

Collective decision-making in honey bees: how colonies choose among nectar sources

Thomas D. Seeley¹, Scott Camazine¹, and James Sneyd^{2*}

¹ Section of Neurobiology and Behavior, Mudd Hall, Cornell University, Ithaca, NY 14853, USA

² Centre for Mathematical Biology, Mathematical Institute, 24–29 St. Giles', Oxford OX1 3LB, UK

Received April 3, 1990 / Accepted September 30, 1990

Summary. A honey bee colony can skillfully choose among nectar sources. It will selectively exploit the most profitable source in an array and will rapidly shift its foraging efforts following changes in the array. How does this colony-level ability emerge from the behavior of individual bees? The answer lies in understanding how bees modulate their colony's rates of recruitment and abandonment for nectar sources in accordance with the profitability of each source. A forager modulates its behavior in relation to nectar source profitability: as profitability increases, the tempo of foraging increases, the intensity of dancing increases, and the probability of abandoning the source decreases. How does a forager assess the profitability of its nectar source? Bees accomplish this without making comparisons among nectar sources. Neither do the foragers compare different nectar sources to determine the relative profitability of any one source, nor do the food storers compare different nectar loads and indicate the relative profitability of each load to the foragers. Instead, each forager knows only about its particular nectar source and independently calculates the absolute profitability of its source. Even though each of a colony's foragers operates with extremely limited information about the colony's food sources, together they will generate a coherent colony-level response to different food sources in which better ones are heavily exploited and poorer ones are abandoned. This is shown by a computer simulation of nectar-source selection by a colony in which foragers behave as described above. Nectar-source selection by honey bee colonies is a process of natural selection among alternative nectar sources as foragers from more profitable sources "survive" (continue visiting their source) longer and "reproduce" (recruit other foragers) better than do foragers from less profitable sources. Hence this colonial decision-making is based on decentralized control. We

suggest that honey bee colonies possess decentralized decision-making because it combines effectiveness with simplicity of communication and computation within a colony.

Introduction

Recently, numerous authors have noted that colonies of advanced social insects constitute higher-order cognitive entities, that is, supraorganismal systems capable of evaluating situations and producing adaptive solutions to problems (Hofstadter 1979; Markl 1985; Seeley and Levien 1987; Wilson and Hölldobler 1988; Franks 1989). Examples of this colony-level problem-solving include a swarm of honey bees selecting the best nest site from a dozen or more possibilities (Lindauer 1955; Seeley 1982), a colony of honeypot ants assessing the strength of a neighboring colony and deciding accordingly whether or not to attack (Hölldobler 1981; Lumsden and Hölldobler 1983), and a colony of army ants choosing a bearing for each day's swarm raid so as to avoid the previous day's foraging zone (Franks and Fletcher 1983; Deneubourg et al. 1989). All such ensemble cognitive performances present us with the puzzle of how the problem-solving abilities of a colony arise from the actions and interactions of the insects composing the colony.

We address this mystery in the context of honey bee colonies choosing among patches of flowers, selectively exploiting the most profitable ones. The ecology of this decision-making can be summarized as follows (reviewed in Seeley 1985). Each year a colony of bees consumes considerable food, approximately 20 kg of pollen and 60 kg of honey. The thousands of foragers in a colony laboriously gather this food from the flower patches dotting the countryside around the colony's hive. Typically a colony will know each day about a dozen or more potential food sources, each with its own level of profit-

* *Present address:* Department of Biomathematics, UCLA School of Medicine, 10833 La Conte Avenue, Los Angeles, CA 90024, USA

Offprint requests to: T.D. Seeley

ability, determined by such variables as the distance from the hive and the abundance and quality of the food. To gather its food efficiently, a colony must deploy its foragers among the flower patches in accordance with their profitabilities.

We begin by documenting the skill with which a colony chooses among nectar sources so that most of its nectar comes always from the richest sources. Then we show how this selective exploitation arises through precise modulation of the rates of recruitment and abandonment for different nectar sources in relation to their profitabilities. This points out the crucial question: how are the rates of these two processes adaptively regulated? After describing the multidimensional modulation of foraging behavior in relation to nectar source profitability, we experimentally analyze how each forager assesses nectar source profitability. The two principal competing hypotheses are that each forager judges by itself the profitability of its nectar source, or that each forager is given this information by the food storer bees in the hive. Next we check our understanding of how the joint actions of a colony's foragers result in producing colony-level decision-making by formulating a mathematical model of this process and comparing the decision-making patterns of simulated and real colonies. We end by discussing the general implications of our investigation.

Methods

1. Colony-level analysis: selective exploitation of nectar sources

A colony composed of individually identifiable bees was presented with two nectar sources with different profitabilities. The colony's differential exploitation of the two sources was measured by determining the total number of different individuals visiting each food source. Also, the different rates of recruitment and abandonment for the two feeders, which ultimately generated the exploitation difference between the two food sources, were determined from records of each bee's visits to the feeders.

Study site. All observations were made at the Cranberry Lake Biological Station (44°09' N, 74°48' W) in northern New York State. This site is surrounded by forests, bogs, and lakes for more than 20 km in all directions, hence forage for bees is extremely sparse and no native honey bees survive there. A full-size colony, kept on platform scales, lost weight (0.50 ± 0.30 kg) on 15 days and gained weight (0.15 kg) on just 1 day during the 16-day study period in June 1989. The scarcity of food enabled us to control the forage collected by our study colony even though its foragers flew freely from the hive.

Study colony. We assembled a colony of individually identifiable bees over a 2-day period, 1–2 June 1989, in Ithaca, as follows. First, at the beginning of each day, approximately 2500 worker bees from a colony of Italian honey bees (*Apis mellifera ligustica*) were shaken into a wire cage. From this, we periodically shook groups of approximately 50 bees into plastic bags and placed them in a refrigerator to immobilize them. After at least 15 min of cooling, the bees in a bag were removed from the refrigerator and poured onto a container of "blue ice", where they stayed chilled during the labelling operation. A bee tag (Opalithplättchen, with 500 number and color combinations) was glued on the thorax of each bee, and a dot of one of eight different colors of paint was

applied to its abdomen. Finally, the bees were gently poured into a cage containing a sugar water feeder and the mother queen. This procedure was repeated several times a day for 2 days until 4000 bees were labelled.

At the end of the second day, the labelled workers and their queen were transferred to a two-frame observation hive identical to the one described in Seeley (1989). The bottom frame contained a mixture of brood (eggs and larvae), honey, and pollen, and the top frame was empty except for a few cells of pollen. On 4 June the colony was moved to Cranberry Lake and left undisturbed for 4 more days, though bees were trained to the feeders to set up the experimental array and to provide food for the colony. On the evening of 8 June, the colony's population was censused by counting the number of bees inside 10 randomly selected 2.5×2.5 cm grid squares on each side of the observation hive: the colony contained approximately 3450 bees. Rainy weather prevailed for the next 10 days, during which all we could do was provide food at the feeders whenever the bees could fly. This kept the colony fed and ensured that the dozen or so bees trained to each feeder would continue visiting the feeders. By the time the weather cleared (19 June) the colony had grown noticeably; fortunately the foragers were still all labelled bees. A census on the evening of 19 June indicated a population of approximately 4200 bees.

Feeders and experimental layout. The feeders were pneumatic feeding dishes identical to those described in a previous paper (Seeley 1989). The observation hive and the two feeders were placed in an approximately linear arrangement, with the hive in the center and the feeders 400 m to the north and south, in small clearings. Both food sources contained the scent anise in a vented reservoir beneath the feeder and also in the sucrose solution (60 μ l of anise extract per liter).

Measuring forager group size, and recruitment and abandonment rates. We recorded which bees visited each food source during every half-hour period throughout two 8-h sets of observations. We accomplished this using roll call sheets listing the identification codes of all 4000 bees and crossing off the identification codes of all bees seen at a feeder during each half hour. Each sheet therefore showed which individuals visited a particular feeder at least once during a 30-min period, and how many in total did so. This number we call the "forager group size." Comparisons between roll call sheets for a feeder also revealed when (to the nearest 30 min) individuals were first sighted at (i.e., were recently recruited to) the feeder or were last sighted at (i.e., were soon to abandon) the feeder. From these data we calculated the per capita recruitment rate or abandonment rate for each feeder for each half hour by dividing the number of recruits or deserters counted during that half hour by the forager group size for the previous half hour.

2. Individual-level analysis: behavior modulation in relation to nectar source profitability

Two colonies were established in adjacent observation hives and 30 bees from each colony were trained to visit separate feeders at the same distance from the hives. The profitability of one (the experimental) colony's feeder was systematically changed during the day and the behavioral adjustments of its foragers were recorded. Meanwhile, the profitability of the other (the control) colony's feeder was left unchanged and the behaviors of its foragers were recorded as a check for possible confounding changes in the ambient conditions.

Study site, bees, experimental layout, and feeders. This experiment was conducted in July 1987 in connection with other experiments already published (Seeley 1989). It involved the same study site, the same two colonies in observation hives, the same experimental layout, and the same feeders as were described in the prior report.

