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# Comparisons of forager distributions from matched honey bee colonies in suburban environments

**Abstract** We conducted experiments designed to examine the distribution of foraging honey bees (*Apis mellifera*) in suburban environments with rich floras and to compare spatial patterns of foraging sites used by colonies located in the same environment. The patterns we observed in resource visitation suggest a reduced role of the recruitment system as part of the overall colony foraging strategy in habitats with abundant, small patches of flowers. We simultaneously sampled recruitment dances of bees inside observation hives in two colonies over 4 days in Miami, Florida (1989) and from two other colonies over five days in Riverside, California (1991). Information encoded in the dance was used to determine the distance and direction that bees flew from the hive for pollen and nectar and to construct foraging maps for each colony. The foraging maps showed that bees from the two colonies in each location usually foraged at different sites, but occasionally they visited the same patches of flowers. Each colony shifted foraging effort among sites on different days. In both locations, the mean flight distances differed between colonies and among days within colonies. The flight distances observed in our study are generally shorter than those reported in a similar study conducted in a temperate deciduous forest where resources were less dense and floral patches were smaller.

## Introduction

Mechanisms of the honey bee's dance language have been studied for a half century (von Frisch 1967). Scout bees leave the hive in search of pollen and nectar. They return with food and communicate, via the dance, information on the odor of and distance and direction to the resource, recruiting other bees from the colony. Little is known about the ecology of this recruitment system (Seeley 1985). How does recruitment fit into the whole colony's foraging strategy?

Visscher and Seeley (1982) addressed this question by mapping the sites foraged by bees from a single colony in a temperate deciduous forest. Each day the colony's foragers visited relatively few of the available floral patches and the colony's efforts shifted among patches on successive days. Scouts surveyed a large area (approx. 113 km$^2$) around the nest and Visscher and Seeley (1982) hypothesized that scouts directed recruits to the most profitable flower patches. Inside the colony, mechanisms of social foraging have been elucidated by creating a simple foraging environment with feeders containing different concentrations of sugar solution at different distances from the hive (e.g. Seeley 1986; Seeley et al. 1991).

In this study, we examined where foragers from matched colonies, two in Florida and two in California, foraged for pollen and nectar in suburban environments characterized by high densities of flowers on trees and in gardens. We had two goals: (1) to compare colony foraging patterns in these habitats with results from the temperate deciduous forest where floral densities were lower, and (2) to compare the distributions of foragers from two colonies located in the same area at the same time. If scouts scour the environment looking for

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profitable resources, and the function of the dance is to focus a colony's foraging efforts on a few most profitable resources, then we expected two colonies faced with the same floral environment to visit the same patches of flowers.

## Materials and methods

Correlations of dance with distance and direction to food patches were used to determine where bees foraged for pollen and nectar (Visscher and Seeley 1982).

### Calibration curve: distance estimated using the dance

The relationship between the duration of a single dance circuit (i.e., one half of the figure-8 waggle dance run) and flight distance can be used to decode where dancers foraged (von Frisch 1967). We used a third order polynomial fit of the data presented by von Frisch (1967, p. 69, Table 6; $r^2=0.998$): $y=89.695-345.256x + 228.224x^2-10.951x^3$, where $x$=duration of a single dance circuit (s) and $y$=distance between the hive and forage site (m) (Fig. 1).

In Florida, we checked the relationship between the calculated and actual flight distances. Bees of the same race that we used in the experiments described below were trained to feeders at several distances up to 1100 m from the hive. They were marked with paint on the thorax while visiting a feeder. At the hive, we counted the number of circuits and timed the dance duration, and then we calculated mean duration of a dance circuit (s/circuit). The observed relationship between distance and circuit duration corresponds well with that predicted by the polynomial function derived from the data of von Frisch (1967) (Fig. 1).

### The experimental protocols

#### General procedures

Two colonies of honey bees (*Apis mellifera*) were studied at each of two suburban locations. The pairs of colonies at each location were in four-frame glass-sided observation hives with 9212 cm² of wax comb and were housed in rooms dimly lit from above by fluorescent lights. The bees had access to the outdoors through a tunnel at the bottom of the hives. Pairs of colonies were approximately matched for population size, brood area, and honey and pollen stores. Observations were made on warm, clear days.

