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The Pattern and Effectiveness of Forager Allocation Among Flower Patches by Honey Bee Colonies

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To gather its food efficiently, a colony of honey bees must allocate its foragers among flower patches in accordance with their profitabilities. Previous empirical studies have revealed the mechanisms of the allocation process, but tell us neither the allocation pattern that results nor its effectiveness. To investigate these topics, we develop a system of differential equations that models the allocation process in a hypothetical colony of bees whose behavior closely approximates the observed behavior of real bees. We find that our hypothetical colony tends toward a specific allocation of foragers among flower patches, one in which each forager experiences the same rate of "value" accumulation regardless of which patch she is visiting (the equal value rate allocation). Moreover, we show that no allocation brings value to the hypothetical colony's hive more than twice as quickly as the equal value rate allocation. To test the accuracy of our model and its predictions about the allocation patterns of honey bee colonies, we use the model to generate predictions about the patterns of dancing and other variables for different flower patches that should be observed in real colonies. The results of one empirical test confirm the model's prediction that at equilibrium the foragers from different patches will experience equal rates of value accumulation.

1. Introduction

As flower patches bloom and wither, a honey bee colony adjusts the allocation of its foragers to focus on the more profitable sources of food. (See Darwin, 1877; Butler, 1945; Weaver, 1979; Visscher & Seeley, 1982.) A recent study (Seeley *et al.*, 1991) has demonstrated that this food-source selection is essentially a process of natural selection as foragers from more profitable sources "survive" (i.e. continue visiting their sources) longer and "reproduce" (i.e. recruit other foragers) more effectively. One important aspect of this colony-level allocation process that remains unclear is the pattern of forager allocation that results.

In this paper we consider a hypothetical colony whose foragers follow the simple rules of honey bee foraging behavior identified in various empirical studies (for examples see, Boch, 1956; Núñez, 1966, 1970, 1982; Waddington, 1982, 1985; Seeley *et al.*, 1991). We find that our hypothetical colony tends toward a specific allocation of foragers among flower patches. We call this allocation the equal value rate allocation and we show that it leads to effective collection of food. In particular, we

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show that no allocation can be more than twice as effective as the equal value rate allocation.

2. Honey Bee Foraging

A typical colony consists of approximately 20 000 workers, one queen and a few drones. The workers collect water, pollen and nectar. They also clean, repair and protect the hive and regulate its temperature. Finally, workers tend to the queen and the young. The tasks a worker performs are in part a function of her age: early in life she works in the hive, later in life she forages (for a review of honey bee biology, see Winston, 1987).

A forager collecting nectar tends to specialize. Not only does she return to the same patch of flowers again and again, but she also consistently visits flowers of the same species within the patch. Thus, each forager masters the special skills required to collect nectar from her particular patch and species of flower.

After collecting nectar, the forager returns to the hive. There she seeks out a food storer bee who takes the load from her and carries it to workers in the colony or stores it in the honey combs. The size of a forager's nectar load is a positive function of the profitability of her food source and is influenced by such food source variables as distance from the hive, sugar concentration of the nectar, and abundance of nectar at the flowers.

Before returning to her patch, the worker may perform waggle dances to recruit foragers to her flower patch. Workers close enough to follow her dance can learn the location and scent of the flowers at her patch.

Most workers locate a forage patch by following waggle dances, but some foragers, called scouts, do not. Instead, they search independently for good sources. Scouts serve the function of providing the colony with information about new forage patches.

2. A Model of Interference

Since each forager tends to specialize, returning to the same patch again and again, we can at any time imagine each forager to be uniquely associated with a particular patch. Let $\mathscr{F}$ denote the set of flower patches and for each patch $x \in \mathscr{F}$ let n_x be the number of bees specialized to x. An allocation then is a non-negative vector $\boldsymbol{n} = (n_x : x \in \mathscr{F})$, describing the number of foragers allocated to each patch. (Table 1 summarizes the definitions of this and other variables used in the model.)

We let r_x denote the rate at which foragers return from patch x as a function of the number allocated to it. These functions will be likely to differ at different patches. For example, r_x will depend on how long it takes a forager to fly from the hive to patch x and back. It might also depend on the distance between individual flowers at the patch, the types of flowers in the patch, and so forth.

If bees forage independently at patch x, neither interfering with nor assisting each other, then the rate at which bees return from the patch is proportional to the number n_x of foragers allocated to the patch. Generally, however, foragers interfere with each

TABLE 1

Definitions of variables used in the model

Variables	Definition (units)
n_x	Number of bees foraging at patch x (bees)
N	Total number of active foragers (bees)
r_x	Rate at which foragers return from patch x (bees/hr)
f_x	Per capita rate of diversion from patch x (diversions/hr/bee)
g_x	Average duration of a dance for patch x (dance circuits/return to hive)
T_x	Round-trip time to patch x; "trip time" (hr)

other at a patch or at the hive, or both. For example, the greater the number of foragers working a patch, the greater the chance that a forager lands on a flower recently harvested by one of her nestmates. Thus we assume that $r_x(n_x)/n_x$, the average number of trips a forager makes per unit time, is a non-increasing function of n_x, the number of foragers allocated to the patch. This will be the case unless foragers can facilitate one another's food collecting at the patch, which is unlikely.