The only difference between the present experiment and the one reported in Fig. 2 of Seeley 1989 was that, in the present case, the fullness of the experimental colony's honey combs was kept constant and the profitability of its feeder was varied, whereas, before, the fullness of the experimental colony's honey combs was varied and the profitability of its feeder was kept constant.

Measuring recruitment and recording the behaviors of foragers. Recruitment from each colony was measured by training 30 bees to a feeder using standard techniques (von Frisch 1967), labeling these bees (the recruiters) with individually identifiable paint marks, and counting the number of unlabeled bees (the recruits) appearing at the feeder every 15 min. Each recruit was captured in a plastic bag (to minimize release of alarm pheromone) shortly after its arrival at the feeder, and was frozen at the end of the day.

Roll calls of the labeled bees at 30-min intervals indicated the number of recruiters at each feeder; this number dropped below 30 for the experimental colony when the profitability of its feeder was lowered and some bees abandoned it. The probability of visiting the feeder was calculated by dividing the number of labeled bees visiting the feeder by 30, that is, the number of labeled bees that visited the feeder when all did so.

Measurements were also made of several variables of the in-hive behavior of the labelled bees from the experimental colony. This involved following one (randomly selected) labelled bee at a time from when it entered the hive to when it exited it. One variable was the "time to start of unloading," which is the time interval between entering the hive and beginning to transfer nectar to a food storer bee. The "time to end of unloading" is the time interval between entering the hive and completing the transfer of nectar to food storers. The "time in hive after unloading" is the time interval between finishing unloading nectar and leaving the hive. Another variable was "dance circuits per bee per return to the hive," which was measured by counting the dance circuits each bee performed during its time inside the hive. The "probability of dancing" was calculated by dividing the number of bees that danced by the total number of bees that were followed (i.e., sample size). Finally, the "foraging tempo," measured in units of trips to the feeder per bee per 30 min, was calculated by first dividing the number of labelled bees visiting the feeder by the number of labelled bees entering the hive per min (measured with ten 1-min counts of labelled bees coming in the entrance). This quotient indicates the average time per roundtrip to the feeder. Next, 30 min was divided by the roundtrip time to determine the number of trips to the feeder that each bee was making in 30 min.

Statistical test. A single classification ANOVA (Sokal and Rohlf 1981) was performed for each variable for which there was an estimate of the mean and variance, i.e., all variables except for the probability of visiting the feeder, the probability of dancing, and foraging tempo.

3. Individual-level analysis: assessing nectar source profitability

Two feeders were established, one with a relatively dilute sugar solution but located near the hive, and the other with a more concentrated sugar solution but positioned far from the hive. Bees were trained to forage from each feeder, and their behaviors inside the hive, especially the strength of their recruitment dances, were monitored to determine which feeder was judged more profitable. The answer reveals whether it is the food storers or the foragers that assess nectar source profitability.

Study site, bees, experimental layout, and feeders. This experiment was performed in Ithaca, New York, using a small colony of Italian honey bees in a two-frame observation hive housed inside a laboratory building. The hive and feeders were identical to those described

in a previous study (Seeley 1989). Both feeders were positioned along a rarely used road (one 50 m and the other 1250 m from the hive) that traverses flat, treeless agricultural fields; hence, both feeders had virtually identical exposure to wind and sun. Fifteen bees were trained to each feeder using standard techniques (von Frisch 1967). Each bee was labeled with paint marks coding individual identity and which feeder she was visiting. Recruits to each feeder were captured in plastic bags to prevent forager build-up at the feeders.

Recording the behaviors of foragers. Labelled foragers were followed one at a time inside the observation hive from time of arrival to departure. Measurements were made, as previously described, of the time to start of unloading, the dance circuits per bee per return to the hive, and the probability of dancing.

Statistical tests. We used *t*-tests, either Student's or the test for equality of two proportions using arcsine transformations (Sokal and Rohlf 1981).

Results

1. Colony-level analysis

Pattern: selective exploitation of nectar sources. Figure 1 shows that when a colony was given a series of choices between two feeders with different profitabilities, it consistently focused its collection efforts on the more profitable feeder. The net result was that the colony steadily tracked the richest source of nectar in the changing array. Note that the measure of foraging effort shown in Fig. 1 – the total number of different individuals visiting the feeder in a half hour – underestimates the colony's response differential to the two feeders. This is because the poorer feeder (0.75 mol/l), relative to the richer feeder (2.50 mol/l), was not only visited by fewer bees, but also was visited at a lower rate by each bee (see data on foraging tempo in Table 1).

Process: tuning the rates of recruitment and abandonment. Because the size of a group is determined by the history of additions to and subtractions from the group, it was clear a priori that the changes in forager group size shown in Fig. 1 reflect changes in the rates of recruitment (additions) and abandonment (subtractions) for each feeder. The complete picture of the recruitment and abandonment dynamics for the two feeders is shown in Fig. 2. On the morning of 19 June, there was essentially no recruitment to or abandonment of the north feeder (1.00 mol/l), and the forager group size here rose only to 12 bees, namely the ones that had foraged here the previous day. At the south feeder (2.50 mol/l), however, there was strong recruitment, especially early in the morning when the feeder was still lightly exploited, and little abandonment, so the forager group size increased dramatically, rising from 0 to 91 bees in 4 hours. Then in the afternoon, the south feeder (now 0.75 mol/l) received negligible recruitment but intense abandonment, so that its forager group size fell back to just 10 bees by the end of the afternoon. Meanwhile, the north feeder (now 2.50 mol/l) had become the target of strong recruitment but little abandonment, with the net result that

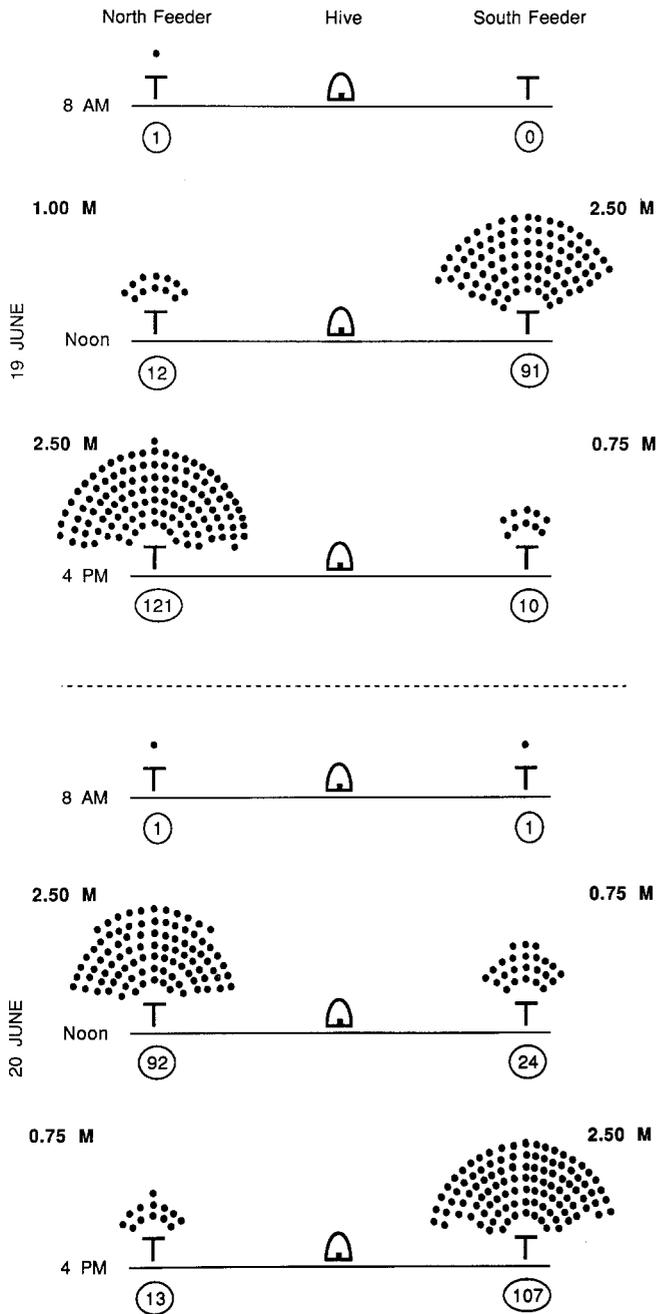


Fig. 1. The basic decision-making phenomenon. When given a choice between two food sources with different profitabilities, the colony consistently directed most of its foraging effort onto the richer one. The number of dots above each feeder denotes the forager group size for that feeder, i.e., the number of different bees that visited the feeder in the half hour preceding the time shown on the left. For several days prior to the start of observations, a small group of bees was trained to each feeder (12 and 15 bees for the north and south feeders, respectively), thus on the morning of 19 June, the two feeders had essentially equivalent histories of low-level exploitation. The feeders were located 400 m from the hive and were identical except for the concentration of the sugar solution

the forager group size here rose from 12 to 121 bees. Similar patterns of reciprocal recruitment and abandonment, in accordance with food source profitability, were recorded on the second day as well. One difference between the data for 19 and 20 June, however, was an

unexpectedly large forager group size – as many as 32 bees – for the poorer (south, 0.75 mol/l) feeder on the morning of 20 June. This morning surge in foragers to the poorer feeder arose because bees that had foraged here the previous morning came out to reconnoitre the site of their prior success, not because bees were recruiting nestmates to the 0.75 mol/l solution at this feeder. Virtually all of the bees (46 out of 48) that visited the south feeder on the morning of 20 June had foraged there the previous morning. Also many (18 out of 48) of these bees ceased visiting the feeder within an hour of their first visit, so that the bees were actually *abandoning* this feeder at a rather high rate from 9:30 a.m. to 12 noon (see Fig. 2).