Pairs of hives were observed simultaneously. Observers rotated between hives each 15 min. To randomly select dances for observation, we used a grid of 5-cm squares drawn on the glass over the area where dancing occurred. We chose a random number cor-

responding to a grid square, and if a bee was dancing inside that square we quantified her dances; if no bee was dancing, then we chose another square. Using a stopwatch, we timed the duration of a series of dance circuits and recorded the orientation of the dances in relation to vertical. Flight distance was calculated for each dance using the calibration curve (Fig. 1). The direction indicated in each dance was calculated by adding the sun azimuth at the time the dance was recorded to the angle of the dance. Dancers carrying pollen were scored as pollen foragers. Bees not carrying pollen were assumed to be nectar foragers. Finally, the inferred location of each forage site was mapped for each hive on each day.

### Site-specific methodologies

Observations in Florida were made between 0830 and 1030 hours on 14–17 March 1989 on the main campus of the University of Miami, Coral Gables. Within the bees' flight range there were numerous residential gardens and flowering trees. The two colonies, designated FL1 and FL2, had approximately 12,000–15,000 bees. Three observers rotated between the four viewing areas (i.e., the two sides of each hive). Dance direction was determined by drawing the dance path on a sheet of clear plastic overlay with a ruler, and later measuring its angle with a protractor. Each dance record consisted of 5–15 circuits.

Observations in California were made in the agricultural research area of the University of California, Riverside campus, surrounded by residential areas, between 0800 and 1600 hours on 19 – 22 February 1991. Colonies CA1 and CA2 each had approximately 10,000 bees. Incoming bees were channeled to one side of the hive by a wedge at the entrance, and passages between sides were blocked within 20 cm of the entrance, so that most dances took place within a 50 × 45 cm area on one side of each hive. Two observers rotated between these two viewing areas. To speed the detection of dances, if a bee was not dancing in a selected grid square, the surrounding 8 squares were scanned. If no dances were occurring in these, another square was randomly chosen. Dance direction was recorded as one of 16 "compass points" (eg., upward =N; 22.5°=NNE, etc.). A microcomputer programmed as a stopwatch and data logger was used on the last 3 days of the experiment to record individual dance circuit times comprising a bout of dancing. Each bee was observed until she left the hive, or until at least four consistent bouts of four or more dance circuits were observed. Individual circuit times (or mean circuit times for each bout during the first 3 days) were examined for inconsistent values. Outlier values were discarded (fewer than 10% of observations) and a mean circuit time calculated for each bee.

### Statistics

Foraging distances were not normally distributed. For parametric statistics we used a square root transformation to normalize the Florida (FL) data and a log transformation to normalize the California (CA) data. Means and analyses of variance were computed using the transformed data. The transformed means and 95% confidence intervals were transformed back to linear scale to describe location and dispersion in our data on flight distances (thereby resulting in asymmetrical 95% confidence intervals).

## Results

### Florida study

As judged from the dances sampled inside the hives, the mean distances (95% C.I.) that bees traveled for
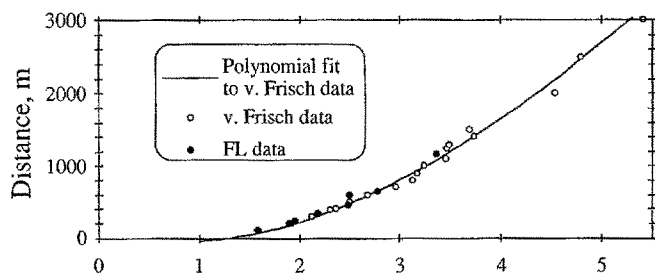


