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Division of Labor Between Scouts and Recruits in Honeybee Foraging

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Summary. The proportion of a honeybee colony's foragers which locate forage patches by independent scouting, as opposed to following recruitment dances, varies between about 5 and 35%, depending on forage availability. Experienced foragers scout more than do novice foragers. The cost of finding a forage patch is greater for recruits than scouts, but the patches found by recruits are evidently superior to those found by scouts. The honeybee's combined system of recruitment communication, scout-recruit division of labor, and selectivity in recruitment, apparently enhances a colony's overall foraging efficiency by guiding a large majority of a colony's foragers to good forage patches.

Introduction

Over the past 60 years, Karl von Frisch and his associates have assembled a detailed understanding of the honeybee's dance language system of recruitment communication (reviewed by von Frisch 1967; Michener 1974; Gould 1976). In contrast, the division of labor which the dance language makes possible – between foragers which search independently for food sources (scouts) and those which are guided to a food source by following recruitment dances (recruits) – has received relatively little attention (Oettingen-Spielberg 1949; Lindauer 1952). The ecological significance of the dance language, however, is probably only understandable in light of the scout-recruit division of labor (Oster and Wilson 1978; Heinrich 1976, 1979). More specifically, the fact that most foragers are guided to forage patches, rather than finding them by random searching, appears to be a central component in the social foraging strategy of honeybee colonies (Visscher and Seeley 1982).

In this paper I explore the scout-recruit division of labor by addressing the following three questions: (1) What are the proportions of scouts and recruits in a colony's forager force? (2) What determines whether a forager behaves as a scout or recruit? (3) How does the scout-recruit division of labor affect a colony's foraging energetics?

Materials and Methods

My basic experimental procedure was as follows: (1) train a small group of labelled foragers from an observation hive to a feeding station, (2) monitor the foraging tempo of each forager for 2 days, (3) shut off the feeding station and watch the labelled bees back in the observation hive to determine how each individual finds her next forage patch (whether by scouting or following recruitment dances, or both). I compared the search times of scouts and recruits by continuously recording on videotape all departures from and returns to the observation hive by labelled individuals. Search times were converted to search costs using standard energetic calculations.

Study Sites. The 7 trials of this experiment were performed in 3 locations: Appledore Island, Maine (42°59′N, 70°37′W; 4 trials; see Seeley 1977), the Marsh Botanical Gardens of Yale University, New Haven, Connecticut (41°19′N, 72°56′W; 2 trials), and the Yale Forest, Union, Connecticut (41°57′N, 72°07′W; 1 trial; see Meyer and Plusnin 1945).

Observation Hive. In order to observe all instances of dance following by the labelled bees, I used an observation hive in which all the dances were performed in a small area on one side of the comb. This hive was essentially a scaled-down version (internal dimensions 46 × 50.5 × 4.5 cm) of the hive described by Visscher and Seeley (1982). Diffuse illumination of the hive at all times prevented disorientation of the bees' recruitment dances. Each summer the hive was stocked with Italian bees (*Apis mellifera ligustica*). At full strength the observation colony contained about 6,000 bees.

I recorded the labelled bees' departure and arrival times at the observation hive by mounting a color video camera (JVC G-71USJ; video recorder: JVC HR-6700U) equipped with close-up lenses over a transparent plastic entrance tunnel

(5.0 cm wide, 3.3 cm tall, and 47 cm long). A digital watch mounted outside the tunnel but within the camera's field-of-view provided time records on the videotapes. Good color resolution among the labelled bees' markings was achieved by painting a large white dot plus a slightly smaller, concentric, colored dot of PLA enamel paint on the thorax or abdomen, or both, of the labelled bees. Fiber optics provided cool illumination of the entrance tunnel. I forced the bees to always walk on the entrance tunnel's floor by coating the tunnel's walls and ceiling (except beneath the camera) with petroleum jelly.

