, and a_1 increases rapidly while the a_2 approaches zero. At the end of 4hr the input parameters for the two sources are switched and the evolution of the distribution computed. The bees quickly adjust in a way that a_1 is rapidly depleted to

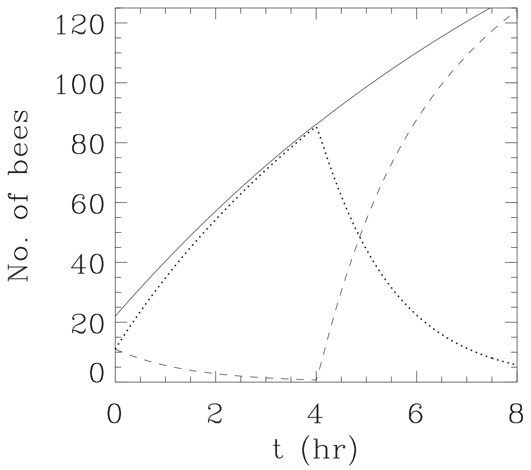

Fig. 2.— The modified SCS model describes the evolution of the forager distribution in the experiment of Seeley et al. 1991, where the foragers converge to the first source with the highest value (dotted line) and abandon the second (dashed line). At the end of 4 hours, when the concentration of the sucrose solution is switched between the two sources, making the first source lower valued, the number at the first source rapidly drops to 6 individuals and the second source is selected by the hive where 124 individuals converge at the end of 8hr. The solid line shows the evolution of the total number of foragers N. The evolution of the distribution matches the experimental results in figure (3) of Camazine & Sneyd (1991).

6 individuals and the foragers at the second source increase to a maximum of 124. The evolution of the distribution is accurately described by the modified SCS model.

5.2. The Bartholdi et al. Experiment

Here we use the data from Bartholdi et al. (1993) and show how the bees distribute the foragers between the two nectar sources whose values are equal, though their profitabilities are different. The mean initial distribution of $(10,10)$ foragers was noted to evolve to a final mean steady state forager distribution of $(20.9 \pm 0.8, 39.0 \pm 2.2)$. We first show that the parameters in Bartholdi et al (1993) map onto the parameters of the modified SCS model, and hence on to our definition of the value. The values of the two sources monitored are 0.70 and 0.84, almost identical. We trace the evolution of the distribution in two different cases: (i) when the assumption that there are only two nectar sources available in the field, and (ii) when there are an arbitrary number of nectar sources all with values much smaller than the monitored sources. Both these cases accurately reproduce the steady state distribution of the Bartholdi et al. experiment.

In section (3) we showed that when only two nectar sources with equal values $v_1 = v_2$ are present in the field the evolution of the distribution for $\alpha = \beta = 2$ follows equation (23), and the asymptotic value of the distribution given by equation (24). When $a_{10} = a_{20} = 10$ and the asymptotic value of $N_{tot} = 60$, the steady state distribution is $(20,40)$, very close to the experimental values. Figure (1) shows that when $\alpha = \beta = 1.84$ the exact experimental results can be obtained. At $\alpha = \beta = 1.84$ the steady state distribution in figure (1) is $(20.96, 39.04)$. We shall now, estimate α and β (or more precisely, the input-parameters x_1, x_2, y_1, y_2), from the observations.

In the notation of Bartholdi et al. (1993) $f_x \equiv f^i_x p_{ai}$ of our notation, is the per capita abandonment from source $x \equiv i$ measured in abandonments/bee/hr, $n_x \equiv a_i$ is the number of bees foraging at the ith source and $g_x \equiv \tau_i/(t_{ui} p_{di})$ is the dance duration for source i, measured in dance circuits/return; t_u is the time per dance circuit. The returning rate of bees from the source i is $r_x \equiv p_{ai} a_i$, and the return time $T_x \equiv 1/p_{ai}$. If the choosing probability f^i_f is defined differently from equation (5) as