**Fig. 1** Best fit curve of data (*open circles*) from von Frisch (1967, Table 6) used to calculate distance indicated by the waggle dance. *Closed circles* indicate data collected in Coral Gables, Florida, USA
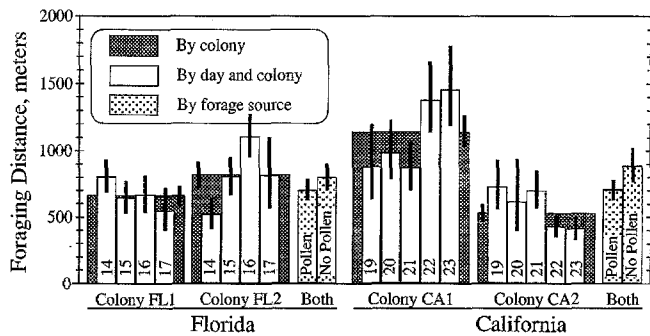
**Fig. 2** Mean flight distance and 95% confidence intervals for the four experimental colonies. Flight distances of pollen and nectar foragers are pooled for each colony and portrayed for each day and for all days pooled. Flight distances of pollen foragers and of nectar foragers are presented separately for all observations in Florida (FL) and California (CA)

pollen and nectar from colonies FL1 and FL2 during 4 days were 664 m (601–731, n=195) and 821 m (735–912, n=220), respectively (Fig. 2). These two distributions of flight distances were significantly different (Table 1). Flight distances differed significantly among days and the interaction between colony number and day of observation (day×colony) was significant (Table 1). The distance flown by bees for pollen (706 m, 638–778, n=242) and for nectar (802 m, 714–895, n=173) were not significantly different (Fig. 2, Table 1).

The scatter of foraging sites is shown on the maps in Fig. 3. Bees foraged most frequently in the suburban residential areas in the north-east and north-west quadrants, less frequently to the south-west, and rarely on the University of Miami campus to the south-east where there were relatively few patches of flowers. "Patch" here refers to a cluster of inferred forage locations, which, given errors inherent in this mapping method (Visscher and Seeley 1981), could be a single point in space or separate nearby points.

A closer examination of the patterns indicates that the two colonies usually did not use the same patches on the same day, although some patches were shared. There are several examples where the two colonies did not share patches. On 14 March, colony FL1 foraged at a site 250–400 m to the south-west, but few dances in colony FL2 indicated this patch. At the same time, colony FL2 foraged approximately 1000 m north while no dances in colony FL1 indicated this site. On 15 March six dances in colony FL2 indicated a patch 300

m north-west while just one dance indicated this patch in colony FL1. On 16 March a patch 300 m to the north-west was indicated by 11 dancers in colony FL2 while no bees in colony FL1 indicated this site. The clearest indication of a shared patch was seen 100–300 m to the east on 17 March. This patch was not visited by either colony on 16 March but 20–30% of the dancers sampled on 17 March indicated this patch (suspected to be a group of flowering palm trees). Also on 17 March, both colonies foraged at a patch 600–900 m north-north-west of the hive.

Within each colony bees shifted among patches on different days. For example, a patch 300 m to the north-west was visited heavily on 15 and 16 March by colony FL2, but it was not foraged on 14 and 17 March. In colony FL1 the entire north-east quadrant was indicated by just three bees on 14 March, but on 15 and 16 March patches in the quadrant were visited heavily.

## California study

Flight distances differed significantly between colonies CA1 and CA2: 1138 m (1035–1251, n=219) and 534 m (484–588, n=218), respectively (Fig. 2, Table 1). There was a significant day×colony interaction. The striking differences in foraging patterns of the two colonies are clearly shown on 22 and 23 February (Fig. 3). The bees from CA1 were scattered widely over long distances, while in CA2 the flight distances were shorter and foraging sites were more concentrated. The bees flew significantly different distances for pollen (703 m, 645–767, n=240) and nectar (895 m, 785–1020, n=200) (Fig. 2, Table 1).

The two colonies rarely shared patches on the same day. An exception was on 20 and 21 February when both colonies used a patch about 300 m to the south-west. These colonies, although closely matched, visited different sites for food and flew very different distances.