These results indicate that colonies are highly skilled at adjusting the rates of recruitment and abandonment for each nectar source in relation to its profitability, and that it is the precise modulation of these rates which generates a colony's selective exploitation of superior nectar sources. This raises the next question: what do individual bees do to produce this adaptive tuning of their colony's rates of recruitment and abandonment?

2. Individual-level analysis

Pattern: behavior modulation in relation to nectar source profitability. The data presented in Table 1 illustrate the ability of bees to finely adjust several components of their foraging behavior in accordance with nectar source quality. On the one hand, when the quality was high (as when the feeder was loaded with the 2.0 mol/l sucrose solution), the bees continued visiting the food source, worked quickly, and danced vigorously, thereby bringing additional nestmates to help exploit their rich find. On the other hand, when the nectar source quality was low (0.5 mol/l solution, or less), the bees tended to abandon the source or, if they did continue foraging there, they behaved relatively slowly and did not perform recruitment dances. This set of responses resulted in a drop in the number of bees at the feeder. Setting the feeder at intermediate levels of quality elicited behavioral responses of intermediate strength, with correspondingly intermediate rates of recruitment to or abandonment of the feeder. Note that simultaneous measurements of recruitment rate for a control colony showed no significant changes, which implies that the ambient conditions were stable during the observations and, therefore, that the behavioral changes documented in Table 1 were solely in response to changes in food source profitability.

Process: assessing nectar source profitability. How does a forager assess the profitability of its nectar source? Three hypotheses come to mind. First, each forager might acquire this information by making direct comparisons of nectar sources. This would require that a forager visit several nectar sources to judge the relative value of the source from which it is foraging. Second, each forager might rely instead upon indirect comparisons made by the food storer bees inside the hive. Each

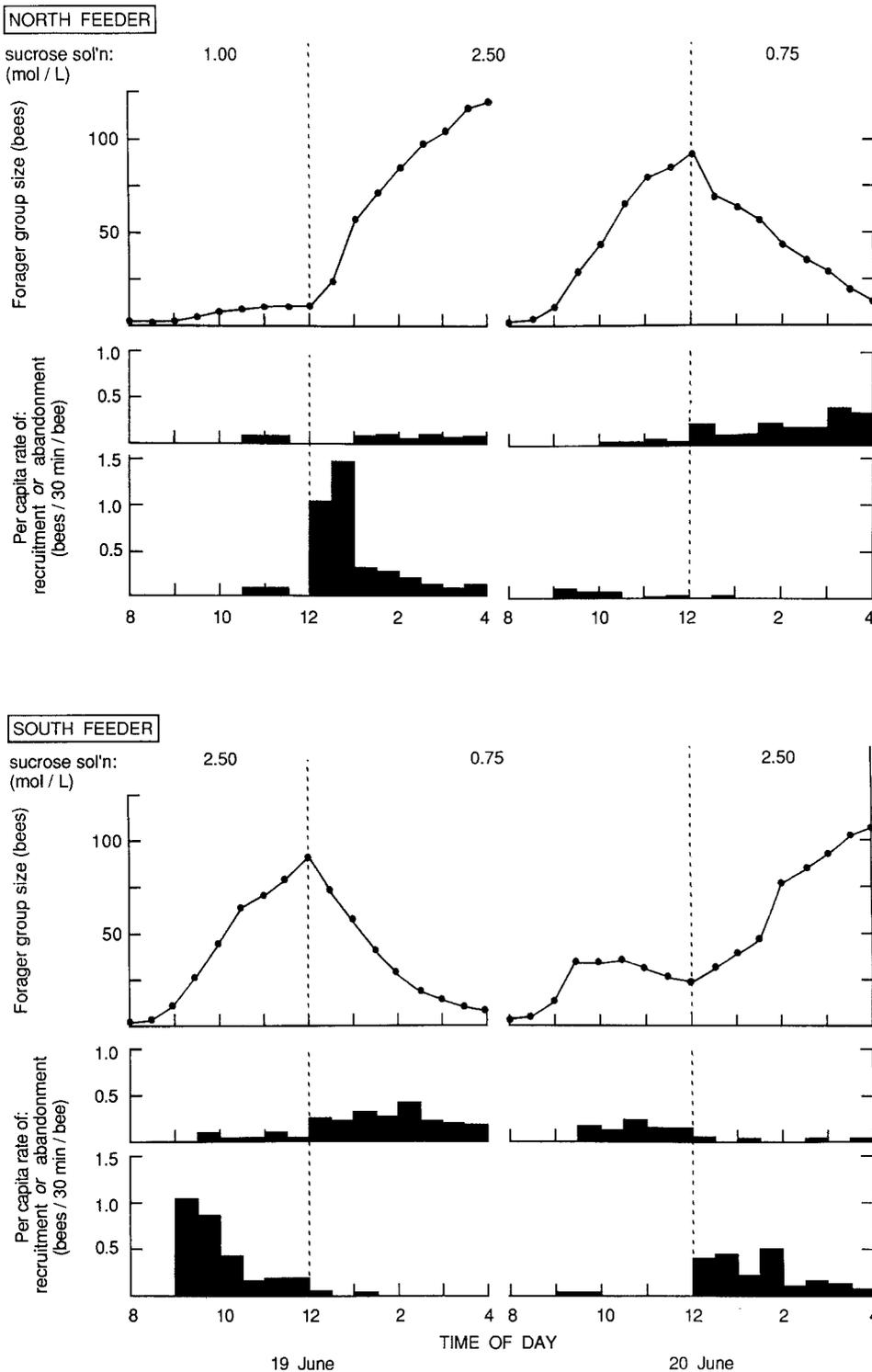


Fig. 2. The colony's responses to the two nectar sources in detail. Values of forager group size denote the number of different individuals that visited each feeder during the previous half hour. Per capita rates of recruitment or abandonment represent the number of recruits or deserters recorded for a 30-min interval divided by the forager group size for the start of the interval. At the start of the observations, 12 and 15 bees had experience at the north and south feeders, respectively, and so provided an initial link between the colony and each feeder. These bees returned to their respective feeders on the morning of 19 June, but were not counted as recruits. Likewise, any bee that had visited a feeder during the afternoon of 19 June was not counted as a recruit if it appeared at the same feeder on the morning of 20 June, hence the increase in forager group size at the two feeders without strong recruitment on the morning of 20 June. This figure illustrates the precise regulation of a colony's recruitment and abandonment rates in relation to nectar source profitability, with the result that the colony's foraging efforts tracked the richer nectar source

food storer bee unloads foragers from various nectar sources, and it has been suggested (Boch 1956; Lindauer 1961, 1975) that food storers compare the nectar loads they receive and preferentially unload foragers bearing the most profitable nectar. A forager's ease in getting unloaded would, according to this hypothesis, inform it of the relative quality of its nectar source. A third possibility is that no comparisons are made, neither by foragers nor by food storers; instead, each forager knows only about its particular nectar source, and its

nervous system can calculate the absolute quality of its source. This hypothesis is closely analogous to Lindauer's (1955) idea that a scout bee, without previous experience in house-hunting, can assess the quality of a nest site through reference to an "*angeborenes Schema eines Nistplatzes*." [Note that in the case of foraging, food source quality is not the sole factor influencing a bee's behavior. Other factors, such as the colony's need for food and the seasonal availability of forage, determine the levels of food source quality that are the