Experimental Procedure. Each trial lasted for 5 days. On the first day, 15 foragers were trained to a feeding station (von Frisch 1967, Fig. 18) 60 m from the observation hive. My training procedure involved placing a small square of bee comb filled with 2 M sucrose solution in the hive entrance, then, when 1–4 bees had begun feeding from the comb, quickly carrying the bees and comb to the feeding station. Just one of these artificial scout bees was allowed to continue foraging from the station; all the other foragers which eventually worked the station found it by being recruited to it. This procedure ensured that at most only one of the foragers was not experienced in finding a food source by following recruitment dances. When 14 recruits had found the feeding station, and had been labelled as described above, I reduced the sugar concentration by appropriate dilutions of a stock 2 M sucrose solution until I arrived at a solution which would sustain the forager's interest, but not induce further recruitment. Occasional newcomers were killed by placing them in ethanol. Finally, at 17.00 h, I shut off the feeding station.

On days 2 and 3, I maintained food at the station from 08.00 to 17.00 h, periodically adjusting the sugar concentration as described above. I checked that each labelled bee continued to work the feeding station by making hourly roll calls at the station. On both days, between 10.00 and 14.00 h, I recorded on videotape each labelled bee's departures and arrivals at the observation hive.

On days 4 and 5, I kept the feeding station shut off and watched the bees at the observation hive from 06.00 to 18.00 h, recording on audiotape any instances of marked bees following dances or returning with forage. By the start of day 4 of each trial, a few labelled bees had died, leaving 11.1 ± 3.6 bees to monitor. Whenever a labelled bee followed a dancer, I recorded the time, dance angle, dance tempo, and forage type using the techniques described by Visscher and Seeley (1982). Whenever a labelled bee returned to the hive, I inspected her legs for pollen and followed her closely to see if she would unload nectar, perform dances to indicate her forage patch, or both. Usually bees which had found forage indicated this within seconds of entering the hive; bees either carried pollen loads or excitedly pressed through surrounding bees with their mandibles spread, trying to find a bee willing to receive nectar. Throughout the observation periods of days 4 and 5, the videotape system automatically recorded all departure and arrival times of the labelled bees. Also, I recorded the number of dancing bees by making 5 counts of the dancers each hour. Finally, after nightfall on day 5, when all the bees were in the hive, I would open the observation hive and collect the labelled bees for morphological analysis.

During trials 5, 6 and 7, I monitored the forage availability by recording the daily weight changes of 2 nearby, full-sized colonies on platform scales (Detecto, Model 4510KG).

Data Analysis. Transcribing the videotapes from days 2 and 3 revealed the number of foraging trips made by each labelled bee during each day's 4-h recording period.

Transcribing the audiotapes from days 4 and 5 yielded a history of each labelled bee's behavior in finding a new forage patch. Some bees returned with forage without following any dances; such bees were classified as 'scouts'. All other bees followed dances before returning with forage, but I classified a dance-follower as a 'recruit' only if the bee indicated by her own dancing that she had visited the same forage patch as was advertised by the dances she had followed. Dance information was interpreted using the techniques described in Visscher and Seeley (1982). Although all dances followed by labelled bees were vigorous and clearly indicated a patch location, frequently the labelled bees' dances were feeble, consisting of just a few circuits. Such dances only provided good information about patch direction, and in these cases I considered a match between the two bees' dances in patch direction alone as indicating that the labelled bee had used dance information to find a forage patch. Occasionally, a labelled bee which had followed dances indicated by her own dances that she had not foraged at the patch corresponding to the dances she had followed. Such bees were also classified as 'scouts'. Still other labelled bees which had followed dances never danced upon finding forage. They were classified as 'ambiguous'.

Transcribing the videotapes from days 4 and 5 yielded data on the time which each labelled bee spent outside the nest searching for a new forage patch. Trips made before a bee returned with forage were assumed to have been devoted entirely to searching, but only a fraction of the trip on which the bee discovered forage could have been devoted to searching. Some time must have been spent collecting the forage. I estimated the time devoted to searching on the discovery trip by subtracting from the total duration of the discovery trip the average duration of trips following the discovery trip, since these trips would involve little or no searching.

Observing Foraging Bees. To calculate the energy expended in searching for a forage patch, I needed to estimate the percent time in flight once a forager has found a patch. Accordingly, between 25 May and 2 October 1982, I followed foraging bees on plants of 16 species. For each species, I gathered data from at least 5 different foragers, following them for a total of 30 min while noting aloud and tape recording whether the bee was perched on a flower or in flight. Transcribing these tapes with the aid of the TIME command in the advanced BASIC language of an IBM PC microcomputer yielded values of percent time flying and perching.