## Discussion

### Forest-suburban Comparisons

One goal of our study was to compare the foraging of a colony in a New York temperate deciduous forest

**Table 1** Analysis of variance performed on the foraging distances. Data were transformed to improve normality and homoscedasticity; square root of distance was used for Florida (FL) data and log distance for California (CA) data.

| Source of Variation | Florida | | | California | | |
|---|---|---|---|---|---|---|
| | df | F value | P value | df | F value | P value |
| Colony | 1 | 4.280 | 0.0392 | 1 | 79.259 | 0.0001 |
| Day | 3 | 3.214 | 0.0229 | 4 | 0.005 | 0.9999 |
| Day×colony | 3 | 7.352 | 0.0001 | 4 | 11.440 | 0.0001 |
| Resource (pollen or nectar) | 1 | 1.807 | 0.1796 | 1 | 4.062 | 0.0445 |

(Visscher and Seeley 1982) with foraging by colonies in an environment with a different spatial pattern and abundance of flowers. We observed differences in both foraging distances and distributions of bees among resource patches.

Foraging distance.

The flight distances we inferred from dances in this study were shorter than those recorded in the temperate forest. In the forest, the mean±SD of daily median distances was 2178±1543 ($n$=34 days) (P. K. Visscher, unpublished work). For colonies FL1, FL2, CA1 and CA2, respectively, they were 750±73 ($n$=4 days), 935±269 ($n$=4), 1413±372 ($n$=5), and 745 ±192 ($n$=5). Higher densities of flowers in our areas may explain this pattern. Flight distances would be expected to be a function of the proximity of flowers to the hive and of the quality of nearby patches relative to those farther away. Short flight distances also have been observed in fields of agricultural crops where the density of flowers is high (Free 1970). Finally, flight distance may be a function of colony size because smaller

colonies have fewer foragers (Michener 1974), and our colonies were smaller than the one used by Visscher and Seeley (1982).