Table 1. Information on the protocol, ambient conditions, and results of the experiment documenting the modulation of foraging behavior in relation to nectar source profitability

| Time period (hours) | 0915–1045 | 1100–1230 | 1245–1415 | 1430–1600 | Significance |
|-------------------------------------|------------|-----------|-----------|-----------|--------------|
| <i>Experimental colony</i> | | | | | |
| Sucrose solution (mol/l) | 2.00 | 1.50 | 1.00 | 0.50 | |
| Probability of visiting feeder | 1.00 | 1.00 | 1.00 | 0.60 | |
| Foraging tempo (trips/bee/30 min) | 6.1 | 6.2 | 6.0 | 3.9 | |
| Probability of dancing | 0.80 | 0.59 | 0.26 | 0.00 | |
| Dance circuits/bee/return to hive | 9.8 ± 15.4 | 5.4 ± 4.9 | 1.6 ± 3.9 | 0.0 | <0.001 |
| Recruitment to feeder (bees/15 min) | 10.3 ± 5.4 | 5.6 ± 4.0 | 2.2 ± 1.6 | 0.0 | <0.001 |
| Time to start of unloading (s) | 13 ± 7 | 12 ± 6 | 14 ± 7 | 28 ± 30 | <0.01 |
| Time to end of unloading (s) | 68 ± 39 | 50 ± 16 | 46 ± 11 | 64 ± 24 | <0.05 |
| Time in hive after unloading (s) | 23 ± 18 | 20 ± 20 | 22 ± 15 | 51 ± 32 | <0.01 |
| Sample size (bees followed) | 25 | 30 | 34 | 25 | |
| <i>Control colony</i> | | | | | |
| Sucrose solution (mol/l) | 1.50 | 1.50 | 1.50 | 1.50 | |
| Recruitment to feeder (bees/15 min) | 8.0 ± 1.5 | 7.5 ± 3.6 | 7.7 ± 3.6 | 7.3 ± 1.9 | >0.75 |
| <i>Ambient conditions</i> | | | | | |
| Temperature (°C) | 25.0–28.0 | 28.0–29.0 | 27.5–28.5 | 27.5–28.0 | |

thresholds for such behaviors as returning to and dancing for a food source (Lindauer 1948; Seeley 1986, 1989). Hence a given level of nectar source quality will elicit different behavioral responses under different conditions.]

Which of these three possible mechanisms operates in the bee hive? The first proposed mechanism (H1: direct comparisons hypothesis) is rendered highly improbable by the following observations from the beginning of the experiment depicted in Figs. 1 and 2. On the morning of 19 June, the bees from the south feeder recruited strongly to their feeder with its 2.50 mol/l sucrose solution while the bees from the north feeder scarcely recruited at all to their feeder with its 1.00 mol/l solution. Clearly, the foragers working these two feeders had correctly assessed the profitability of each food source. But did the assessment process depend upon bees making direct comparisons of these two food sources? Evidently not. The records of which individuals visited which feeder reveal that of the 117 bees total that visited the two feeders during the morning of 19 June, only two of them visited *both* feeders. These two bees both switched from the poorer feeder (north) to the richer feeder (south) late in the morning (see Fig. 2). Hence only a tiny minority of the foragers had knowledge of both feeders; the vast majority must have arrived at an assessment of the profitability of these feeders without making direct comparisons between them. (It should be noted that the two feeders were essentially the only two nectar sources available to the bees in the study colony. One indication of this is that on 19 June the scale hive colony lost 0.50 kg, which is virtually the same weight loss recorded for the previous 3 days (0.45, 0.55, 0.60 kg) when the weather was cold and rainy and the bees could not even fly from the hive.)

To distinguish between the second hypothesis (H2: indirect comparisons mediated by food storer bees) and

third hypothesis (H3: no comparisons), we compared the responses of foragers to two feeders that were arranged so that the two hypotheses gave opposite predictions about which feeder the bees would judge more profitable. To understand the design of this experimental layout, we must focus on a critical feature of H2, namely its implication that a nectar source's profitability is evaluated simply as a function of the sugar concentration of its nectar. This follows from the basic premise of H2 that it is the food storer bees that make the evaluations, coupled with the reasonable assumption that the only variable affecting a nectar source's profitability that food storer bees might know about is the sugar concentration of its nectar. We feel that this assumption is valid because whereas it is clear that food storer bees can easily acquire information about the sugar concentration of a source's nectar, simply by tasting the nectar as they receive it from a forager, there is no evidence that food storer bees acquire information about the other variables influencing the energetic profitability of a nectar source – including distance from hive to source, abundance of nectar at the source, difficulty of feeding at the source, direction in relation to the wind, and wind speed. For example, although a food storer bee could conceivably acquire information about the distance between the hive and a forager's nectar source (by following dances performed by the forager), it is clear that this happens rarely, if at all. Food storer bees almost never attempt to follow dances performed by foragers they have unloaded (e.g., see Fig. 6 in Seeley 1989). Moreover, a forager rarely even provides the food storer that has unloaded it with any dances to follow; 58 different foragers gathering nectar and pollen from natural flower patches were observed making a total of 153 returns to the hive with forage, and in only 11 (7%) of these returns were dances performed (data from bees followed in the study Seeley and Visscher (1988)). Likewise, there are no signs that

| Variable | 50 m | | 1250 m | |
|---|------------------------|------------------------|--------|--------------------------|
| | 0.75 mol/L | 1.00 | or | 2.50 mol/L |
| Time to start of unloading (s) | 11 ± 4 ^a | 37 ± 26 ^b | | 12 ± 4 ^a |
| Probability of dancing | 0.50 ^a | 0.10 ^b | | 0.73 ^a |
| Dance circuits per bee per return to hive | 4.5 ± 6.3 ^a | 0.6 ± 0.3 ^b | | 14.6 ± 19.6 ^c |
| Sample size (bees followed) | 22 | 20 | | 22 |

Fig. 3. Experimental design and results of the test for how foragers assess the profitability of a nectar source. Fifteen bees were trained to forage at each of the two feeders, and their responses to these feeders were observed. The bees from the 50-m, 0.75-mol/l feeder unloaded their nectar more quickly and danced more strongly than did those from the 1250-m, 1.00-mol/l feeder. This implies that assessments of nectar source profitability are made by the forager bees, which have knowledge of the many variables affecting the energetic profitability of a nectar source, rather than by the food storer bees, which know only one variable, the sugar concentration of the nectar

food storer bees acquire information about the other variables influencing the energetic profitability of a nectar source – such as nectar abundance, direction in relation to the wind, and wind speed – since food storers remain inside the hive where they have no direct access to information about these variables, and they have no known means of gaining information about these variables indirectly from the foragers.

In contrast to H2, H3 predicts that a nectar source's profitability is assessed as a function of many variables. This is because this hypothesis assumes that the foragers are making the assessments, and foragers of course have direct access to information about the multiple variables affecting the energetic profitability of a nectar source.

The experimental layout shown in Fig. 3 is such that H2 and H3 give opposite predictions about the relative profitabilities (as judged by the bees) of the two feeders, and hence about the bees' relative responses to these feeders. Consider what each hypothesis predicts about the bees' responses to the 50-m, 0.75-mol/l feeder relative to those for the 1250-m, 1.00-mol/l feeder. H2 predicts that the bees foraging from the 50-m, 0.75-mol/l feeder will assess its profitability as relatively low because its sugar concentration is relatively low, and thus predicts that these bees will dance relatively little. H3, however, predicts that the bees visiting the 50-m, 0.75-mol/l feeder will assess its profitability as relatively high because its much shorter distance from the hive will more than compensate for its lower sugar concentration, and therefore predicts that these bees should dance relatively strongly. Which prediction is correct? As we see in Fig. 3, the bees from the 50-m, 0.75-mol/l feeder danced much more

strongly than did the bees from the 1250-m, 1.00-mol/l feeder. These results strongly contradict H2.

This rejection of H2 is reinforced by the average times to start unloading for the different forager groups. First, note that the bees from the 1250-m, 1.00-mol/l feeder took more time to begin unloading than did the bees from the 50-m, 0.75-mol/l feeder. This runs contrary to H2, which assumes that food storer bees preferentially unload foragers bringing in more concentrated nectar. Second, note that foragers from the 50-m, 0.75-mol/l feeder and the 1250-m feeder, when reloaded with a 2.50-mol/l solution, began unloading equally quickly, despite the huge difference in concentration between their sugar solutions. This too contradicts the basic assumption of H2. However, both of these patterns in unloading times are consistent with H3. The first pattern evidently is the result of the foragers from the 1250-m, 1.00-mol/l feeder concluding that their feeder's profitability was low and slowing their foraging tempo (see Table 1), in part by not seeking to unload their nectar immediately upon entering the hive. The second pattern apparently reflects the bees from both the 50-m, 0.75-mol/l feeder and the 1250-m, 2.50-mol/l feeder judging that their feeder was high in profitability and deciding to forage with high tempo, which included seeking to unload nectar immediately upon entering the hive.

3. Model of collective decision-making

We now formulate a mathematical model of nectar-source selection by honey bee colonies, based on the empirical work just presented. The model enables us to see more clearly the colony-level consequences of the individual-level behavior patterns described above. It therefore provides a test of the idea that the colony-level decision-making can be accounted for simply in terms of an assemblage of bees, in which each bee independently modulates its behavior in accordance with the profitability of its nectar source. We check the validity of the ideas expressed in the model by comparing the pattern of exploitation of two unequal nectar sources that is predicted by this model with the pattern of exploitation that was actually observed.