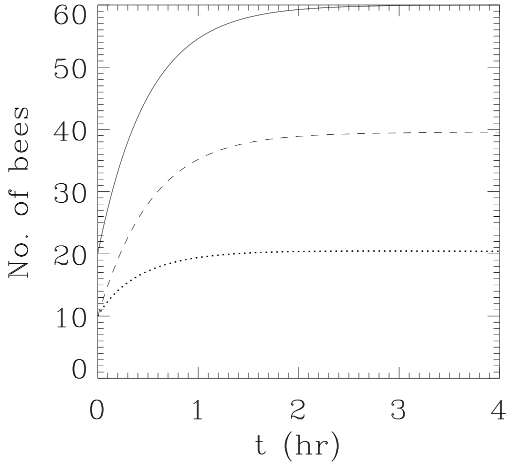

Fig. 3.— The initial distribution of foragers with $(a_{10}, a_{20}) \equiv (10,10)$ is allowed to evolve for a two source model whose values are given by the experimental values in Table 1 of Bartholdi et al. (1993); $v_1 = 0.70$ and $v_2 = 0.84$, with $\alpha = 1.58$ and $\beta = 1.89$. The dotted line traces the evolution of a_1, dashed line that of a_2 and solid line of N which rises from $N_\circ = 20$ to $N_{tot} = 60$. The forager distribution at 4 hrs is $(20.42, 39.57)$, accurately matches the Bartholdi et al. experiment. The hive distributes its foragers between the two almost equal valued sources. Twice the number of foragers forage at the second source whose $x-$value is twice that of the first.

$$f^i_f = \frac{g_x r_x}{\sum_{x=1}^{m} g_x r_x} \equiv \frac{\tau_i p_{ai} a_i/(t_{ui} p_{di})}{\sum_{j=1}^{m} \tau_j p_{aj} a_j/(t_{uj} p_{dj})}, \quad (35)$$

then $x_i = \tau_i p_{ai}/(t_{ui} p_{di})$ instead of $x_i = \tau_i f^i_d (1 - f^i_x)(p_{ai}/p_{di})$ of equation (12). In the Bartholdi et al. (1993) definition of f^i_f (equation 35) and notation, the equal value translates to

$$v_i = \frac{g_x}{f_x T_x} \equiv \frac{\tau_i}{f^i_x t_{ui} p_{di}}, \quad (36)$$

and the experimental values of their Table 2 yields $v_1 = 18.4$ and $v_2 = 22.0$.

The choosing probability in equation (12), on the other hand, provides the value according to our definition as in equation (15). Table 2 of Bartholdi

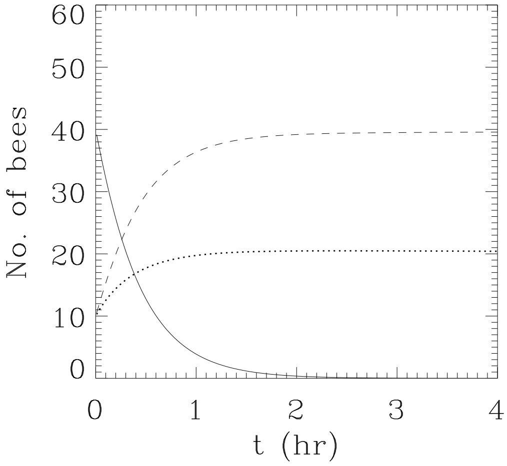

Fig. 4.— The experimental values in Table 1 of Bartholdi et al. (1993) are used as input-parameters along with a fictitious nectar source a_3 with its parameters $x_1 = 0.1x_2$ and $y_1 = 100y_2$, so that $v_3 = 0.001v_1$, and $v_1 = 0.7 \approx v_2 = 0.84$. The set of equations (14) are solved numerically. The solutions depict how the number of foragers at each source evolve from the initial distribution of $(a_{10}, a_{20}, a_{30}) \equiv (10, 10, 40)$ to the steady state distribution of $(20.42, 39.57, 0)$. Solid line shows a_3 which is abandoned because its value is small compared to the first two sources, dotted line is a_2 and dashed line is a_3, where all the foragers eventually distribute themselves with $a_2 > a_1$ because $x_2 > x_1$.

et al. (1993) supplies the input-parameters $\tau_1 = 0.073t_{u1}p_{d1}$, $\tau_2 = 0.117t_{u2}p_{d2}$, $p_{a1} = 1/0.165$ hr^{-1}, $p_{a2} = 1/0.140$ hr^{-1}, $f_x^1 = 0.024 * 0.165$, and $f_x^2 = 0.038 * 0.140$. The values of the duration of each dance circuit t_{ui} are obtained by obtaining a least squares fit to the data in Table (13) of von Frisch (1967). The two sources are equidistant at 350m from the hive, the least squares fit gives $t_{u1} = t_{u2} = 2.3$s. We make one reasonable assumption, that all the foragers that do not abandon the source, dance for it, instead of returning to the source without dancing. In other words, $f_d^i = 1$. The values of the two sources turn out to be $v_1 = 0.70$ and $v_2 = 0.84$. The value derived directly from the modified SCS model differ from the equal value of the Bartholdi et al. definition, but the ratio v_1/v_2 are the same in both definitions.