Forage patches

Visscher and Seeley (1982) and Schneider (1989) concluded that the foraging patterns they observed suggest that a colony monitors a large area and focuses its foraging effort on a small number of flower patches. These conclusions were based on the concentration of foragers on relatively few patches, and on the rapid turnover of the patches in use. In this study, the forage maps do not display as strong a pattern of concentration on a few patches. For example, on the maps for CA1 on all days and for FL1 and FL2 on 15 and 16 March, the forage patches are widely scattered and are often represented by a single dance record. On other days there is considerable clumping, such as in CA2 on 21–23 February, or the FL colonies on 17 March. This difference in dispersion of foragers may arise from differences in the spatial patterning of flowers. The areas surrounding our colonies had many residential gardens
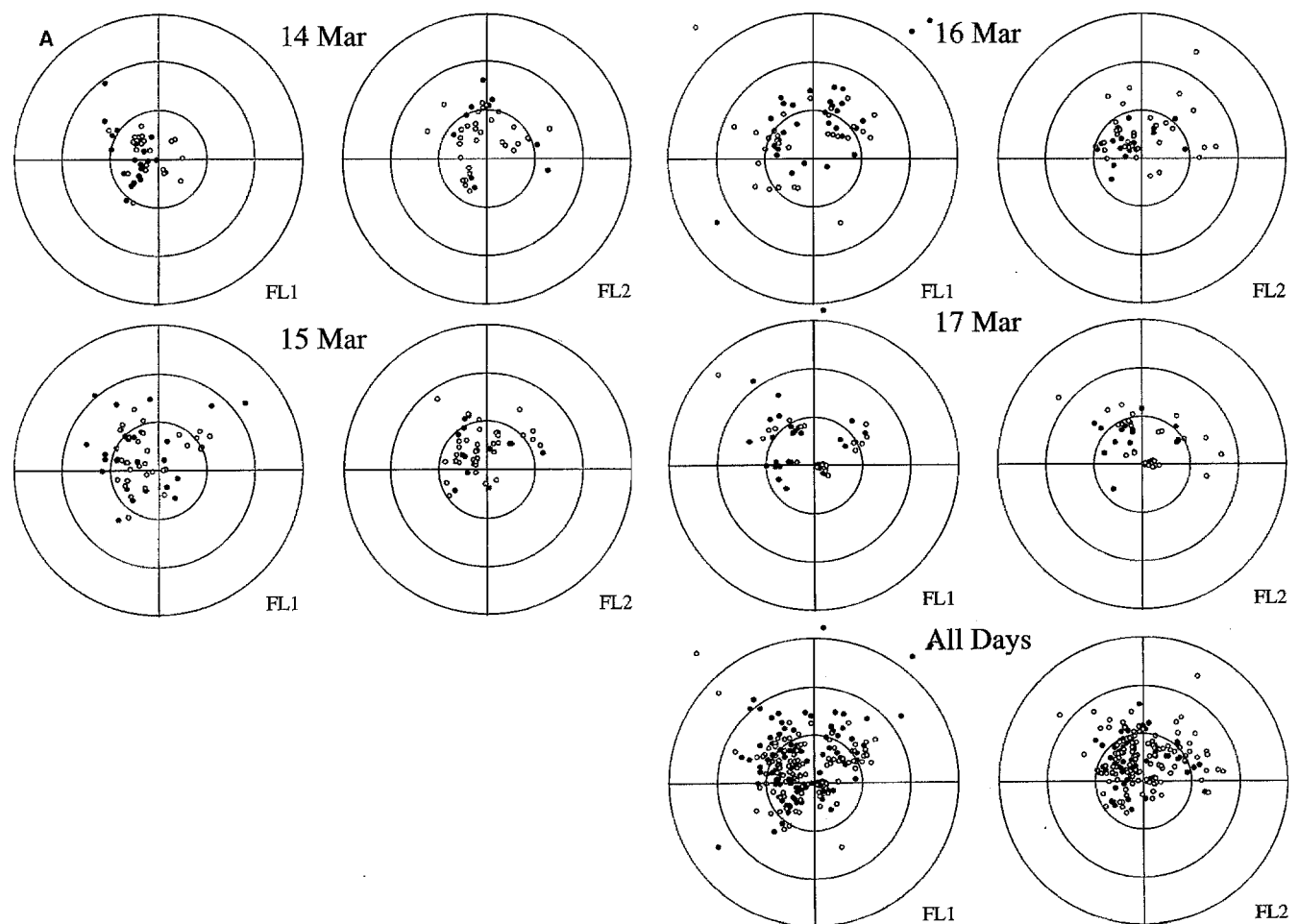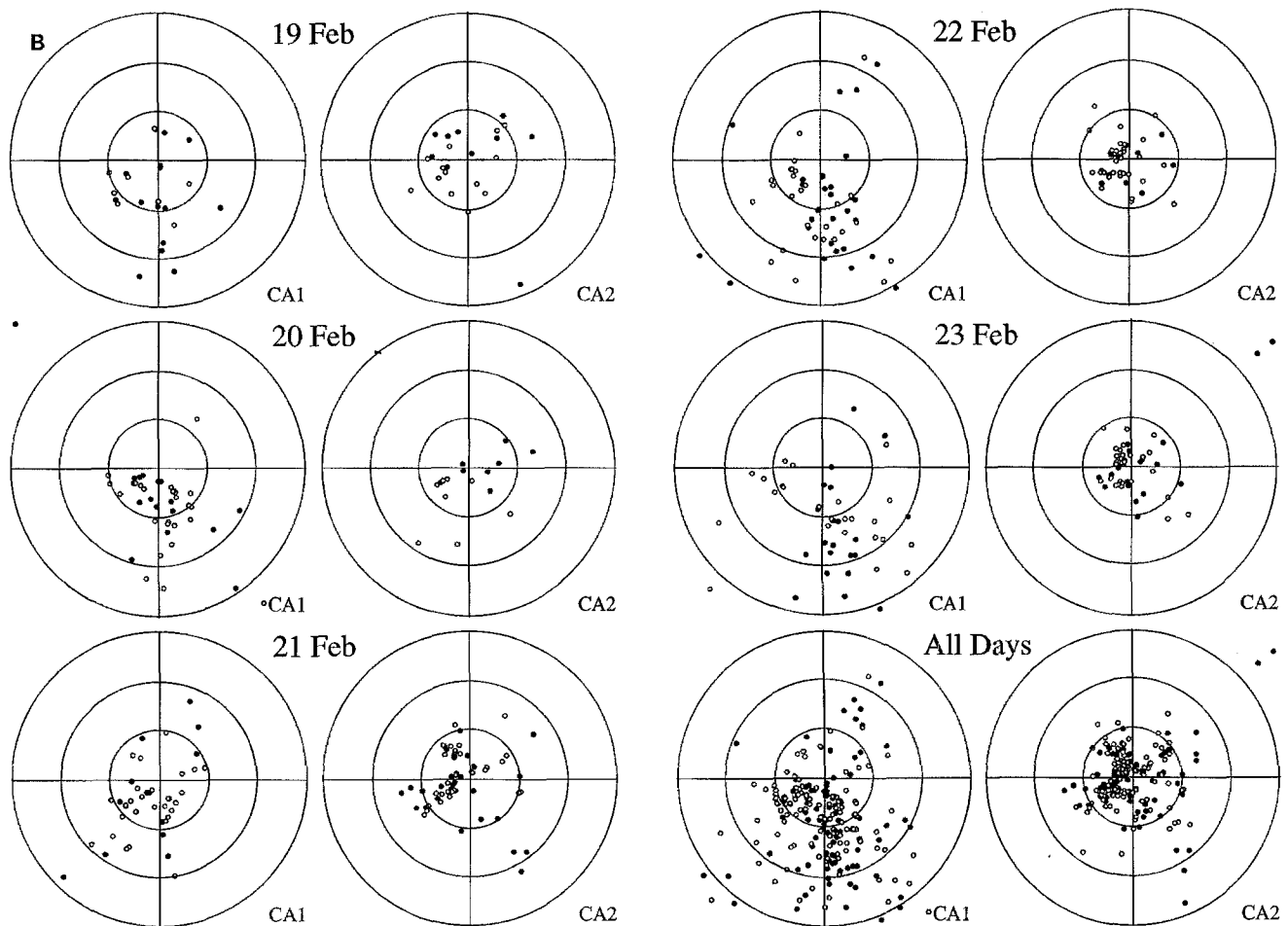