Although foragers do interfere with each other, we assume that this interference does not reduce the total rate of foraging at the patch. That is, we assume that the foraging rate r_x is a non-decreasing function of n_x, the number of foragers allocated to the patch. This will normally be the case unless the number of foragers at the patch becomes so great that congestion hinders foraging.

3. A Hypothetical Colony

To understand the allocation of foragers precisely, we introduce a hypothetical colony of bees whose behavior we carefully define to approximate the observed behavior of real bees.

We assume that a forager returning from a patch either goes back to the same patch, or else is diverted from the foraging process. For example, a forager might be diverted to rest, or eat, or defend the hive, or she may simply abandon the patch. We assume that each forager is diverted from patch x at the same average rate f_x. The value of f_x can depend on n_x but this dependence must be in terms of some quantity (such as the energetic efficiency of nectar collection) that individual foragers can assess. For simplicity of notation, we write f_x rather than the more cumbersome $f_x(n_x)$.

A diverted worker stops foraging for a while and then re-enters the foraging process as a potential new recruit. We assume that workers are diverted and re-enter the process at the same average rate so that the average number of active foragers remains constant.

We assume that any worker re-entering the foraging process is recruited to patch x with probability equal to the fraction of all dancing that is currently for patch x (see Seeley & Towne, 1992). If all dances are the same length then the probability that she goes to a given patch is simply the fraction of all dances that are for that patch. If the average duration of each dance for patch x is g_x, then the probability that a recruit goes to patch x is proportional to $g_x r_x(n_x)$, the total *amount of dancing* for the patch in a fixed period of time, rather than the total *number of dances* for the patch. Again, g_x can be a function of n_x, but the dependence of g_x on n_x must be in terms of quantities individual foragers can assess.

Finally, scouts in our hypothetical colony behave exactly as other foragers except they do not wait to be recruited but instead search independently for a new forage patch. We assume that a scout has a positive probability of going to each patch in $\mathscr{F}$ each time she searches.

4. The Equal Time Allocation

To understand the allocation that results from the behavior patterns just described, we develop a system of differential equations that models the allocation process in our hypothetical colony. The differential equations only approximate our hypothetical colony. First, they model foraging activity as a continuous process and so ignore the fact that bees are indivisible. Second, they are deterministic: For a given set of flower patches there is a unique allocation of bees to which this process will converge. The allocation process in our hypothetical hive, on the other hand, is stochastic: It will not remain fixed at any single allocation for an extended period of time, but instead will hover about a steady-state allocation. Nevertheless, the system of differential equations is animated by the same dynamics that drive the allocation process in our hypothetical colony and so understanding one provides insight into the other.

As a first step in developing a model of the allocation process in our hypothetical colony, we consider a simpler colony in which all dances are the same duration, say 1 unit of time, and each forager is diverted at the same average rate $\bar{f}$. We later extend the system to describe our more realistic hypothetical colony.

When all dances are the same duration, an allocation n leads to dancing for patch x at the rate $r_x(n_x)$ and so to dancing for all patches at a combined rate of

$$R(n) = \sum_{x \in \mathscr{F}} r_x(n_x). \tag{1}$$

Thus, of all workers re-entering the foraging process during a sufficiently long period of time, the fraction

$$\frac{r_x(n_x)}{R(n)}$$

are recruited to patch x on average.

We assume that after a sufficiently long period of time, the number of active foragers is fairly constant, hovering about the value N. So, for each allocation n,

$$N = \sum_{x \in \mathscr{F}} n_x. \tag{2}$$

To achieve this, workers must re-enter the foraging process at the same average rate they are diverted from it. Thus, foragers re-enter the foraging process at the rate $\bar{f}N$

and new foragers are recruited to patch x at the rate:

$$\bar{f}N\frac{r_x(n_x)}{R(n)}. \tag{3}$$

Since each bee is diverted at the rate $\bar{f}$, the rate at which foragers are diverted from patch x is:

$$\bar{f}n_x. \tag{4}$$

Combining (3) and (4) gives the following system of differential equations describing how the allocation changes with time:

$$\dot{n}_x=\bar{f}N\frac{r_x(n_x)}{R(n)}-\bar{f}n_x. \tag{5}$$

This system reaches a steady-state allocation† in which the rates of recruitment and diversion balance out exactly, so the number of bees allocated to each patch remains constant and

$$\frac{n_x}{r_x(n_x)}=\frac{N}{R(n)} \tag{6}$$

for each active patch x.

The ratio $n_x/r_x(\bar{n}_x)$, referred to as the average trip-time T_x, is the average time it takes a forager to fly from the hive to patch x, collect nectar, return to the hive and unload. So, in steady state when all dances are the same duration, the average trip-time T_x of each active patch x must be equal to the average trip-time $\bar{T}=N/R(n)$ of the allocation.