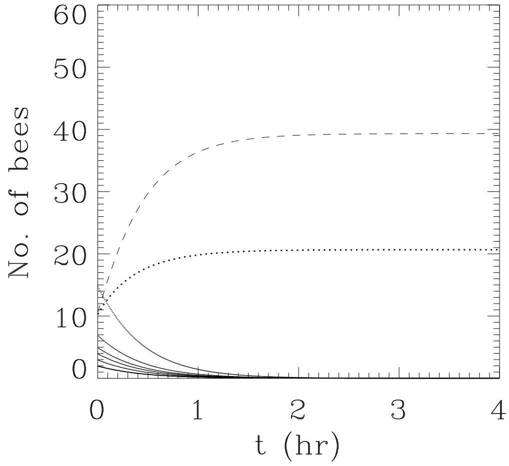

Fig. 5.— The exercise in figure (4) is repeated for 10 sources where the first 2 sources have the experimental values of Bartholdi et al. (1993) the remaining sources have $x_i = 0.1x_1$, $y_i = 100y_1$, for $i = 3, 4, ..., 10$. The initial distribution of $(10, 10, 15, 2, 2, 2, 3, 4, 5, 7)$ evolves to $(20.42, 39.57, 0, 0, 0, 0, 0, 0, 0, 0)$. The hive abandons all the sources with smaller value and distributes all its foragers between the two sources with equal and maximum values.

The values are not identical, but are almost equal. We shall see that the modified SCS model accurately describes the final distribution of foragers. The input-parameters estimated as above give $x_1 = 0.0169$, $x_2 = 0.0319$, $y_1 = 0.024$ and $y_2 = 0.038$, with $\alpha = 1.58$ approximately equal to $\beta = 1.89$. Solving equation (19) with the initial values of $(a_{10}, a_{20}) \equiv (10, 10)$ and N evolving as equation (8) with $k = 2$ so that $N_\circ = 20$ evolves to the asymptotic value of 60 in 4hr, yields the dotted curve for a_1 and dashed curve for a_2 in figure (3). The distribution at 4hr is given by $(20.42, 39.57)$. The experimental values of Bartholdi et al. (1993) are accurately reproduced by the modified SCS model.

The two nectar source model yields the final distribution when the total number of available foragers increases from an initial value $N_\circ = 20$ to $N_{tot} = 60$ within roughly an hour or two. However, with an arbitrary number of sources in the field the total number of available foragers could either follow the evolution above, or can be constant at $N_\circ = N_{tot} = 60$. In either case, the observed steady state distribution is obtained if the value of all other available sources are smaller than the two experimental sources; $v_i << 0.70, \forall i \neq 1, 2$.

For 3 sources, let the third source have $x_3 = 0.1x_1$, $y_3 = 100y_1$, giving $v_3 = 0.001v_1$. We numerically solve the set of differential equations (14) with the initial distribution $(10, 10, 40)$ and a constant $N = N_\circ = 60$ to get the evolution of the distribution as shown in figure (4); dotted line is a_1, dashed line is a_2, and solid line is a_3. The foragers abandon source 3 leaving all the 60 foragers to distribute themselves between the first two sources with exactly the same distribution as for the two nectar source model $(20.42, 39.57, 0)$.

This exercise can be done for any number of nectar sources. Figure (5) shows a 10 source model with the initial distribution of $(10, 10, 15, 2, 2, 2, 3, 4, 5, 7)$ evolves to $(20.42, 39.57, 0, 0, 0, 0, 0, 0, 0, 0)$, when $x_i = 0.1x_1$, $y_i = 100y_1$ for $i = 3, 4, ...10$, so that $v_i << v_1, v_2$ for $i \geq 3$. The bees choose the source with the maximum value, and in the process if the maximum value is equal for a number of different sources, they distribute themselves between the maximum equal valued sources.

6. Cross-Inhibition Between Forager Groups

The parameters that the value depends on could vary with time, making the value time-dependent. In such a case the colony adjusts the forager allocation in real time between the various food sources. Such a mechanism has been shown experimentally in Seeley (1995). This mechanism by which the hive achieves an increase in the number of foragers at the nectar site which has increased its profitability by decreasing the foragers at another less profitable source is called cross-inhibition (section 5.13 of Seeley 1995). In the Seeley (1995) experiment, two identical sucrose feeders were placed equidistant from a colony. For almost 2.5hr essentially equal number of bees visited the two locations. At the end of 2.5hr when one source is replaced by twice the concentration of sucrose solution, the number of foragers quickly increased from 25 bees to approximately 67 bees, while suppressing the number at the second source from 25 to roughly 6 bees.