**Fig. 3** Continued

**Fig. 3** Polar coordinates of the foraging positions inferred from waggle dances in two adjacent hives in **A** Coral Gables, Florida, 14–17 March 1989, and **B** Riverside, California, 19–23 February 1991. *Concentric rings* denote distance (1-km intervals) from the hives at the center of the plot. *Open circles* indicate pollen foragers and *closed circles* indicate nectar foragers (no pollen carried during dance). On the CA plots, 8 of 219 records are out of range for the colony CA1 and 3 of 218 for the colony CA2

and flowering trees. This situation led to many relatively small patches of flowers. Although we made no quantitative comparison of the habitats, the large scale flower densities were almost certainly higher and flower patches more available in our habitats than in the New York forest.

A pattern of many small, rich (or equal) patches of flowers would be expected to have two interesting effects on foraging. First, a large proportion of patches would be above the profitability threshold for individual foragers and so individuals will continue to exploit them. Second, small, as compared to large patches, would be more difficult for recruits to locate, so they would more likely go to the "wrong" patch. This would further disperse the colony's foraging effort. It may be that in a foraging environment like ours, recruitment is less important in assembling information and precisely directing the colony's foraging. Less food might be retrieved as a result of recruitment, and a smaller proportion of the colony's foraging directed by recruitment. Because recruits often take several unsuccessful

trips after following dances and before finding food (Seeley and Visscher 1988), a relatively rich habitat with high dispersion of patches would increase the proportion of recruits that found a patch different from the one visited by the recruiting bee whose dances they followed.