Biological basis of the model. We will start with a pool of foragers that are not yet committed to one of the nectar sources available outside the hive. Each of these uncommitted bees (hereafter called “follower bees”) locates a nectar source by following the recruitment dances of a nestmate that is already committed to a patch of flowers. Now consider the behavior of one follower bee as it begins its day by following dances (Fig. 4). Within the dance floor region of the hive are bees dancing for two nectar sources (*A* and *B*). Our bee follows a dancer for nectar source *A* and is recruited to this source. Having located source *A*, it gathers a load of nectar and returns to the hive. After unloading its nectar to a food storer bee, the forager proceeds with one of three options, illustrated by the arrows after the two branch points (diamonds). The first is (1) to abandon the nectar

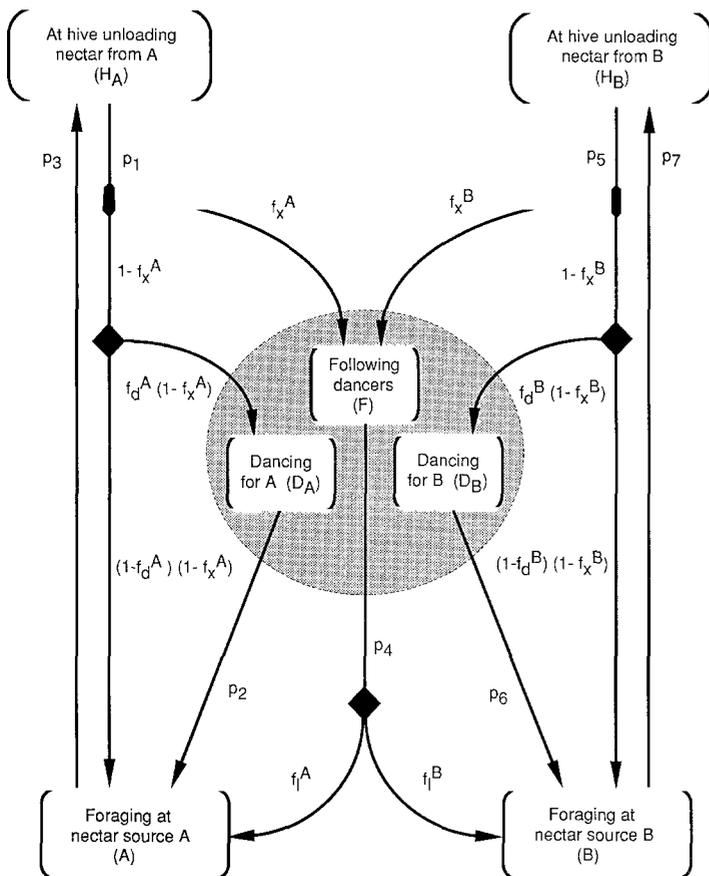


Fig. 4. Graphical representation of the mathematical model of how honey bee colonies choose between two nectar sources (A and B). The model is based on the following empirically determined cycle of foraging behavior. A bee begins foraging by following nestmates performing recruitment dances, then arrives at a food source and gathers a load of nectar, and finally returns to the hive and unloads the nectar. At this point it repeats the cycle, though now with the option of continuing to forage from its current nectar source (and perhaps even dancing for this source), rather than following dances to locate a new source. The black diamonds along the arrows denote decision points. The grey circle represents the dance floor area inside the hive. At any given moment, each forager is in one of the seven compartments shown (H_A , H_B , F , etc. denote both the respective compartments and the number of foragers in these compartments). The model predicts a distribution of the foragers among the seven compartments over time as a function of the rate constant (p_i) associated with each compartment and the probabilities (f_x^A , f_x^B , etc.) associated with each of the five branch points. Empirical studies have revealed the behaviors of individual bees. A computer simulation of this model enables us to see the colony-level implications of these individual-level behavior patterns and thereby test our understanding of the way that these behavior patterns combine to produce a colony's ability to choose among nectar sources

source and return to the pool of follower bees. If, however, she elects to continue with her nectar source, then she has two other options, either (2) to perform recruitment dances before heading back to the flowers, or (3) to return to the flowers directly without attempting to recruit nestmates. Many variables of nectar sources – including nectar sweetness, nectar abundance, nectar accessibility, and distance from the hive (Seeley 1986 and references therein) – influence foragers as they choose

among these options. But in this model, as in the study of behavioral modulation above, we will work with nectar sources that differ only in their sugar concentration. Note too that this model does not consider changes in the response thresholds of the foragers in relation to changes in foraging conditions (Lindauer 1948; Seeley 1986, 1989); hence, it represents the process of nectar-source selection under a fixed set of foraging conditions (weather, forage abundance, colony need, etc.).

Mathematical structure of the model. The essential features of the biology just described can be incorporated in a mathematical model of a colony choosing between two nectar sources as follows. First, we assume that at any moment each forager must be in one of the seven compartments shown in Fig. 4. These compartments are:

1. H_A : unloading nectar from nectar source A
2. H_B : unloading nectar from nectar source B
3. D_A : dancing for nectar source A
4. D_B : dancing for nectar source B
5. A : foraging at nectar source A
6. B : foraging at nectar source B
7. F : following a dancer

More formally, a bee is considered in one of these seven compartments until the moment she enters her next compartment. Thus, for example, the time spent in D_A includes both the time spent dancing for and the time needed to return to nectar source A . Note that the dance floor (shaded area in Fig. 4) holds three compartments, one (D_A) containing bees dancing for source A , one (D_B) containing bees dancing for source B , and one (F) holding bees following a dancer. Note too that Fig. 4 consists of two separate cycles, one for each food source, with the follower compartment (F) the only intersection point for the two cycles. Thus bees from one nectar source can switch over to the other source only by passing through the dance floor and following a dancer for the other nectar source. Figure 4 suggests that the dance floor lies at the heart of the decision-making process. Whatever information transfer occurs among the foragers is assumed to happen here.

Two variables affect the proportion of the total forager force that is in each of the seven compartments: (1) the rate at which individual foragers move from one compartment to another and (2) the probability that a forager takes one or the other fork at the five branch points (diamonds) in Fig. 4). The fraction of bees leaving a compartment in a given time interval is denoted by the appropriate rate constant p_i . For example, the rate constant for bees leaving compartment A is p_3 and the fraction of the bees at nectar source A that leave in a time interval Δt is equal to $p_3 \Delta t$. The values of the rate constants p_i will be calculated from experimental data in the next section.

Now let us consider what determines the probabilities of the different behaviors at each of the five branch points in Fig. 4. The first branch point occurs after a bee has unloaded her nectar in the hive. At this point

Table 2. Parameter values for the model of a colony choosing between two nectar sources, as shown in Fig. 1. *A* and *B* correspond to the 2.50-mol/l and the 0.75-mol/l feeders, respectively. For full definitions of the parameters, see the text and Fig. 4

| Parameter: definition | Value | Reference |
|---|---------|---------------------------------------|
| T_1 : time from start of unloading to start of following, dancing, or foraging, <i>A</i> foragers | 1.0 min | Table 1 ^a |
| T_2 : time from start of dancing to start of foraging, <i>A</i> foragers | 1.5 min | Table 1 |
| T_3 : time from start of foraging to start of unloading, <i>A</i> foragers | 2.5 min | Table 1 |
| T_4 : time from start of following dancers to start of foraging, <i>A</i> and <i>B</i> foragers | 60 min | Seeley and Visscher 1988 ^b |
| T_5 : time from start of unloading to start of following, dancing, or foraging, <i>B</i> foragers | 3.0 min | Table 1 ^a |
| T_6 : time from start of dancing to start of foraging, <i>B</i> foragers | 2.0 min | Table 1 |
| T_7 : time from start of foraging to start of unloading, <i>B</i> foragers | 3.5 min | Table 1 |
| f_x^A : probability of abandoning <i>A</i> , per foraging trip | 0.00 | Table 1 |
| f_x^B : probability of abandoning <i>B</i> , per foraging trip | 0.04 | Table 1 ^c |
| f_d^A : probability of dancing for <i>A</i> | 1.00 | Table 1 |
| f_d^B : probability of dancing for <i>B</i> | 0.15 | Table 1 |

^a Since the probability of dancing upon return from *A* is 1.00, T_1 can be more precisely defined as the time from start of unloading to start of dancing. Conversely, since the probability of dancing upon return from *B* is near zero, T_5 can be defined as essentially the time from start of unloading to start of following or foraging

^b This paper reports that in order to find a rich patch of flowers by following dances, on average a bee spends a total of 121 min outside the hive searching for targets indicated by dances. The total time spent inside and outside the hive will be somewhat greater still. The value given here, 60 min, is less than these estimates because in the Fig. 1 experiment the recruitment targets (feeders) were only 400 m from the hive, whereas in Seeley and Visscher (1988) the recruitment targets (natural flower patches) were on average 1600 m from the hive

^c f_x for the 0.75-mol/l feeder was calculated as follows. Table 1 shows that a bee's probability of continuing to visit (=not abandoning) a 0.75-mol/l feeder after 30 min was approximately 0.80. Because each forager made approximately 5 trips to the feeder in 30 min, this implies that $(1-p)^5 = 0.80$, where p = the probability of abandoning the feeder per trip. Solving this equation yields $p = 0.04$

she may abandon the nectar source and return to the dance floor to follow another dancer. The probability that a bee does so is denoted by the function f_x , which we call the abandoning function. In general, the value of f_x will depend on the profitability of the nectar source; thus, f_x^A denotes the probability that a bee leaving H_A will abandon nectar source *A* and become a follower bee (*F*). Abandonment diminishes the number of bees committed to a nectar source and provides a pool of uncommitted bees that follow dancers for one nectar source or the other.