The modified SCS model can describe the evolution shown in figure (5.35) of Seeley (1995). Since the input-parameters are not available we use some typical values as parameters α, β, and y_1. The initial distribution in lower figure (5.35) of Seeley (1995) is $(15, 18)$. The sources are identical and equidistant in the first phase of the experiment, hence the values of the sources are equal and α should be equal to β; we choose $\alpha = \beta = 1$. We then take typical values of f_x^1 to be 0.1 and $p_{a1} = 1./2.5\text{min}^{-1}$, to get $y_1 = 0.04$. The initial total number of foragers $N_\circ = 33$ asymptotically approaches a value of roughly 60 (figure 5.35 Seeley 1995) in the first phase of the experiment, so we let N vary according to equation (8) with $k = 1.5$ so that N increases from 33 to 60 within the 2.5hr of the first phase of the experiment. This is a two nectar source model and the solutions are given by equation (19). The solutions are computed and plotted in figure (6). The dotted line is a_1, dashed line is a_2 and solid line is N. The number of foragers are close to each other and hover around $25 - 30$ foragers at the end of 2.5hr.

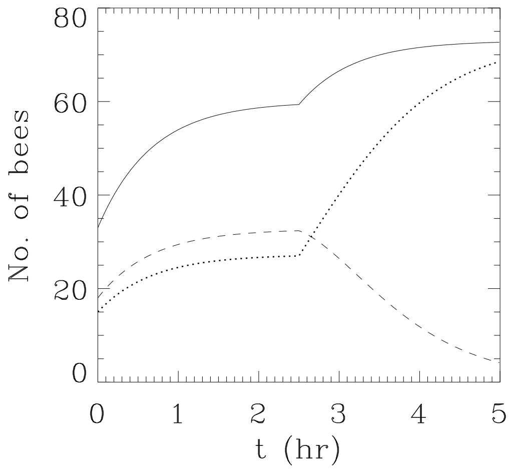

Fig. 6.— Two equal valued sources are visited by an almost equal number of foragers, as shown by the dotted line for the first source and dashed line for the second; solid line shows the total number. At the end of 2.5 hours when the value of the first source is doubled the hive quickly adjusts its forager distribution by increasing the number at the first source and simultaneously decreasing the number at the second source. Thus cross-inhibition is a natural extension of self-organization through the modified SCS model.

In the second phase of the experiment, the sucrose concentration of the first source was doubled. Though we do not know the exact functional dependence of the abandonment probability f_x on profitability, we know it must decrease f_x, hence we naively assume that $f_x^1 = 0.05$; half its original value of 0.1. This doubles $\alpha = f_x^2 p_{a2} / f_x^1 p_{a1}$. The total number of foragers in the experiment which is at 60 in the beginning of the second phase increases to 73. Hence, with $N_\circ = 60$ and $N_{tot} = 73$ we solve for a_1 and plot the forager distribution for the second half of the experiment. When the value of the first source is doubled the hive increases the foragers at the higher valued source to roughly 69 foragers and simultaneously decreases the foragers at the second source to 4. Cross-inhibition is a natural extension of the source selection and forager distribution of self-organization, through the modified SCS model.

7. Discussion

Bees collectively decide on the selection of the nectar sources and the distribution of foragers among them. This coordinated activity among several thousand bees is achieved without any central authority. Each individual bee follows a set of simple rules based on a set of parameters that she can measure. We shall call these parameters the source-parameters $(s_1, s_2, ..., s_p)$ and the forage context-parameters $(c_1, c_2, ..., c_q)$ (figure 5.22 of Seeley 1995). For instance, a few of the source-parameters include the location of the source, sugar content of the nectar, and travel time to the source. Some of the context-parameters are the nectar influx, weather, and time of the day. The source parameters instruct the forager about the profitability of the source, whose knowledge is solely confined to the forager (Seeley et al. 1991). The foragers derive quantities like the threshold profitability from the context-parameters (Seeley 1994).