The differences we observed between the foraging of adjacent, matched colonies suggest that comparative data on the distribution of foragers need to be interpreted with caution. Schneider (1989) studied the distributions of foraging African honey bees in Botswana and compared their foraging distances with those of European bees in New York (Visscher and Seeley 1982). Schneider concluded, albeit with some caution, that African bees forage over a smaller area and tend to forage closer to the hive than do European bees. However, in our study, bees from the two matched FL colonies, foraging in the same resource environment, exhibited different flight distances on different days, and bees from one CA colony flew, on average, twice the distance of bees from its matched colony. In

quite different environments, the foraging patterns of European honey bees vary tremendously, as shown by the comparison of our results with those of Visscher and Seeley (1982). Even Schneider (1989) used two colonies at different times in the same location and recorded very different flight distances. This variety of findings suggests caution in making comparisons between subspecies and between genetic lines of bees when the results are taken at different times, in different places. Such comparisons require replicate colonies of both races in the same place and at the same time.

## Patch turnover

Over successive days the distribution of foragers from each of our colonies changed. This pattern was reported by Visscher and Seeley (1982) and Schneider (1989). The rapid turnover of resources can support the idea that recruitment serves to pool information and increase the average richness of sites visited by focusing foraging on rich new finds. The daily shifts in the colonies' foraging efforts could be viewed as a contradiction to the idea that the recruitment system played a lesser role in our colonies. However, daily change in pattern would also be expected in groups of animals without a recruitment system, such as bumblebees, if the individual foragers are sensitive to the profitability of flowers and accept and reject flowers (and whole patches of flowers) based on their profitability. Thus, the observed shifting pattern of resource use is also consistent with a recruitment system that plays a lesser role in directing foragers.

The critical role of recruitment for colony-level foraging is that, by reducing search costs, recruitment makes it profitable to switch earlier from a declining resource. In a habitat with many small rewarding patches this relative advantage would be smaller because search costs of bees locating new resources, either without dance information or as a "mistake" after following dances, are already low.

Another potential ecological role of recruitment is that it may allow colonies to rapidly exploit bonanzas in competition with other nectarivores. This kind of effect is illustrated in our study by the sudden shift of much of the foraging of both FL1 and FL2 to a new small patch on 17 March. Thus it may be that even in an environment where recruitment has less impact much of the time, colony food collection may be strongly affected by recruitment to particularly rich resources, and the colony's ability to compete with other pollen/nectar feeders may be enhanced.

## Adjacent colony comparisons

Another of the principal goals of this study was to compare the distribution of foragers in similar colonies for-

aging at the same time in the same habitat. Implicit in the picture developed by prior studies is the expectation that if colonies pool reconnaissance from an exhaustive survey of the available forage around their nests, and focus their foraging on the richest of the sites they have found, then the sites visited by two colonies in the same environment should be the same. This expectation is strongly contradicted by our findings. The distributions of foragers from adjacent hives are strongly dissimilar except in the FL colonies on 17 March. Below we discuss two possible explanations for different foraging patterns of adjacent colonies: that the colonies find different resources and that they choose different resources.

## Find different resources

Different patches may have been chosen by different colonies because the colonies' search is not complete, so that bees from each colony simply found different resources from which to choose. The data of Seeley (1988) indicated that bees can find small isolated food patches, suggesting that a search, even over a large area, is likely to be complete. However, Seeley's study took place in an environment of low resource density. Sampling limitations would probably increase when resources are numerous relative to the capacity of single colonies to discover and exploit them. Our study may have represented such a situation, with so many rich patches in our study sites that it might be unlikely that bees from different colonies would choose the same patch. Nonetheless, strong differences in foraging distance would not be expected to result from this kind of sampling error, without biases with regard to where each colony searched. Recruitment, even when it does not send bees to the same patches advertised by the recruiting bees, probably does provide some positive feedback which helps maintain distribution differences. Colonies with important distant resources are likely to discover other distant resources in the same direction through recruitment errors, since recruits presumably gain and use some information from dances they have followed in searching for forage, even when they are not successful in locating the same patch. Colonies which only exploit nearby sites, however, would be less likely to discover new distant sites through recruit error. Thus, while sampling effects do not predict consistent distance or direction differences in the sites discovered by different colonies, they could provide initial biases which are reinforced by positive feedback and lead to marked differences.

