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## FORAGING STRATEGY OF HONEYBEE COLONIES IN A TEMPERATE DECIDUOUS FOREST<sup>1</sup>

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**Abstract.** To understand the foraging strategy of honeybee colonies, we measured certain temporal and spatial patterns in the foraging activities of a colony living in a temperate deciduous forest. We monitored foraging activities by housing the colony in an observation hive and reading its recruitment dances to map its food source patches. We found that the colony routinely foraged several kilometres from its nest (median 1.7 km, 95% of foraging within 6.0 km), frequently (at least daily) adjusted its distribution of foragers on its patches, and worked relatively few patches each day (mean of 9.7 patches accounted for 90% of each day's forage). These foraging patterns, together with prior studies on the mechanisms of honeybee recruitment communication, indicate that the foraging strategy of a honeybee colony involves surveying the food source patches within a vast area around its nest, pooling the reconnaissance of its many foragers, and using this information to focus its forager force on a few high-quality patches within its foraging area.

**Key words:** *Apis*; central-place foraging; feeding behavior; foraging strategy; honeybee; recruitment communication; social foraging; social insect ecology.

### INTRODUCTION

Increased feeding efficiency through cooperative foraging has often been suggested as a prime mover in the evolution of sociality (Alexander 1974, Wilson 1975, Bertram 1978). Within the social insects, mechanisms of joint food retrieval are particularly striking and diverse. Past studies in this area (reviewed by Wilson 1971, Hölldobler 1977) have primarily analyzed the mechanisms of recruitment communication (such as laying odor trails, piloting other foragers, or performing symbolic dances). Only a relatively few studies (see review by Heinrich 1978; also Cherrett 1968, Johnson and Hubbell 1974, 1975, Bernstein 1975, Rockwood 1976, Davidson 1977, Taylor 1977, 1978, Hubbell and Johnson 1978, Heinrich 1979, Hölldobler and Lumsden 1980) have related these mechanisms to the underlying strategies of foraging as a colony and their ecological significance. ("Strategy" here denotes a set of coordinated adaptations which, taken together, characterize an organism's adaptive solution to an ecological problem, e.g., how to harvest its food efficiently.) This imbalance in studies of insect social foraging is perhaps most striking for honeybees (*Apis* spp.).

When a honeybee worker returns to the colony from a rich food source, she communicates the direction and distance of that source to her nestmates by means of the famous dance language recruitment system. Many of the details of foraging behavior in honeybees, such as how individual bees perform and read the

dances, orient to flowers in the field, and make decisions about the value of available forage, have been analyzed, most notably by Karl von Frisch and his associates (reviewed by von Frisch 1967). It is clear that the dance language provides mechanisms for a honeybee colony to integrate the foraging activities of its many thousands of members. Although von Frisch discusses how these mechanisms might fit together in the colony's choice of forage, relatively little is understood about the overall organization of a colony's foraging, and how this strategy helps facilitate a colony's food collection.

To identify the social foraging strategy of honeybee colonies, we measured certain temporal and spatial patterns in the foraging activities of a full-sized colony living under natural conditions. These include: (1) the spatial distribution around the nest of the food source patches used by a colony, (2) the temporal pattern of turnover in these patches, (3) the number of patches in use each day, (4) the day-to-day pattern of labor allocation to these patches, and (5) the temporal variation across the summer in overall food availability and colony foraging activity. Knowledge of these patterns, combined with an already intimate understanding of the honeybees' recruitment mechanisms, sheds new light on the social foraging strategy of these insects in terms of energetics, division of labor, and the ecological significance of their unique dance language recruitment system.

### STUDY SITE

Previous field studies of honeybee foraging have concentrated on the interaction of honeybees with agricultural crops (reviewed by Free 1970) or artificial

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feeding stations (von Frisch 1967). Very little is known about the way of life and the ecological interactions of honeybees in a natural habitat. We feel that the temperate forests of North America may provide the best available setting for ecological study of the European races of *Apis mellifera*; feral colonies have probably been abundant in the forests of the northeastern United States since their introduction >300 yr ago (Oertel 1980), but are now rare in Europe (Ruttner 1973), due to competition from a dense population of domestic colonies. This study is concerned with the foraging of honeybees under primarily nonagricultural conditions.