Statistics. Unless stated otherwise, measurements are given as the mean ± one standard deviation. Statistical tests are based on t tests: Student's, the test for equality of two percentages, or the test for significance of a product-moment correlation coefficient (Sokal and Rohlf 1969).

Morphological Analysis. The sizes of individual bees were recorded by measuring head width and wing length using techniques described by Seeley et al. (1982).

Results

The Proportions of Scouts and Recruits

Table 1 shows the observed distribution of 78 experienced foragers among the categories of scout, recruit, and ambiguous. Assuming that the proportion of bees which followed dances but nevertheless scouted (category 1 B) was the same for unambi-

Table 1. Distributions of novice and experienced foragers among three categories (scout, recruit, and ambigous) denoting how each bee located a forage patch

	Novice foragers (data from Lindauer 1952)			Experienced foragers		
	N		%	*N*		%
Scout						
A. Did not follow dances	9	13	8	16	17	22
B. Followed dances, but did not forage at the patch indicated by the dances	4			1		
Recruit Followed dances, and foraged at the patch indicated by the dances		46	29		30	38
Ambiguous Followed dances, but may or may not have foraged at the patch indicated by the dances		100	63		31	40
Total		159 bees	100		78 bees	100

guous (categories 1 B and 2) and ambigous (category 3) dance-following bees, then the total percentage of scouts was 22% + (1/31) × 40% = 23%. Evidently only a clear minority of the foragers found food without being guided by dances to a forage patch. (Because nearly all (97%) of the unambiguous, dance-following bees were recruits, throughout the remainder of the paper I assume all of the ambiguous, dance-following bees were also recruits.)

The figure of 23% scouts among experienced foragers is by no means a fixed proportion. Rather, the proportion of scouts apparently depends heavily upon the foraging conditions. This dependence is suggested by comparing the results of the first and second vs third and fourth trials on Appledore Island. As is shown in Table 2, within a 4-week period the percent scouts changed dramatically, apparently in response to changed foraging conditions. During trials 1 and 2, when little forage was available, approximately 36% of the bees found forage by scouting. In contrast, during trials 3 and 4, when large patches of catnip (*Nepeta cataria*) had come into bloom, the percent scouts dropped to about 5%. I quantified forage availability by counting the number of dancers in the hive at any one time (see Table 2). Comparisons between the daily average in number of dancers in the observation hive and daily weight gain of two nearby, full-sized colonies on scales revealed a significant ($P < 0.05$) positive correlation ($r = 0.82$) between these two variables (data from trials 5, 6, and 7).

Table 2. Comparison between times of poor forage (trials 1 and 2) and rich forage (trials 3 and 4) in the proportion of foragers which found a forage patch by scouting. The proportions of scouts were calculated using the same method which indicated 23% scouts overall (see text and Table 1)

	Trials		Significance of the difference
	1 and 2	3 and 4	
Dates	29 June to 3 July 80 7–11 July 80	21–25 July 80 27–31 July 80	
Proportion of scouts ($\bar{P} \pm$ SE)	0.36 ± 0.09	0.05 ± 0.04	$P < 0.005$
No. of dancers ($\bar{X} \pm$ SD)	0.8 ± 1.0	4.9 ± 2.3	$P < 0.001$
No. of bees	28	22	

Apparently the proportion of scouts is adjusted to the colony's needs. When little forage is available, and thus when there are relatively few high-quality patches being advertised in the hive, more bees search for additional patches than when high-quality patches are widely available and are steadily advertised in the hive.

Were True Scouts Observed?

In the preceding calculation of the percent scouts, I have assumed that the bees which did not follow dances to find a forage patch were true scouts, that is, bees which had searched for new forage patches, and not bees which had simply returned to forage patches which they had worked before being drawn into my study.