Although the differential eqn (5) only approximates the allocation process in the simplified version of our hypothetical colony, both are animated by similar dynamics. If the average trip-time at patch x gets too large, the average forage rate r_x/n_x at that patch drops. As this rate drops, so too does the average amount of dancing each forager at the patch does before she is diverted. This means that each forager from the patch recruits new foragers to take her place at a slower-than-average rate. Thus, the number of new recruits directed to the patch is smaller than the number diverted from it and the number of foragers allocated to the patch declines. As the number of foragers declines so does the average trip-time. Similarly, if the average trip-time from a patch is too small, the larger-than-average amount of dancing for that patch will increase the number of new recruits and with it the average trip-time.

Although the two models are similar, the differences between the deterministic differential equations and the stochastic allocation process are significant. These differences illustrate the importance of scouts. For example, in our hypothetical colony there is a positive probability that all foragers visiting any given patch will be diverted. If this happened and there were no scouts, the patch would be irretrievably

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† See Appendix for a proof.

"forgotten". If our hypothetical colony had no scouts it would ultimately forget all but a single patch. Thus, the scouts in our hypothetical colony not only introduce new forage patches, they also help ensure that current patches are not forgotten.

Although we cannot describe analytically the allocation patterns of our hypothetical colony, the fact that the differential eqn (5) converges indicates that our colony will similarly tend toward a steady-state allocation. In order to better understand this allocation, we consider the colony after a long period of time. Scouts will no longer be identifying new forage locations but will only be rediscovering forgotten patches. In this situation, we argue that the colony will tend toward the steady-state allocation with the property that when any patch not in this allocation is introduced, it is soon forgotten and when any forgotten patch in the allocation is rediscovered, its allocation is soon restored. In other words, scouts will occasionally introduce (poor) patches outside the allocation, but these patches will soon be forgotten and so introducing them will not lastingly change the allocation. On the other hand, the colony will occasionally forget (rich) patches in the allocation, but when scouts re-introduce them they will again become active. In terms of the differential eqn (5) this means that the colony will tend toward a steady-state allocation n active on a set $\mathscr{F}'$ of patches with x in $\mathscr{F}'$ if, and only if, for small $\varepsilon > 0$

$$\dot{n}_x|_\varepsilon = \bar{f} r_x(\varepsilon)\left[\frac{N}{R(n)} - \frac{\varepsilon}{r_x(\varepsilon)}\right] \geq 0; \tag{7}$$

that is, if and only if the average trip-time $\varepsilon/r_x(\varepsilon)$ at patch x with only ε foragers is less than the average trip-time $\bar{T}$ of the allocation. In summary, our simplified colony in which all dances are the same duration and all foragers are diverted at the same average rate, converges to the allocation with

$$T_x = \bar{T}$$

for each patch $x \in \mathscr{F}$ such that $\dot{n}_x|_\varepsilon \geq 0$ and $n_x = 0$ otherwise. Thus, each bee should experience the same average round trip time regardless of what patch she is visiting. We refer to this as the *equal-time allocation.*

5. The Equal Value Rate Allocation

To extend this analysis to our more realistic hypothetical colony in which the average duration of a dance (measured in units of dance circuits per return to the hive) for patch x is given by g_x and the average rate at which a forager is diverted from patch x is given by f_x, observe that an allocation n leads to dancing for patch x at the rate

$$g_x r_x(n_x)$$

and to dancing for all patches at a combined rate of

$$GR(n) = \sum_{x \in \mathscr{F}} g_x r_x(n_x).$$

Thus, of all workers re-entering the foraging process, the fraction

$$\frac{g_x r_x(n_x)}{GR(n)}$$

are recruited to patch x on average.

Since workers are diverted from patch x at rate $f_x n_x$, to ensure that the number of active foragers remains fairly constant, workers must re-enter the foraging process at the average rate

$$\bar{f}N = \sum_{x \in \mathscr{F}} f_x n_x .$$

Thus, the system of differential equations

$$\dot{n}_x = \bar{f}N \frac{g_x r_x(n_x)}{GR(n)} - f_x n_x \quad \text{for each } x \in \mathscr{F}$$

describes the allocation process in our hypothetical colony.

In steady state the average rates of recruitment and diversion must balance and so,

$$\frac{n_x}{r_x(n_x)} = g_x \frac{\bar{f}}{f_x} \frac{N}{GR(n)}$$

for each active patch x. Thus, in steady state the average trip-time of each active patch x must be proportional to $v_x = g_x(\bar{f}/f_x)$, i.e.

$$T_x = v_x \frac{N}{GR(n)}$$

for each active patch and patch x is active if and only if, for small $\varepsilon > 0$,

$$\dot{n}_x|_\varepsilon = f_x r_x(\varepsilon)\left[v_x \frac{N}{GR(n)} - \frac{\varepsilon}{r_x(\varepsilon)} \right] \geq 0.$$

The term v_x is a measure of the value of patch x since as patch quality increases, g_x will rise and $\bar{f}$ and f_x will fall. In summary, our hypothetical colony converges to the allocation with

$$\frac{v_x}{T_x} = \frac{GR(n)}{N}$$

whereby each bee will accumulate value at the same rate regardless of which patch she is visiting. We refer to this as the *equal value rate* allocation.