The study colony was situated near the center of the Arnot Forest (42°17'N 76°39'W, altitude 585 m), a 1637-ha research preserve owned by Cornell University, near the town of Cayuta, Schuyler County, New York, USA. Most of this tract and much of the surrounding area is forested, with forest types ranging from young old-field successional forest to pine (*Pinus strobus*) plantations and mature mixed-hardwood forests (Fig. 1; Odell et al. 1980).

#### METHODS

The heart of our experimental procedure is the daily mapping of a colony's food source patches by reading the recruitment dances of bees in the colony. This was accomplished by establishing a large colony in an observation beehive, calibrating the relationship of forage site distance to recruitment dance tempo, and appropriately sampling, recording, and interpreting the colony's recruitment dances.

##### *Observation hive construction*

Our observation hive (similar to that in Seeley 1979; Fig. 1) had a comb area of 13 496 cm<sup>2</sup> and an internal volume of 40.27 L, chosen to be near the median volume of feral honeybee nests in this region (Seeley and Morse 1976). To enable us to see all recruitment dances in the hive, the entrance was fitted with a block which forced all traffic to enter and leave from one side of the comb. Passage between the two sides of the comb was restricted; all passageways within 60 cm of the entrance were blocked with beeswax. These measures directed all dancers to a well-defined "dance floor" near the entrance on one side of the hive. A grid of 5 cm sided squares, 9 squares high by 10 squares wide, was drawn on the glass of the hive over the dance floor. Counts of dancers throughout the summer indicated that 94% of them danced within this grid. The hive was insulated by removable double glazing, and, when not under observation, by styrofoam panels. Bees entered the hive through a rectangular tunnel 300 mm long, 50 mm wide, and 25 mm high constructed of transparent plastic. The entrance tunnel was fitted with a removable pollen trap consisting of a piece of 5-mm mesh which could be inserted across the entrance tunnel, forcing the bees to squeeze through the holes in the mesh. This knocked the pollen from the corbiculae

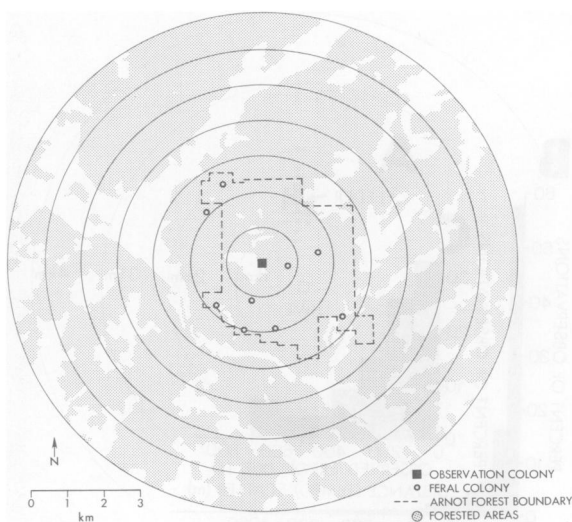


FIG. 1. Map of the study area. Stippled areas are forests; note that most of the area of this map is forested. The feral colonies were censused only within the Arnot Forest; many other colonies undoubtedly are present elsewhere on this map.

of a fraction of the bees. These pollen pellets then fell through the 4-mm mesh floor of the tunnel under the trap. Pollen collections were taken only as needed to secure samples of all pollens seen in the hive; the trap was in place <10% of the time. Since collection efficiency was low, and few bees were stripped of both pollen pellets, the influence of pollen trapping on either the hive's demand for pollen or representation of pollens in our sampling was minimal.