To test this assumption, I compared the percent scouts in trials 5 and 6 vs in trial 7. In trial 7 the experimental colony was moved overnight to a new location before starting the experiment, therefore the labelled bees could not have returned to a prior forage patch when the feeding station was shut off. In trials 5 and 6, the experimental colony was not moved before the experiment began and so the labelled bees could have returned to an earlier forage site. The forage availability was highly similar for all three trials (average daily weight gain of nearby scale hives: 0.24 ± 0.36, 0.05 ± 0.18, 0.14 ± 0.09 kg; trials 5, 6, 7, respectively; all differences between means are not significant ($P > 0.39$)). If the presumed scouts were true scouts, then there should not have been a significant difference between trials 5 and 6 vs trial 7 in the proportion of scouts. If, however, the presumed scouts were simply returning to earlier forage patches, then there should have been a significantly smaller proportion of scouts in trial 7 relative to trials 5 and 6. In fact, the proportion of scouts did not differ significantly ($P > 0.80$) between trials 5 and 6 (30% scouts, $N = 20$) and trial 7 (25% scouts, $N = 8$). Furthermore, the search times did not differ significantly ($P > 0.29$) between the scouts of trials 5 and 6 (97 ± 56 min) and trial 7 (50 ± 11 min). Evidently true scouts were observed in this study.

Factors Determining a Bee's Scout or Recruit Behavior

A logical first step in analyzing why a bee scouts or follows dances to find a forage patch is to distinguish between two general hypotheses about foragers. The first states that foragers are not all equivalent, that there are scout and recruit specialists, and so instances of scouting and recruiting are distributed non-randomly among a group of foragers. The second hypothesis states that all foragers are equivalent, that foragers do not specialize in scouting or recruitment, and therefore that random events determine whether a particular forager, in a given situation, scouts or follows dances to find a forage patch.

My experimental design did not allow repeated determinations of how particular foragers found forage patches, thus I could not directly determine whether certain individuals specialize in scouting or recruitment. However, I could try to determine whether there is anything special about scouts or recruits, and so in this way distinguish between the equivalent and non-equivalent forager hypotheses. I compared the foraging tempos of scouts and recruits during their 2 days of foraging from the feeding station. The scouts' foraging rates averaged higher than those of recruits (scouts, 95.4 ± 12.8; recruits, 74.8 ± 21.4 foraging trips/8 h/bee; $P < 0.01$). Moreover, individual bees were moderately consistent in their foraging rates; $r = 0.654$ for the correlation between the number of foraging trips between 10.00 and 14.00 h on days 2 and 3 of each trial ($N = 28$ bees, $P < 0.0001$). Because a bee's scouting tendency correlates with her recent foraging rate, it appears that there are moderately consistent differences among foragers in tendency to scout or follow dances to find forage patches.

What underlies the variation in scouting tendency? Scouts and recruits do not differ in size (wing length: scouts, 8.86 ± 0.10 mm, recruits, 8.89 ± 0.11 mm, $P > 0.60$; head width: scouts, 3.77 ± 0.04 mm, recruits, 3.81 ± 0.05 mm, $P > 0.13$). To check for a difference in age or foraging experience between scouts and recruits, I compared the percent scouts which I observed among experienced foragers to that observed by Lindauer (1952) who used similar observation techniques but studied foragers finding their first food source (see Table 1). The best estimate of percent scouts among Lindauer's novice foragers is $8\% + (4/50) \times 63\% = 13\%$, which is significantly ($P < 0.03$) less than the 23% which I observed for experienced foragers.

The difference in percent scouts between novice and experienced foragers in probably even greater than the preceding numbers indicate. As was previously noted, the percent scouts varies with changes in foraging conditions, and whereas the observations indicating 13% scouts among novice foragers were made during a forage dearth (Lindauer 1952, p. 325), the observations indicating 23% scouts among experienced foragers were made during both rich and poor foraging conditions. A fairer comparison is that between Lindauer's results and mine from trials 1, 2, 5, 6 and 7, when in all cases little forage was available. In these 5 trials I monitored 53 bees, of which 17 were scouts (16 type A and 1 type B, categories as in Table 1), 18 were recruits, and 18 were ambiguous. The best estimate of the percent scouts is $32\% + (1/19) \times 34\% = 34\%$, which is strikingly different ($P < 0.0004$) from the 13% scouts observed by Lindauer.