6. Effectiveness

In this section we explore the effectiveness of the predicted allocation patterns. We begin by considering the simplified hypothetical colony in which all dances are the same average duration and each forager is diverted at the same average rate. In section 4 we argued that this simple colony tends toward the equal-time allocation. In this section we show that this allocation is quite effective under a wide range of conditions. To begin, we show that no allocation can bring nectar to the hive more than twice as quickly as the equal-time allocation.

THEOREM 1

Let n be any allocation and let n^* be the equal-time allocation. If at each patch x, r_x is non-decreasing and r_x/n_x is non-increasing, then

$$\frac{R(n)}{R(n^*)}\leq 2.$$

Proof

Consider any allocation n. Let $\mathscr{F}_{\leq}$ be the set of patches x for which $n_x \leq n_x^*$ and let $\mathscr{F}_{>}$ be the set of patches x for which $n_x > n_x^*$. Then

$$\sum_{x\in\mathscr{F}_{\leq}} r_x(n_x) \leq \sum_{x\in\mathscr{F}_{\leq}} r_x(n_x^*) \leq R(n^*) \tag{8}$$

since r_x is non-decreasing. Further let $\bar{T}=N/R(n^*)$ be the common average trip-time for the active patches under the equal-time allocation. Since r_x/n_x is non-increasing and $n_x^*=0$ only if $\varepsilon/r_x(\varepsilon)>\bar{T}$ for small $\varepsilon>0$,

$$\frac{r_x(n_x)}{n_x}\leq\frac{1}{\bar{T}}$$

for each $x\in\mathscr{F}_{>}$. Thus,

$$\sum_{x\in\mathscr{F}_{>}} r_x(n_x) \leq \frac{1}{\bar{T}} \sum_{x\in\mathscr{F}_{>}} n_x \leq \frac{N}{\bar{T}} = R(n^*) \tag{9}$$

and, summing (8) and (9) gives the result

$$R(n)=\sum_{x\in\mathscr{F}} r_x(n_x) \leq 2R(n^*). \qquad \square$$

Theorem 1 implies that even with complete information about the return rates r_x, perfect and instantaneous communication and unlimited computational power, it is impossible to find an allocation more than twice as effective as the equal-time allocation. In fact, when naïvely applied, traditional methods of optimization do not provide a similar performance guarantee. For example, even points satisfying the

Kuhn-Tucker necessary conditions for optimality may lead to an arbitrarily bad allocation (see, for example, Hillier & Lieberman, 1990)[†].

The equal-time allocation is generally much better than this bound indicates. Theorem 1 states that as long as the return rates satisfy the two assumptions, it is impossible to contrive a situation in which the equal-time allocation performs less than half as well as possible. In other words, the allocation patterns of our simplified hypothetical colony are effective for an extremely wide range of circumstances[‡].

In our more realistic hypothetical colony the amount of dancing for a patch per return to the hive reflects aspects of the patch other than simply the length of time required to collect a load of nectar. For example, von Frisch (1967) demonstrated that the duration of a dance is influenced by the energy content of the nectar. In a colony capable of distinguishing among food sources in this way, the simple rate at which nectar is collected is no longer an appropriate "currency" or measure of effectiveness. However, if g_x, the average duration of a dance for patch x, is proportional to the energetic profit of the nectar from patch x but each forager is diverted at the same average rate $\bar{f}$, an appropriate current is $GR(n)$, the rate at which the colony collects energy. In this case, the average trip-time to an active patch under the equal value rate allocation is proportional to the energetic profit of the nectar at the patch, i.e. $T_x = g_x N/GR(n)$. Corollary 1 shows that under these circumstances, no allocation brings energy to the hive more than twice as quickly as the equal value rate allocation.

COROLLARY 1

Let n be any allocation and let n^* be the equal value rate allocation. If at each patch x, $f_x = \bar{f}$, $g_x r_x$ is non-decreasing and $g_x r_x / n_x$ is non-increasing, then

$$\frac{GR(n)}{GR(n^*)} \leq 2.$$

Finally, in our most realistic hypothetical colony, where the average duration of dancing for patch x is g_x and the average rate at which each forager is diverted from

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[†] A standard technique for solving constrained optimization problems is to identify points satisfying the Kuhn-Tucker conditions. In some cases these conditions can be shown to be both necessary and sufficient for optimality. In this case, however, the conditions are only necessary for optimality, i.e. any optimal solution must satisfy the Kuhn-Tucker conditions. Therefore, it is not surprising that Kuhn-Tucker points may lead to sub-optimal allocations.

The contrast between the performance guarantees of these two methods is enlightening. Under fairly restrictive conditions, Kuhn-Tucker points are guaranteed to be optimal. When these conditions do not apply, Kuhn-Tucker points may lead to arbitrarily bad allocations. The allocation mechanism of the bees, on the other hand, will only rarely lead to an optimal allocation, but will—under a very wide range of circumstances—guarantee a relatively good allocation.