The second branch point applies to bees that did not abandon their nectar source. It determines what proportion of these bees will dance for their nectar source. Although at this branch point there is no filtering of bees away from nectar sources, the outcome of this branch point affects the probability of a follower bee following dances for each nectar source, as described hereafter. The probability that a bee becomes a dancer for her nectar source is denoted by the function f_d . The function f_d is called the dancing function and, as with the abandoning function, its value for a given bee depends on the profitability of the bee's nectar source, with f_d^A denoting the probability of dancing by a bee foraging at nectar source *A*.

The third branch point arises when bees follow dancers for one or another nectar source. The probability of a follower bee following dances for nectar source *A* or *B* is denoted by the function f_1^A or f_1^B , respectively, which we call the following function. A recent study (Seeley and Towne, in preparation) has shown that follower bees simply follow the first dancer they encounter and that encounters occur at random. Hence, in the situation of just two nectar sources, *A* and *B*, the likelihood

of encountering and following a dancer for nectar source *A* (f_1^A) at any particular moment can be roughly estimated by $D_A/(D_A + D_B)$. However, because D_i includes both bees dancing for *i* and bees that have ceased dancing but are still in the dancing compartment, the ratio $D_A/(D_A + D_B)$ will often be a poor estimate of f_1^A . For example, if nectar source *A* is scarcely danced for but its foragers linger in the hive without dancing, then the ratio $D_A/(D_A + D_B)$ will greatly overestimate the likelihood of encountering a dancer for *A*. It can be much improved by multiplying each D_i in the ratio by the proportion of time that foragers in the dancing compartment *i* are actually dancing, which we will denote as τ_i .

For simplicity in making calculations with the model, we make three further assumptions: (1) the total number of bees foraging is fixed, (2) all bees begin foraging simultaneously, and (3) all the foragers go to either one of two nectar sources. In the appendix we present the set of differential equations that describes this model of colony-level decision-making.

Model parameters. We now calculate estimates of the model's parameters for the situation shown in Fig. 1, namely a colony choosing between two equidistant sucrose solution feeders that are identical, except that one contains a 0.75-mol/l solution and the other contains a 2.50-mol/l solution. Let us first consider the rate constants. These can be calculated from the time required for a bee to get from one compartment to another (i.e., the time spent in the compartment plus the time to get to the next compartment). Each rate constant, p_i , is equal to $1/T_i$, where each T_i is the time required to get from the relevant compartment to next. Values of T_i

appropriate to the foraging situation shown in Fig. 1 are given in Table 2.

The abandoning function (f_x) and the dancing function (f_d) include many variables – such as the profitability of the nectar source, the colony's need for nectar, and the weather conditions – hence it is difficult to give a general description of these functions. However, the values of these functions have been measured (see Table 1) for a set of conditions virtually identical to those under which the Fig. 1 data were recorded: feeders 400 m from the hive, high colony need for nectar, sparse ambient forage, and fair weather. We used the data in Table 1 (with appropriate interpolations and extrapolations) to determine the values of f_x and f_d that are appropriate to simulating the colony's choice between 2.50-mol/l and 0.75-mol/l nectar sources as shown in Fig. 1 (see Table 2).

Values of the following function, f_1 , were calculated for the two nectar sources using the more accurate of the two methods just described. Thus, each D_i was first discounted by the factor τ_i , the proportion of time in D_i that was actually spent in dancing. Each τ_i was calculated by taking the product of the average number of dance circuits and the average circuit time, and dividing it by the total time a bee is in the compartment D_i (T_2 and T_6 for compartments D_A and D_B , respectively). Given that the bees from the 2.50-mol/l and 0.75-mol/l feeders danced on average 14 and 1 circuits, respectively (see Table 1), and each dance circuit for a 400-m target requires approximately 2.4 s (von Frisch 1967), and given values of $T_2=90$ s and $T_6=120$ s (see Table 2), this yields values of $\tau_A=0.38$ and $\tau_B=0.02$, where A and B represent the 2.50- and 0.75-mol/l feeders.

Results of the model. Figure 5 shows the pattern of simulated colonial decision-making obtained by numerical integration of the model's equations with the following starting conditions: A and $B=11$, D_A and $D_B=1$, H_A and $H_B=0$, and $F=101$. These values correspond closely to the starting conditions for the experiment shown in Figs. 1 and 2 in that at 8:00 a.m. on 19 June there were approximately 12 bees committed to each feeder, and during the course of the day a total of approximately 125 different bees visited the two feeders. The pattern generated by the model closely resembles the one generated by the colony of bees; compare Fig. 5 with Fig. 2. As in the case of the experimental data, the plot of the model's results shows consistent increases in the number of foragers on whichever feeder provided a 2.50-mol/l sugar solution, and consistent decreases at the 0.75-mol/l feeder. What is especially important is the comparison between the experimental data and the model's predictions for the afternoon of 19 June. This is because the starting conditions were nearly matched for the field and the model for this time period – 12 and 3 bees committed to the real and simulated north feeder (2.50 mol/l), and 90 and 119 bees committed to the real and simulated south feeder (0.75 mol/l). As the afternoon progressed, both in the field and in the computer, the number of bees foraging from the north feeder in-

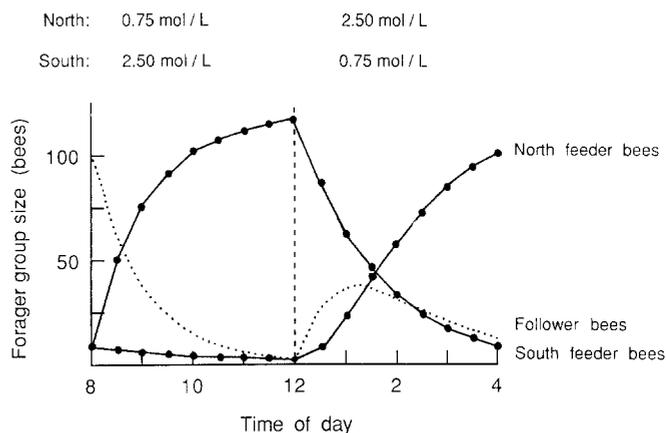


Fig. 5. An example of the nectar-source selection by honey bee colonies predicted by the model shown in Fig. 4. For this simulation the model's parameters were adjusted to correspond to the situation shown in Figs. 1 and 2, namely a colony choosing between two equidistant (400-m) feeders offering either a 0.75 or a 2.50-mol/l sucrose solution ad libitum. The forager group size for each feeder equals the sum of the bees dancing for the feeder (D_A or D_B), the bees at the feeder (A or B), and the bees unloading nectar from the feeder (H_A or H_B). In this simulation, as in reality, the colony always focused the vast majority of its foraging effort on the richer feeder, and was able to respond rapidly to a reversal in the location of the richer feeder. This result supports the model of colony-level decision-making shown in Fig. 4

creased sigmoidally while those foraging from the south feeder decreased exponentially. The maximum rates of increase at the north feeder were 34 and 18 bees/30 min for the experimental and simulation results, respectively, and the corresponding maximum rates of decrease at the south feeder were -19 and -30 bees/30 min. The two sets of results show a less close match in the morning. This is because in the field the north feeder was loaded with a 1.00 rather than a 0.75-mol/l solution, in order to prevent total abandonment of the north feeder, whereas in the simulation the north feeder was loaded with a 0.75-mol/l solution, in order to keep the simulation simple. Also, in the field the bees did not begin foraging simultaneously, whereas in the simulation they all began at 8:00 a.m. sharp.

Discussion

How does the ability of a honey bee colony to choose among nectar sources emerge from the behaviors of thousands of bees? This question, which is the heart of this study, is just one form of the general question of self-organization in biology (Pattee 1976; Nicolis and Prigogine 1977; Haken 1978): how does the adaptive structure and functioning of a living system arise out of the joint actions of its subsystems? Colonies of the advanced social insects express this puzzle especially strongly since they present a clear juxtaposition of two levels of adaptive organization, the colony and the organism, yet it is rarely obvious how the properties of a colony emerge from the collective activities of its constituent insects. Fortunately, colonies of social insects

are unusually favorable subjects for studies of self-organization because, compared with organisms or cells, their dissection and experimental analysis is relatively easy. Nearly 20 years ago Wilson (1971, p 227) identified the special challenge and opportunity that the social insects offer to understanding biological organization when he wrote “the reconstruction of mass behavior from a knowledge of the behavior of single colony members is the central problem of insect sociology.”

1. *Synthesis of the analysis*

This investigation began with careful documentation of the adaptive functioning of the whole system, i.e., nectar-source selection by honey bee colonies. Previous studies (Darwin 1877; Butler 1945; Weaver 1979; Visscher and Seeley 1982) had suggested that colonies can selectively exploit rich food sources and can rapidly shift foragers among food sources following changes in the food source array. The present findings strongly confirm these ideas. Even a cursory glance at the exploitation patterns shown in Figs. 1 and 2 reveals these skills.