Search Costs of Scouts and Recruits

One hypothesis for the adaptive significance of the honeybee's dance language is that it reduces the average cost per forager of locating forage patches. At the heart of this hypothesis is the assumption that finding a patch by scouting is more costly than being guided to a patch by recruitment dances. If this is true, and given the fact that recruitment communication enables most foragers to avoid scouting, then the average cost of finding a patch should be lower in colonies with recruitment communication than in those without it, all else being equal.

To test this hypothesis, I compared the average search times required by scouts and recruits to find their next forage patch after I shut off the feeding station. Each bee's search time was the sum of the time periods spent outside the nest, starting on the morning of day 4 in each trial and ending when the bee returned with food (minus a correction, as described above, for time spent collecting on the discovery trip).

Contrary to expectations, recruits spent more time searching for a forage patch than did scouts: recruits, 138±76 min ($N=20$); scouts, 85±58 min ($N=8$); $P<0.087$. Why was this? One reason is that recruitment was not automatic. Recruits did not find the target patch on their first trip out after following a dancer. Instead, they required 4.8±3.2 (range 1–12) dance-guided search trips, each one lasting 17±11 min. A possible second factor is that some recruits perhaps first scouted for a new patch, then, when this failed, located a patch by following dances. The time records of individual recruits shed light on this second possibility. Each labelled bee's first few trips outside on the morning of day 4 were brief, usually under 5 min. The bees were simply going out to check the feeding station (von Frisch 1923, personal observations). Later in the day, once recruits began following dances and started searching much farther afield than the feeding station, trip durations moved into the 10+ min range. Out of 20 recruits, 4 made one or more (2.5±1.3) trips outside lasting 10+ min before beginning to follow dances, suggesting that about 20% of the recruits did some scouting beyond the feeding station.

To put the difference in search costs between scouts and recruits into meaningful perspective, it is useful to convert it from time units to calories, and then compare this cost difference with the net profit of a typical foraging trip. Recruits required, on average, 53 min more search time than did scouts. A lower bound on the proportion of this search time which was spent in flight can be estimated from the percent time in flight for foragers when in profitable forage patches: 36±17%, range 4–68%. (This estimates a lower bound because a forager working profitable flowers almost certainly flies less than one still searching for flowers. Also, the preceding percentage does not take into account any flight to and from a patch.) Therefore recruits spent, on average, about 19 or more minutes in flight more than did scouts. Given a metabolic rate of 1.42 ml O_2/g/min (Heinrich 1980), a partially loaded bee weight of about 0.1 g (Otis 1982), and a conversion factor of 5.0 cal expended/ml O_2 consumed (Kleiber 1961), then the cost of 53 min of extra searching, assuming 36% flight time, is about 13 cal. (Because the metabolic rate of a resting or walking bee is only a few percent that of a flying bee (reviewed by Kammer and Heinrich 1978), I have ignored energy expenditure during non-flight time.) If the entire 53 min were spent in flight, then recruits would have expended about 38 cal more than scouts in locating a forage patch.

How does this 13–38 cal estimate of the added cost of recruitment compare with the net profit on a foraging trip for nectar? Given an average net nectar gain of 30 µl per foraging trip (von Frisch 1967; Fukuda et al. 1969), and an average energy concentration of 2 cal/µl nectar (Southwick et al. 1981), then the net profit of a foraging trip for nectar is about 60 cal, on average. Thus the added cost of finding a patch by recruitment is roughly 25–65% of the net profit from a foraging trip.

Comparison of Scouts' and Recruits' Forage Patches

The relative qualities of forage patches found by scouts and recruits can be inferred from differences in their foraging behavior after finding a patch. The proportion of trips following the discovery trip in which the forager returned with forage was higher for recruits than for scouts: recruits, 0.95±0.14 ($N=20$); scouts, 0.51±0.47 ($N=8$); $P<0.0005$ ($t=-3.75$ after arcsin transformations of the proportions). Also, the rate of successful trips (forager returns with food) following the discovery trip was higher for recruits than scouts: recruits, 1.22±1.30 ($N=20$); scouts, 0.72±0.94 trips/h/bee ($N=8$); $P=0.067$. Apparently the patches found by recruits had a higher probability of being worth returning to than did the patches found by scouts.