Loaded with knowledge and nectar from the food source, the forager returns to the hive. Among the source-parameters, the coordinates of the source are known to be directly communicated by the dancer to a few follower bees through the waggle dance. Profitability of the source is known to be indirectly communicated by modulation of the dance duration (von Frisch 1967, Seeley 1994); the dance duration increases linearly with the profitability of the source. The followers do not compare the dances, neither does each forager directly compare the alternative nectar sources, nor does each food-storer bee that unloads the nectar from the forager acquire enough information of the profitability of the various sources to transmit any knowledge to the foragers (Seeley & Towne 1992). The lack of direct communication of the profitability leaves the individual foragers poorly informed. Yet, an intelligent colony emerges out of a collection of these poorly informed individuals and the colony of bees selectively exploits the most profitable among the food sources (Butler 1945, Weaver 1979, Visscher & Seeley 1982, Seeley 1986, Seeley et al. 1991).

The SCS model shows that the colony achieves this selection through the process of self-organization. The selection of the source by an unemployed forager is mediated by a probabilistic event on the following floor. A chance encounter of a follower with a dancer sends her off to the source whose coordinates she has just read. The probability of these chance encounters with dancers whose source is the most profitable is the largest, because this dancer happens to spend more time advertising for her source (Seeley 1994). This recruitment to the most profitable source is a runaway process, because the encounter probability increases as the number of dancers advertising for the most profitable source increase, and whose dancers have increased because the number of followers recruited to the source have increased through the larger dance duration. Thereby, the colony collectively achieves the process of selection of the most profitable source, which the poorly informed individual is incapable to perform.

The profitability is not the sole criterion of source selection. The Bartholdi et al (1993) experiment shows that the hive distributes its foragers among two nectar sources with different profitabilities. They theoretically show that the criterion is a quantity, they call, the ‘equal value’. They claim that the colony converges to the ‘equal value’ for each source available in the field, and their theoretical proofs demonstrate that there is no other allocation that is more than twice as effective than the allocation that emerges from an equal value among all sources. In effect, the hive selects all sources in the field and distributes a non-zero number of foragers between them.

The conflicting results in the Seeley et al. (1991) and Bartholdi et al. (1993), converge in the modified SCS model, which successfully explains both experiments. The colony selects a subset of the available sources based on a quantity, which we have called the 'value' of the source, and not solely through the profitability. Apart from the difference in the functional dependence on the input parameters, our source value differs from the Bartholdi et al. 'equal value', in a significant way: the colony does not converge onto the 'value', but each individual forager independently determines the value of her source which remains time-independent. Hence, the colony does not select all sources but a subset of sources that have the maximum values which are equal. The forager distribution among these maximum equal valued sources is very effective as shown by the elegant theoretical proof in Bartholdi et al. (1993).

The modified SCS model unifies the SCS model with the Bartholdi et al (1993) model and describe the source selection and forager distribution by the colony. The modification through the 'no-accumulation hypothesis' reduces the $3m+1$ coupled differential equations in the SCS model to m. This drastic simplification leads to analytic solutions of the modified SCS model and thus further reveals the mechanism that drives the collective decision making process. The modified SCS model shows that profitability is not the principle criterion by which the bees select the sources but a quantity called the 'value' of the source. The value of a source (equation 15) is a function of 4 input-parameters (f_x, f_d, τ, p_d), which in turn must depend solely on the source and context-parameters, including the profitability. A forager determines the value of the source through an internal gauge and indirectly communicates the profitability through the dance duration τ. Not τ alone, but, the total time she spends on the dance floor T_d, and the probability through which she abandons her source f_x, or dances for it f_d, crucially affect the selection process. As a result, nectar sources with different profitabilities can be selected as in the Bartholdi et al. (1993) experiment, because the the value gauge of the bees yields an equal value to the two sources.

Once the forager determines the input-parameters she has individually estimated the value of her source, whose knowledge is in her sole possession. Through her decision whether to dance or abandon the source, through the duration she would want to spend on the dance floor, and through the fraction of that time she would dance, she contributes to the collective decision making so that her colony deploys the right number of foragers to survive and maintain its prosperity. The value gauge carried by each bee, is in essence, a master gauge with sub-units. The sub-units are the abandonment probability gauge, the dancing probability gauge, dance duration gauge and the dance floor time gauge. The dance duration gauge is known to be a linear function of source profitability (Seeley 1994). Future experiments would tell us how the other sub-units depend on the source and context parameters. Knowing this functional dependence of the rest of the sub-units is to know the exact 'simple behavioral rules' followed by each individual that shapes the self-organization process. This would tell us why the colony distributes all foragers among a subset of sources chosen by their maximum equal value. The knowledge of all the gauges would allow us to predict the evolution of the distribution of foragers among the flower patches for a given hive, through the modified SCS model.

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