[‡] On first inspection, the performance guarantee "half as well as possible" may not seem remarkable. However, in comparison with other similar performance guarantees, it is rather good. For example, the best known heuristic for the symmetric traveling salesman problem invokes some of the most powerful techniques of discrete mathematics and still only guarantees a tour no more than 1·50 times as long as the optimum. Simpler heuristics are still rather involved and can only guarantee a tour that is at most twice as long as the optimum.

patch x is f_x, the choice of currency is more difficult. In fact, several currencies have been proposed (such as net energetic efficiency, net rate of energy intake, etc) and the question of which is most appropriate remains without a conclusive answer.

We suggest that the notion of a simple currency (such as net energetic efficiency) for foraging is perhaps inappropriate, at least at the colony level. Natural selection among honey bee colonies probably does not favor simply efficiency *or* rate of energy collection. Rather, it is more likely that colonies that are able to balance various foraging considerations, such as energetic efficiency *and* rate of energy intake, will have an evolutionary advantage, because ideally a colony will gather as much food as possible as efficiently as possible. Thus, in evaluating the effectiveness of honey bee allocation patterns the appropriate currency may be rather complex. Corollary 2 shows that the equal value rate allocation is effective with respect to the currency:

$$VR(n) = \sum_{x \in \mathcal{F}} v_x r_x(n_x),$$

which we call the "rate of value accumulation".

COROLLARY 2

Let n be any allocation and let n^* be the equal value rate allocation. If at each patch x, $v_x r_x$ is non-decreasing and $v_x r_x / n_x$ is non-increasing, then

$$\frac{VR(n)}{VR(n^*)} \le 2.$$

Depending on the specific relationship between v_x and the flower patch, Corollary 2 leads to different conclusions about honey bee foraging behavior. One appealing interpretation is that v_x is proportional to the energy efficiency of foraging at patch x. In this case $VR(n)$ is a measure of foraging success (accumulation of value) which combines considerations of both efficiency and rate of foraging. For example, if a colony's foragers are efficient, but have a low rate of foraging trips, or if they have a high rate of foraging trips but forage inefficiently, the colony's rate of value accumulation will be low. Achieving a high rate of value accumulation requires that the colony's foragers be allocated among patches in a way that produces fairly high levels of both foraging efficiency and rate of foraging trips. Corollary 2 states that no allocation is more than twice as effective in maximizing the colony's rate of value accumulation as the equal value rate allocation. This does not prove that rate of value accumulation is the appropriate currency in studying honey bee foraging, rather it shows *how* honey bee foraging behavior can lead to foraging success at the colony level.

7. Testing the Model

Let us now focus our attention on the model for our most realistic hypothetical colony, which yields the prediction that at equilibrium there will be an equal value rate allocation. We can view the equal value rate allocation from the perspective of dancing. Since $GR(n)$ is the total amount of dancing in a unit of time and N is the number of foragers, $\bar{D}=GR(n)/N$ is the average amount of dancing each bee does per unit time.

Further, since $1/\bar{f}$ is the average length of time a forager spends before being diverted, $\bar{D}/\bar{f}$ is the average amount of dancing a forager does before being diverted. Equation (6) then says that for each active patch x,

$$\frac{g_x}{f_x}\frac{r_x(n_x)}{n_x}=\frac{\bar{D}}{\bar{f}}.$$

But

$$\frac{D_x}{f_x}=\frac{g_x}{f_x}\frac{r_x(n_x)}{n_x}$$

is the average amount of dancing each forager allocated to patch x does before being diverted. Indeed, if too few foragers are allocated to patch x, then each bee at x will do more dancing than average, thus recruiting more foragers. So, if this analysis is correct, in steady state the average amount of dancing per bee before abandoning a patch will be the same for each active patch. This remains to be checked empirically.

Further, viewing (7) from this perspective gives

$$\dot{n}_x|_\varepsilon=f_x\varepsilon\frac{\bar{f}N}{GR(n)}\left[\frac{g_x}{f_x}\frac{r_x(\varepsilon)}{\varepsilon}-\frac{\bar{D}}{\bar{f}}\right]\geq 0; \tag{10}$$

from which we see that patch x is predicted to be active if and only if a single forager allocated to it recruits more effectively on average than her nestmates from other patches. This prediction, like the previous one, can be checked using standard techniques of training bees from an observation hive to experimental feeders (as in von Frisch, 1967) and observing the patterns of dancing in the hive (as in Seeley *et al.*, 1991).