Discussion

The most thought-provoking finding of this study is that search costs were greater for recruits than scouts. Insofar as this is generally true, it falsifies the hypothesis that the dance language helps minimize the average cost per forager of locating forage patches.

Probably a better approach toward understanding the ecological significance of the dance language is to view it in the broader context of the overall strategy of foraging by honeybee colonies. The essence of this strategy seems to be that a colony operates as an information center in which the reconnaissance of foragers is pooled and processed to focus the colony's efforts on a few, high-quality forage patches (von Frisch 1967, p. 246; Visscher and Seeley 1982). Recruitment communication via the dance language is one element of honeybee social organization which makes this strategy possible. Three other essential elements are (1) the scout-recruit division of labor such that most individuals find forage patches by following recruitment dances, (2) feedback to foragers concerning whether or not to change forage patches (Lindauer 1954), and (3) regulation of dancing so that only the best patches are advertised by dances (Lindauer 1954; Boch 1956). The net result of the joint operation of these various elements seems to be that the majority of a colony's foragers (the recruits) invest relatively heavily in locating rich forage patches while a small minority (the scouts) invest less in searching, find poorer patches on average, but occasionally make the critical discoveries of new, rich patches. Presumably the net rate of food collection per forager, averaged over all foragers, is higher with than without this elaborate social organization, especially when there is wide variance in patch quality and top-quality patches are widely scattered. The previously-stated differences between scouts and recruits in foraging behavior after finding a forage patch support this interpretation of the dance language's functional significance by suggesting that recruits find higher-quality patches than do scouts.

Given the conditions under which the observations reported here were made, it is not clear that scouts always have lower average search costs than recruits. The first two trials with videorecording (trials 5 and 6) were conducted in a botanical garden located in a neighborhood with many flower gardens, while the third trial with videorecording (trial 7) was conducted in a 3,200+ ha forest during the goldenrod (*Solidago* spp.) bloom. In all three trials it may have been fairly easy for scouts, searching at random, to find patches. When forage is sparser, scouts may have to spend much more time searching. In contrast, the search costs of recruits may vary relatively little with changing foraging conditions. Recruits search specifically for known patches and so do not depend on random encounters with patches.

Several earlier studies have reported on the number of search trips required by recruits to find patches (Esch and Bastian 1970; Mautz 1971; Gould 1976). However, because these prior studies involved recruitment to artificial feeders at most a few hundred meters from the hive, it is unclear whether they confirm or contradict the pattern of repeated searches reported here, in which recruitment was to real patches of flowers 1,340 ± 960 m from the hive. When the recruitment target was a wide array of feeders, recruits found a food source on their first search trip (Gould 1976). When the target was just a single feeder, recruits required 1–10 search trips (2.5 ± 2.3 trips for a feeder 200 m distant) (Esch and Bastian 1970; Mautz 1971).

Many authors have discussed the idea that animal groups may function as information centers (Fisher 1954; Ward 1965; Zahavi 1971; Ward and Zahavi 1973; Krebs 1974; Bayer 1982). These are usually thought to help reduce the cost of finding food.The present study suggests that animals may form information centers which actually raise the cost of finding a food source but provide an overall advantage in foraging by helping individuals locate especially rich food sources. This second function of information centers is probably less common than the first because it requires not only sharing information about food sources, but also mechanisms for deciding which food sources are the most profitable.

It is well known than honeybee colonies have the ability to choose among forage patches and so focus their foraging on the richest patches (Butler 1945; Boch 1956), but the precise mechanisms of forage patch selection are still poorly understood. They therefore represent a major gap in our understanding of the honeybee's social foraging strategy. Because most foragers locate forage patches by following recruitment dances, studies of colonial decision-making about forage patches must logically focus on what regulates recruitment intensity to particular patches. Numerous factors are already known to influence a forager's tendency to dance (reviewed by von Frisch 1967), including the relative ranking of a patch's nectar concentration, the patch's distance from the nest, and the ease of foraging at the patch. But the precise ways in which these and other patch properties are jointly evaluated in estimating each patch's relative profitability, and the precision of colonial patch selection, remain important mysteries in honeybee foraging behavior.

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