## Choose different resources

If colonies do find the same resources, but allocate foragers differently among them, this could reflect colony

specific payoffs in the resources at different sites. Such a situation could arise from colonies having different nutritional needs. We examined this possibility in our data by comparing the proportions of pollen foragers in the dance records to see whether more foraging was allocated to pollen collection in one colony than in the other. In CA colonies there was no significant difference (CA1 52% vs CA2 58%, $x^2=1.69$, $P=0.19$), but in FL colonies there was a difference (FL1 68% vs FL2 50%, $x^2=13.3$, $P=0.0003$). Different nutritional needs could account for some of the difference in foraging patterns we saw, but this does not explain differences in the location of nectar sources exploited.

Colony-specific payoffs might also be influenced by historical factors. Once a colony discovers and begins to exploit a resource, their efficiency at foraging on it probably increases. At the same time, the available reward decreases because of foraging bees. Thus, foragers from the second colony to discover the resource would realize lesser initial benefits than encountered by the first colony, and greater costs than the bees from the first colony which continue to work the resource, leading to a strong difference in colony payoff.

## Conclusions

The patterns we observed in resource visitation by similar colonies foraging in the same environment suggest some alterations in our picture of honey bee recruitment. A colony's foraging behavior, quantified as where bees fly for food, is likely determined by many factors including the nutritional status of the colony, the distribution of pollen and nectar, the colony size, random aspects of the process of gathering information on resources, and the foraging behavior and density of competing bees. Heritable variation may also play a role (Page and Robinson 1991). The status of several environmental factors may influence the role of the recruitment system. When resources are plentiful and arrayed in small patches, the recruitment system may be less important in influencing the colony's acquisition of food than when forage is scarce or there are rich bonanzas. Errors in recruitment may play an important role in the foraging dynamics of colonies, and this role is likely to be dependent on the distribution of resources available. Recruitment behavior need not underlie shifts in the foraging behavior of groups, but does have the potential to enhance the competitive success of honey bee colonies by making such shifts more rapid, enabling exploitation of ephemeral, rich rewards, enhancing tracking of a changing resource landscape, and making more efficient discovery and selection of resources of higher average quality than would otherwise be exploited.

This study suggests several questions that should be addressed with field studies to advance our understanding of the role recruitment plays in the ecology of foraging honey bees. What are the economics of switching from a declining resource and discovering and exploiting a new one? How do foraging rewards for experienced bees and newcomers change with time in patches of flowers? How much is resource collection affected by experimentally obstructing recruitment communication? Is the whole colony's foraging reflected in the recruitment dances or is a large proportion of foraging proceeding without recruitment? Results of studies designed to answer these questions will complement knowledge on the mechanisms by which honey bees perform and read dances, and how they process information about resource availability and colony needs, and increase our understanding of the behavioral ecology of honey bee dance language.

## References

Free JB (1970) Insect pollination of crops. Academic Press, New York
Frisch K von (1967) Dance language and orientation of bees. Belknap Press, Cambridge, Massachusetts
Michener CD (1974) The social behavior of the bees. Belknap Press, Cambridge, Massachusetts
Page RE, Robinson GE (1991) The genetics of division of labour in honey bee colonies. Adv Insect Physiol 23:117–169
Schneider SS (1989) Spatial foraging patterns of the African bee, *Apis mellifera scutellata*. J Insect Behav 2:505–521
Seeley TD (1985) Honeybee ecology: a study of adaptation in social life. Princeton University Press, Princeton
Seeley TD (1986) Social foraging by honey bees: how colonies allocate foragers among patches of flowers. Behav Ecol Sociobiol 19:343–354
Seeley, TD (1988) The effectiveness of information collection about food sources by honeybee colonies. Anim Behav 35:1572–1575
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
Seeley TD, Camazine S, Sneyd S (1991) Collective decision-making in honey bees: how colonies choose among nectar sources. Behav Ecol Sociobiol 28:277–290
Visscher PK, Seeley TD (1982) Foraging strategy of honeybee colonies in a temperate deciduous forest. Ecology 63:1790–1801

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