One can also test the model by checking the prediction that at equilibrium bees from different food sources will have equal rates of value accumulation. This test would involve setting up two food sources which differ in distance from the hive or concentration of the sugar solution (or both), letting the colony's exploitation of the two feeders come to equilibrium, and then measuring, for each feeder's foragers, the average amount of dancing per return to the hive (g_x), the average drop out rate (f_x), and the average trip-time (T_x) for foragers from each feeder. If the model is correct, then the following prediction will hold:

$$\frac{g_1}{f_1T_1}=\frac{g_2}{f_2T_2}.$$

We have performed one test of this prediction. On July 4, 1991, we presented a honey bee colony with two sucrose solution feeders which were identical in distance from the hive (350 m, one north and one south of the hive) but differed in the concentration of the sugar solution (2·00 and 2·50 mol l^{-1}, respectively). The two feeders were the only sources of food available to the colony. The bees were housed in an observation hive, so we could record the number of dance circuits for each feeder, and all of the bees were labeled for individual identification, so we could monitor individual foragers and detect diversions from each feeder [see Seeley *et al.* (1991) for details of the study site, materials and methods]. At 09:00 the feeders were loaded with their sugar solutions, and by 11:00 the colony had reached an equilibrium distribution of foragers between the two feeders. This equilibrium was maintained for the next 4 hr: north feeder 20·9 ± 0·8 bees, south feeder 39·0 ± 2·2 bees ($X \pm$ S.D.). During the 4 hr equilibrium period we measured;

(1) the average trip-time of foragers by measuring the trip-times of 20 randomly chosen foraging trips to each feeder,

(2) the total number of dance circuits performed for each feeder by steadily monitoring the dancing in the hive, and

(3) the number of diversions from each feeder by performing roll calls every half hour of the bees visiting each feeder. A bee was judged to have abandoned a feeder if she was not recorded on two consecutive roll calls for the feeder.

The results of these measurements, together with the calculations of g_x, f_x and g_x/f_xT_x, are summarized in Table 2. Our measurements reveal a close match between the model's prediction and reality. Although the two feeders differed markedly in initial profitability, such that the richer feeder ended up with nearly twice as many foragers and received more than three times as many dance circuits as the poorer one, at equilibrium the two feeders differed only slightly (by a factor of 1·20) in their values of g_x/f_xT_x. Indeed, if there had been just one more diversion from the south feeder (seven instead of six), then the two feeders would have had equivalent values of g_x/f_xT_x.

TABLE 2

Test of the model's prediction that at equilibrium a colony's foragers are all allocated among food sources such that the rate of value accumulation is the same for all food sources

Variable	North	South
Sugar concentration (mol l^{-1})	2·00	2·50
Number of foragers, n_x (bees)	20·9	39·0
Average trip time, T_x (hr)	0·165	0·140
Total trips to feeder in 4 hr, $n_x(4/T_x)$	507	1114
Total dance circuits in 4 hr	37	130
Dance duration, g_x (dance circuits/trip)	0·073	0·117
Number of diversions in 4 hr (bees)	2	6
Per capita diversion rate, f_x (diversions/bee/hr)	0·024	0·038
g_x/f_xT_x	18·4	22·0

A colony was presented with two feeders that differed in profitability, the system was allowed to come to equilibrium, and the variables needed to test the predictions were measured during a 4 hr equilibrium period.

8. Conclusions

The foundation for this investigation was a reasonably complete picture of the behavioral mechanisms whereby a colony of honey bees allocates its foragers among flower patches, selectively exploiting those with greater food rewards. We knew that this is in essence a process of natural selection with foragers from rich food sources surviving (continuing to visit) longer and reproducing (recruiting nestmates) better (see Seeley *et al.*, 1991; Camazine & Sneyd, 1991). However, our knowledge of the allocation pattern that results was extremely limited. Because a colony's foragers fly far (up to 10 km) from the hive, it is impossible to determine a colony's allocation pattern under natural conditions through direct measurements, and no attempt had been made to determine the allocation patterns indirectly using a mathematical model. Furthermore, our understanding of the effectiveness of a colony's allocation patterns in enabling it to gather its food successfully was virtually nil. The present study was undertaken to help fill these gaps.

Before reviewing the specific findings of the paper, we wish to emphasize two important aspects of the general approach we have taken.

First, our mathematical model is not at all an hypothesis about how the allocation process works, rather it is a quantitative description of the allocation process as revealed by various empirical studies (for example, Seeley *et al.*, 1991). Hence, our model does not analyze the mechanism of the allocation process; instead it examines the logical implications of this process. In particular, it sheds light on the distribution pattern of foragers among flower patches and on the effects of this pattern on the colony's foraging success.

Second, this mathematical analysis does not rely on any assumption about what currency the bees are trying to maximize in their foraging, either at the individual or at the colony level. Instead, it starts simply with the known behavior patterns of bees and derives a system of differential equations describing the dynamics in the number of bees at each patch. This in turn reveals a measure of patch quality, value v_x, whose total rate of accumulation is evidently maximized (or nearly so) by the bees. The important point is that this measure of foraging success is a product, not a premise, of this study.

With respect to the allocation patterns of a colony's foragers, we predict that given enough time the forgers will become distributed according to the equal value rate allocation. Under this distribution, the average per capita rate at which value is accumulated from a flower patch becomes the same for each active patch. For example, if a patch starts out with two few foragers, its value will be disproportionately high (i.e. its foragers will have a higher than average dancing rate and a lower than average abandonment rate). This will result in an increase in the number of foragers working the patch. Conversely, if a patch has too many foragers, it will lose foragers due to a disproportionately low value (i.e., its foragers will have a lower than average dancing rate and a higher than average abandonment rate). Such gains and losses in the number of foragers will eventually bring the per capita rate of value intake from each active patch to the shared, equilibrium level, as was observed in our empirical test of the model.