The next step was to explain these colonial foraging patterns in terms of the behaviors of individual bees. Fortunately, these two levels of description are directly bridged by the fact that the colony-level patterns (numbers of foragers allocated to each food source) are a direct result of two processes (recruitment to and abandonment of food sources) that are rather easily understood in terms of bee-level behavior patterns. Hence the key to linking the colonial and organismal descriptions of nectar-source selection was understanding how individual bees modulate their colony's rates of recruitment and abandonment to different nectar sources in accordance with their different levels of profitability.

By recording the behaviors of bees visiting a feeder, and periodically changing the profitability of the feeder, we were able to assemble a detailed picture of the multi-dimensional modulation of foraging behavior in relation to nectar source profitability (Table 1). Behaviors that the bees vary include the strength of waggle dancing, the tempo of visits to the food source, and the likelihood of returning to the food source. Other investigators (von Frisch 1967, p 45; Nunez 1966, 1970, 1982) have analyzed subsets of these behavioral variables in a similar fashion and have reported comparable patterns of behavior modulation in accordance with food source profitability. Therefore, we feel that the patterns shown in Table 1 are general for bees. In broad terms, as food source profitability increases, the duration of dancing increases, the tempo of foraging increases, and the probability of abandoning the food source decreases.

This begs the question: how does a forager assess the profitability of its nectar source? Three hypotheses (H1–H3) were examined. The first (H1) is that each bee makes this assessment by visiting several nectar sources and directly comparing its nectar source with others to estimate its relative profitability. A priori this seems improbable because in nature the flower patches exploited by a colony are widely scattered over an area extending

several kilometers from the hive (Visscher and Seeley 1982) and are not easily located, even by bees that are directed to the patches by recruitment dances (Esch and Bastian 1970; Mautz 1971; Seeley and Visscher 1988). More importantly, our data contradict H1, at least as a mechanism commonly used by bees. Of 117 bees involved in generating the pattern of selective exploitation on the morning of 19 June (see Figs. 1 and 2), only 2 visited more than one nectar source.

What about the second hypothesis (H2), that the food storer bees compare the profitabilities of different nectar loads and indicate (by the willingness to accept nectar) to each forager the relative profitability of its forage? According to this hypothesis, nectar source quality is assessed by bees simply as a function of the sugar concentration of the nectar, since this is evidently all that a food storer bee knows about a nectar source. But as the experiment reported here (Fig. 3) has shown, bees evaluate nectar source profitability as a function of variables besides sugar concentration, such as distance from the hive. This result falsifies H2. This conclusion is reinforced by the reports of Boch (1956) and Waddington (1982, 1985) that foragers adjust the strength of dancing in response to multiple variables affecting the energetic profitability of a nectar source – such as distance from the hive, difficulty of obtaining the nectar, and nectar abundance – not just sugar concentration.

By process of elimination, our results support the third hypothesis (H3) that each forager independently assesses the profitability of its nectar source and does so without reference to other nectar sources. This information processing evidently works as follows. In visiting a flower patch, a nectar forager takes in information about the energetic gains and costs associated with foraging at the patch – as determined by such variables as the distance from the hive, sugar concentration of the nectar, and nectar abundance – and integrates this information to arrive at an estimate of the overall energetic profitability of its patch. Each forager's nervous system is evidently calibrated so that it knows whether this level of profitability is low, high, or some point in between. Nectar sources that rank low will generally elicit abandonment of the source, and nectar sources that rank high will generally elicit recruitment to the source, though the precise levels of profitability that are the thresholds for abandonment and recruitment are adjusted by the foragers as a function of other variables independent of any one nectar source, such as the colony's nutritional status (Lindauer 1948; Seeley 1989), the seasonal forage availability (Lindauer 1948; Seeley 1986), and the weather conditions (Schuà 1952; Boch 1956). If all the foragers in a colony have shared rules for determining the profitability of nectar sources and for adjusting the response thresholds, then even though the foragers operate independently and with limited information, they will generate a coherent colony-level response to different food sources, wherein better food sources are recruited to and heavily exploited while poorer ones are abandoned. To be sure, the details remain obscure about the information processing inside a bee as it assesses the profitability of a nectar source,

especially how this calculation is performed by the central nervous system; however, what is now clear is that each nectar forager makes its own, independent assessment of the profitability of its nectar source and that it makes this assessment based only on local information from her particular nectar source. Hence, paradoxically, global order emerges from the actions of many independent actors, and moreover, none of the actors possesses an overview of the total operation (though they do possess shared information about the rules for assessing nectar source profitability and about such variables as the colony's nutritional state and the weather).

We now know a good deal about how bees modulate their behavior in relation to nectar source profitability, but is this behavioral modulation, performed by all the foragers in a colony, really sufficient to account for the nectar-source selection ability of the colony as a whole? Evidently it is. The computer simulation of decision-making by a colony wherein each forager simply adjusts her behavior according to the profitability of her nectar source and, when being recruited to a new nectar source, follows a dancer chosen at random from among the dancing foragers, yields patterns of nectar source exploitation that are remarkably similar to what was observed experimentally (Figs. 2 and 5). This does not imply that the rather simple model (Fig. 4) underlying these simulations contains a complete description of the decision-making process. Nevertheless, the match between the model's predictions and reality certainly suggests that this model captures the essence of the decision-making process. This can be thought of as a kind of natural selection among alternative nectar sources as foragers from higher profitability sources "survive" (continue visiting their source) longer and "reproduce" (recruit other foragers) better than do foragers from lower profitability sources. The net result is that the percentage of a colony's forager population associated with a nectar source will automatically increase if the profitability of the nectar source is relatively high, and will inevitably decrease if its profitability is relatively low. Hence, inside a bee hive, as in the natural world in general, the blind process of natural selection generates impressive order, and we need not invoke any higher-level decision-maker (no overseer) to explain this order.

2. *The rationale for decentralized control*

This conclusion is important, for it points out that the control of a colony's foraging behavior is highly decentralized. Indeed, it seems clear that it is distributed among *all* of the foragers in the colony, with each bee independently adjusting its behavior to what is appropriate to its own food source, and the colony-level decision-making arising automatically out of the resultant dynamics in recruitment and abandonment. Decentralized control of colony functioning has been reported in a number of contexts, including recruitment to food sources in fire ants (Wilson 1962), queen rearing and

thermoregulation in honey bees (Baird and Seeley 1983; Heinrich 1985), nest building in polybiine wasps (Jeanne 1986), food-source selection in pavement ants (Pasteels et al. 1987a, b), and raiding in army ants (Deneubourg et al. 1989; Franks 1989), to cite just a handful of examples. It seems that distributed control will prove the rule, at least in the advanced eusocial species where colony populations are generally on the order of 10^3 or larger [there is good evidence of centralized control in the primitively eusocial insects such as paper wasps, *Polistes*, where colonies usually contain less than 10^2 individuals (Reeve and Gamboa 1983)]. Why might this be?

More precisely, what factors have favored or disfavored the evolution of decentralized control for large societies? Considering first the reasons that would seem to disfavor decentralized control, there is no question that omitting a central authority leaves a group prone to conflicting actions among its members as individuals respond to their different, local situations rather than the shared, global condition of the group as a whole. Colonies of social insects frequently demonstrate this problem, for example, when an ant colony changes nest sites and some workers carry brood out of the old site while others carry them back in again (Wilson 1971, p 224). Also, without anyone supervising a group, redundancies within the group are likely to arise, especially for any activity that requires a long time to produce negative feedback effects to regulate the number of individuals undertaking the activity. Furthermore, the absence of a strong central authority within a group probably hampers its ability to amount a rapid, *global* response to a critical stress, such as an attack by a predator. On the other hand, distributing the control of a group widely among its members almost certainly enhances its ability to make a rapid, *local* response to a stress because it eliminates the need for time-consuming communication between the peripheral sensor/effector individuals and the central decision-making individuals. Also, distributing the control may often make the group less prone to incapacitating damage since the group's functioning will not depend critically on the status of a small subset of supervisory individuals.

We suspect, however, that the principal reason that decentralized control has evolved in colonies of advanced social insects is that it is a means for a society to achieve a high degree of organization without highly sophisticated communication and computation devices (Hayek 1945; Simon 1981). If the large colonies of social insects were run by a central authority, then each colony would have to possess an elaborate communication network so that information about the entire colony could flow adequately to the central planners, and so that orders from the central planners could be transmitted back to the appropriate members of the colony. Equally importantly, the central planning body would have to possess extremely sophisticated information-processing abilities to perform the difficult calculations needed to integrate information about the entire colony and produce orders that would result in a rational allocation of the colony's resources. Both of these complex devices

of social coordination are avoided in colonies with decentralized control wherein individuals make relatively simple decisions using information that is directly at hand. Although this may seem like a decidedly crude way to build a well organized society, this study of the honey bee society illustrates that it can be remarkably effective.