It is worth noting that the equal value rate allocation of the foragers among flower patches should be identical to the ideal free distribution (see Fretwell & Lucas, 1970; Fretwell, 1972), assuming that foragers assess patch profitability in terms of rate of value accumulation, since both distributions will result in all individuals experiencing equal rates of value accumulation. This is interesting because the behaviorial mechanisms for producing these two distributions are extremely different. Whereas the equal value rate allocation arises out of the actions of bees acting only on *local* knowledge of the available flower patches (i.e. each bee knows about the profitability of just one patch and adjusts her foraging behavior accordingly), the ideal free distribution would arise if each forager possessed *global* knowledge of the available flower patches and could freely and independently choose among the patches, selecting the one where she could achieve the highest rate of value accumulation. Hence it appears that the honey bee's social organization enables a colony to produce, with bees possessing extremely limited information, a labor distribution among flower patches that is as good as would be produced if the bees were omniscient about the patches.

Does this equal value rate allocation, with its resultant equalization in the rates of value accumulation for all active patches, result in efficient exploitation of food sources by a honey bee colony? Evidently it does. Corollary 2 indicates that even with complete information, perfect and instantaneous communication and unlimited computational power, the colony could at best double its total rate of value accumulation. The value of a patch [as defined in this study: $v_x = g_x(\bar{f}/f_x)$] is a positive function of its profitability, which for nectar sources seems to be measured in terms of the maximum energetic efficiency that a bee can achieve in working the patch (net joules gained per joule expended; Schmid-Hempel *et al.*, 1985; Seeley, 1986; Wolf & Schmid-Hempel, 1990). Hence Corollary 2 implies that whereas each bee behaves in a manner consistent with maximizing the *efficiency* of energy accumulation, the colony allocates foragers among patches in a manner that tends to keep it near the maximum possible *rate* of (efficient) energy accumulation. In other words, it appears from this analysis that a honey bee colony strikes a balance between intake efficiency and intake rate by having each bee forage efficiently as an individual, and deploying these efficient individuals among the patches of flowers in a manner that tends to maximize the colony's total rate of food collection. Natural selection has presumably favored colonies that can gather their food efficiently yet sufficiently during the brief summer season to enable them to survive the forthcoming winter, grow rapidly in the spring, and so reproduce vigorously the following summer. All told, this requires a colony to extract some 20 kg of pollen and 60 kg of honey each year from the flowers in the surrounding countryside (see Seeley, 1985). The analysis reported here strongly suggests that the honey bee's social organization for allocating foragers among flower patches is highly effective in helping a colony meet this large need for food.

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APPENDIX

Theorem 2

Suppose that for each patch $x \in \mathcal{F}$

$$h_x(n) = \frac{v_x r_x(n)}{n}$$

is a continuous, strictly decreasing function of such that[†]

$$\lim_{n\to 0} h_x(n) = \infty$$

and

$$\lim_{n\to\infty} h_x(n) = 0.$$

Then, regardless of the initial allocation, the system defined by (5) *converges to the equal value rate allocation.*

Proof

For $\bar{r} > 0$, define $n_x(\bar{r})$ to be the unique solution to

$$h_x(n) = \bar{r}.$$

Note that this system has a unique solution since h_x is strictly decreasing,

$$\lim_{n\to 0} h_x(n) = \infty \quad \text{and} \quad \lim_{n\to\infty} h_x(n) = 0.$$

Note too, that if $\bar{r}_1 < \bar{r}_2$, then $n_x(\bar{r}_2) < n_x(\bar{r}_1)$. Thus,

$$N(\bar{r}) = \sum_{y\in\mathscr{F}} n_y(\bar{r})$$

is a strictly decreasing function of $\bar{r}$ and there is a unique solution r^* such that

$$N(r^*) = \sum_{y\in\mathscr{F}} n_y(r^*) = N.$$

The allocation $n(r^*)$ is the equal value rate allocation[‡].

Define the potential function $V(n)$ to be:

$$\sum_{y\in\mathscr{F}} \max\{0, n_y - n_y(r^*)\}.$$

Note that V attains its minimum at $n = n(r^*)$. Further, although V is not everywhere differentiable, its right derivative with respect to the system (5) is given by

$$\dot{V}_+(n) = \sum_{y\in\mathscr{F}^+(n)} \dot{n}_y$$

where $\mathscr{F}^+(n)$ is defined to be the set of $y\in\mathscr{F}$ such that either

(1) $n_y > n_y(r^*)$ or

(2) $n_y = n_y(r^*)$ and $\dot{n}_y > 0$.

[†] The first condition is meant to reflect the role of scouts. Even when no foragers are allocated, scouts visit the patch. If $g_x r_x$ is continuous and strictly positive at zero, then $h_x \to \infty$ as $n \to 0$. The second condition is merely a matter of convenience. To ensure this we might simply fix $v_x r_x(n) = v_x r_x(N)$ for all $n > N$.

[‡] So, if bees had computers and knew the profitabilities and return rates at each patch, they could compute the equal value rate allocation by performing binary search over values of $\bar{r}$.

We show that $\dot{V}_+(n) < 0$ for $n \neq n(r^*)$ and hence v is decreasing over time. Consider an allocation n. For each $x \in F^+(n)$, $n_x \geq n_x(r^*)$ and so $h_x(n_x) \leq r^*$. Further, since $n \neq n(r^*)$, we have that $n_x > n_x(r^*)$ and $h_x(n_x) < r^*$ for some $x \in F^+(n)$. Thus, from the definition of h_x, we have that

$$\sum_{y\in\mathscr{F}^+(n)} g_y r_y(n_y) < r^* \sum_{y\in\mathscr{F}^+(n)} f_y n_y. \tag{A.1}$$

Likewise, for each $x \notin \mathscr{F}^+(n)$, $n_x \leq n_x(r^*)$ and so $h_x(n_x) \geq r^*$. It follows that

$$\sum_{y\notin\mathscr{F}^+(n)} g_y r_y(n_y) \geq r^* \sum_{y\notin\mathscr{F}^+(n)} f_y n_y. \tag{A.2}$$

Combining (A.1) and (A.2), we have that

$$\left(\frac{\sum_{y\notin\mathscr{F}^+(n)} f_y n_y}{\sum_{y\in\mathscr{F}^+(n)} f_y n_y}\right) \sum_{y\in\mathscr{F}^+(n)} g_y r_y(n_y) < \sum_{y\notin\mathscr{F}^+(n)} g_y r_y(n_y)$$

and so,

$$\frac{\bar{f}N}{\sum_{y\in\mathscr{F}^+(n)} f_y n_y} \sum_{y\in\mathscr{F}^+(n)} g_y r_y(n_y) < \sum_{y\in\mathscr{F}} g_y r_y$$

from which we conclude that

$$\dot{V}_+(n) = \sum_{y\in\mathscr{F}^+(n)} \dot{n}_y = \sum_{x\in\mathscr{F}^+(n)} \left[\frac{\bar{f}N g_x r_x(n_x)}{\sum_{y\in\mathscr{F}} g_y r_y(n_y)} - f_x n_x\right] < 0.$$

Next, we note that along any path $C = \{n(t)\colon t \geq 0\}$ of (5),

$$V(n(t)) - V(n(0)) = \int_0^t \dot{V}_+(n(\tau))\,\mathrm{d}\tau. \tag{A.3}$$

This follows from the fact that

$$\begin{aligned}\int_0^t \dot{V}_+(n(\tau))\,\mathrm{d}\tau &= \sum_{y\in\mathscr{F}} \int_{\{\tau:\, y\in\mathscr{F}^+(n(\tau))\}} \dot{n}_y\,\mathrm{d}\tau \\ &= \sum_{y\in\mathscr{F}} \left[\max\{0, n_y(t) - n_y(r^*)\} - \max\{0, n_y(0) - n_y(r^*)\}\right] \\ &= V(n(t)) - V(n(0)).\end{aligned}$$

We will use these facts to show that the process (5) converges to $n(r^*)$ regardless of the initial allocation.

Consider a path $C = \{n(t)\colon t \geq 0\}$ of (5). Since V is non-negative and strictly decreasing along the path C,

$$\lim_{t\to\infty} V(n(t))$$

exists and is some non-negative number m.

We prove that $m=0$ as follows. Suppose, on the contrary, that $m>0$. Since V is continuous and $V(n(r^*))=0$, there is $\varepsilon>0$ such that for each allocation n in a ball B of radius ε about $n(r^*)$, $V(n)<m$. Consider the compact set R of all allocations not in the relative interior of B. Since $\dot{V}_+$ is continuous and negative on the compact set R, it attains a maximum, $-k<0$ on R.

Since $V(n(t))$ is a strictly decreasing function of t along the path C and

$$\lim_{t\to\infty} V(n(t))=m,$$

along C, $C\subseteq R$.

Thus, $V_+\leq -k<0$ for all $t\geq 0$ and

$$\begin{aligned} V(n(t))-V(n(0)) &= \int_0^t \dot{V}_+(n(\tau))\,\mathrm{d}\tau \\ &\leq -\int_0^t k\,\mathrm{d}\tau \\ &= -kt. \end{aligned}$$

It follows then that

$$V(n(t))\leq V(n(0))-kt$$

for all $t\geq 0$, from which we conclude that

$$\lim_{t\to\infty} V(n(t))=-\infty,$$

contradicting the fact that V is non-negative. Thus, we may conclude that

$$\lim_{t\to\infty} V(n(t))=0,$$

and hence that

$$\lim_{t\to\infty} n(t)=n(r^*).$$

As this is true on any path C, we have that (5) converges to $n(r^*)$ regardless of the initial allocation.