Acknowledgements. This project has been supported by the U.S. National Science Foundation, through grants BNS-8606778 and BNS-8916006 to Tom Seeley and through a graduate fellowship to Scott Camazine; and by the U.S. Department of Agriculture, through Hatch grant NY(C)-191407. We gratefully acknowledge this support. We also thank Dr. Wolfgang Kirchner (University of Würzburg) for suggesting the design of the experiment that tests whether or not food storer bees preferentially unload foragers bearing nectar loads of high sugar concentration (H2). Bill Shields, Director of the Cranberry Lake Biological Station, and everyone else at the CLBS, deserve our deepest gratitude for providing us with a field setting for the experiments that was ideal, both ecologically and psychologically. Finally, one of us (T.D.S.) wants especially to thank Mary Eickwort, Oliver Habicht, Scott Kelley, and Samantha Sonnak, who steadfastly tended the feeders during the experiments, despite the heavy attacks by blackflies, and Robin Hadlock Seeley, who made it possible for T.D.S. to go to Cranberry Lake and perform the critical study with the colony of labelled bees despite pressing needs at home.

References

- Baird DH, Seeley TD (1983) An equilibrium theory of queen production in honeybee colonies preparing to swarm. *Behav Ecol Sociobiol* 13:221–228
- Boch R (1956) Die Tänze der Bienen bei nahen und fernen Trachtquellen. *Z Vergl Physiol* 38:136–167
- Butler CG (1945) The influence of various physical and biological factors of the environment on honeybee activity. An examination of the relationship between activity and nectar concentration and abundance. *J Exp Biol* 21:5–12
- Camazine S, Sneyd J (1991) A mathematical model of colony-level nectar source selection by honey bees: self-organization through simple individual rules. *J Theor Biol* (in press)
- Darwin CR (1877) The effects of cross and self fertilization in the vegetable kingdom. Appleton, New York
- Deneubourg JL, Goss S, Franks N, Pasteels JM (1989) The blind leading the blind: modelling chemically mediated army ant raid patterns. *J Insect Behav* 2:719–725
- Esch HA, Bastian JA (1970) How do newly recruited honey bees approach a food site? *Z Vergl Physiol* 68:175–181
- Franks NR (1989) Army ants: a collective intelligence. *Am Sci* 77:138–145
- Franks NR, Fletcher CR (1983) Spatial patterns in army ant foraging and migration: *Eciton burchelli* on Barro Colorado Island, Panama. *Behav Ecol Sociobiol* 12:261–270
- Frisch K von (1967) The dance language and orientation of bees. Harvard University Press, Cambridge
- Haken H (1978) Synergetics – an introduction. Springer, New York Berlin Heidelberg
- Hayek FA (1945) The use of knowledge in society. *Am Econ Rev* 35:519–530
- Heinrich B (1985) The social physiology of temperature regulation in honeybees. *Fortschr Zool* 31:393–406
- Hofstadter DR (1979) Gödel, Escher, Bach: an eternal golden braid. Basic Books, New York
- Hölldobler B (1981) Foraging and spatiotemporal territories in the honey ant *Myrmecocystus mimicus* Wheeler (Hymenoptera: Formicidae). *Behav Ecol Sociobiol* 9:301–314
- Jeanne RL (1986) The organization of work in *Polybia occidentalis*: costs and benefits of specialization in a social wasp. *Behav Ecol Sociobiol* 19:333–341
- Lindauer M (1948) Über die Einwirkung von Duft- und Geschmacksstoffen sowie anderer Faktoren auf die Tänze der Bienen. *Z Vergl Physiol* 31:348–412
- Lindauer M (1955) Schwarmbienen auf Wohnungssuche. *Z Vergl Physiol* 37:263–324
- Lindauer M (1961) Communication among social bees. Harvard University Press, Cambridge
- Lindauer M (1975) Verständigung im Bienenstaat. Fischer, Stuttgart New York
- Lumsden CJ, Hölldobler B (1983) Ritualized combat and intercolony communication in ants. *J Theor Biol* 100:81–98
- Markl H (1985) Manipulation, modulation, information, cognition: some of the riddles of communication. *Fortschr Zool* 31:163–194
- Mautz D (1971) Der Kommunikationseffekt der Schwänzeltänze bei *Apis mellifica carnica* (Pollm.). *Z Vergl Physiol* 72:197–220
- Nicolis G, Prigogine I (1977) Self-organization in nonequilibrium systems. Wiley, New York
- Núñez JA (1966) Quantitative Beziehungen zwischen den Eigenschaften von Futterquellen und dem Verhalten von Sammelbienen. *Z Vergl Physiol* 53:142–164
- Núñez JA (1970) The relationship between sugar flow and foraging and recruiting behaviour of honey bees (*Apis mellifera* L.). *Anim Behav* 18:527–538
- Núñez JA (1982) Honeybee foraging strategies at a food source in relation to its distance from the hive and the rate of sugar flow. *J Apic Res* 21:139–150
- Pasteels JM, Deneubourg J-L, Goss S (1987a) Self-organization mechanisms in ant societies (I): Trail recruitment to newly discovered food sources. In: Pasteels JM, Deneubourg J-L (eds) From individual to collective behavior in social insects. Birkhäuser, Basel, pp 155–175
- Pasteels JM, Deneubourg J-L, Goss S (1987b) Transmission and amplification of information in a changing environment: the case of insect societies. In: Prigogine I, Sangleier M (eds) Law of nature and human conduct. G.O.R.D.E.S., Bruxelles, pp 129–156
- Pattee HH (1976) Physical theories of biological co-ordination. In: Grene M, Mendelsohn E (eds) Topics in the philosophy of biology, vol 27. Boston studies in philosophy of science. Reidel, Boston, pp 153–173
- Reeve HK, Gamboa GJ (1983) Colony activity integration in primitively eusocial wasps: the role of the queen (*Polistes fuscatus*, Hymenoptera: Vespidae). *Behav Ecol Sociobiol* 13:63–74
- Schua L (1952) Untersuchungen über die Einfluß meteorologische Elemente auf das Verhalten der Bienen. *Z Vergl Physiol* 34:258–277
- Seeley TD (1982) How honeybees find a home. *Sci Am* 247(Oct):158–168
- Seeley TD (1985) Honeybee ecology. Princeton University Press, Princeton
- Seeley TD (1986) Social foraging by honeybees: how colonies allocate foragers among patches of flowers. *Behav Ecol Sociobiol* 19:343–354
- Seeley TD (1989) Social foraging in honey bees: how nectar foragers assess their colony's nutritional status. *Behav Ecol Sociobiol* 24:181–199
- Seeley TD, Levien RA (1987) A colony of mind. The beehive as thinking machine. *The Sciences* 27:38–43
- Seeley TD, Visscher PK (1988) Assessing the benefits of cooperation in honeybee foraging: search costs, forage quality, and competitive ability. *Behav Ecol Sociobiol* 22:229–237
- Simon HA (1981) The sciences of the artificial, 2nd edn. MIT Press, Cambridge
- Sokal RR, Rohlf FJ (1981) Biometry, 2nd edn. Freeman, San Francisco
- Visscher PK, Seeley TD (1982) Foraging strategy of honeybee colonies in a temperate deciduous forest. *Ecology* 63:1790–1801

- Waddington KD (1982) Honey bee foraging profitability and round dance correlates. *J Comp Physiol* 148:297–301
- Waddington KD (1985) Cost-intake information used in foraging. *J Insect Physiol* 31:891–897
- Weaver N (1979) Possible recruitment of foraging honeybees to high-reward areas of the same plant species. *J Apic Res* 18:179–183
- Wilson EO (1962) Chemical communication among workers of the fire ant *Solenopsis saevissima* (Fr. Smith). 1. The organization of mass-foraging. *Anim Behav* 10:134–147
- Wilson EO (1971) *The insect societies*. Harvard University Press, Cambridge
- Wilson EO, Hölldobler B (1988) Dense heterarchies and mass communication as the basis of organization in ant colonies. *Trends Ecol Evol* 3:65–68

Appendix

This section presents the set of differential equations that describe the rate of change of the number of bees in each compartment shown in Fig. 4 over time. The symbols in these equations are defined in the text accompanying Fig. 4. For a more detailed discussion of the model represented by these equations, see Camazine and Sneyd (1991).

$$\begin{aligned}
 dA/dt &= (1-f_a^A)(1-f_x^A)p_1H_A + p_2D_A + f_1^Ap_4F - p_3A \\
 dD_A/dt &= f_a^A(1-f_x^A)p_1H_A - p_2D_A \\
 dH_A/dt &= p_3A - p_1H_A \\
 dF/dt &= f_x^Ap_1H_A + f_x^Bp_5H_B - p_4F \\
 dB/dt &= (1-f_a^B)(1-f_x^B)p_5H_B + p_6D_B + f_1^Bp_4F - p_7B \\
 dD_B/dt &= f_a^B(1-f_x^B)p_5H_B - p_6D_B \\
 dH_B/dt &= p_7B - p_5H_B
 \end{aligned}$$