##### *Hut for observation hive*

To protect the observation hive from sun, rain, and cold, it was housed in a 2 × 1.7 × 2 m hut with a roof constructed of translucent corrugated fiberglass panels (Barclite 400, white). These diffuse sunlight sufficiently to eliminate light-dependent misdirection (von Frisch 1967) in the recruitment dances. The 95% confidence interval (calculated by the methods of the Watson test, Batschelet 1965) for the mean vector bearing of nine dances of bees trained to a feeder 80 m from the hive was small (176.45° ± 3.56°) and included the feeder direction (177°), indicating that the bees oriented their dances exclusively with respect to gravity, reflecting the changing sun azimuth, but not the sun's angle relative to the comb, as they would have if they had seen the sun while inside the hive.

##### *Bees used and calibration of the distance-tempo curve*

Our bees came from the apiaries at Cornell University. Though their precise racial composition cannot be specified, they were probably hybrids of *Apis mellifera ligustica* with *A. m. caucasica*, *A. m. carnica*, and *A. m. mellifera*. The bees were dark brown. The colony, which numbered ≈20 000 individuals, was

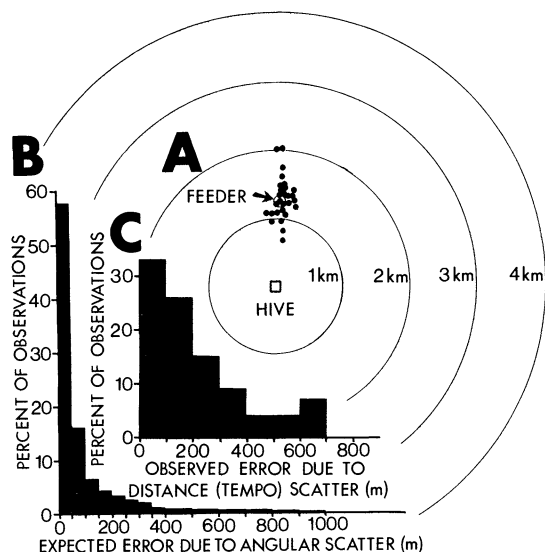


FIG. 2. (A) Scatter of recorded dances for a known feeder location. (B) Expected frequency distribution of errors due to angular scatter for the distances in this study. (C) Observed frequency distribution of errors in the indication of distance.

placed in the forest on 6 June 1980, and had 6 d to orient before we began observations.

Since the relationship between dance tempo (the speed with which circuits of the recruitment dance are performed) and distance to a food source varies among honeybee races (von Frisch 1967), we needed to calibrate our bee colony. We did this by training bees to a feeding station a known distance from the hive (using techniques similar to those described by von Frisch 1967 and Gould 1976), marking the bees visiting the feeding station, and timing their dances (as described below) in the observation hive. This was repeated at nine distances between 100 and 1500 m;  $41.7 \pm 15.8$  dance bouts (here and throughout, numbers of this form denote the mean  $\pm 1$  SD) of five circuits each were timed for each feeder distance. To translate dances to distances beyond those used to calibrate our bees, we used the data of von Frisch (1967:69), with which ours converged (Visscher 1982).

#### Dance selection and recording techniques

To randomly sample the colony's dances, we selected squares of the dance floor grid with a random number table, until a square in which a bee was performing a recruitment dance was selected (5% of the numbers corresponded to the area outside the grid). We timed this bee's dance circuits with an electronic lap timer until she left the hive, or until we had consistent times from at least four bouts containing four or five dance circuits each. We recorded the angle of the waggle run relative to vertical as 1 of 32 divisions of a circle.

For each dance the information recorded included time of day, angle of dancing, durations and number of circuits for several bouts of dancing, and color of pollen, if any, borne on the bee's corbiculae. Overall, we recorded  $2.54 \pm 1.32$  bouts per bee with  $3.99 \pm 1.19$  dance circuits per bout. We recorded the dances of bees continually from 0800 to 1700 each day for four 9-d periods spanning the 1980 summer: 12–20 June, 9–17 July, 28 July–5 August, and 19–27 August.

#### Construction of forage maps

Maps of the sites for which we observed recruitment dances were constructed as follows. The sun azimuth at the time of each dance recording was computed using a program for the Hewlett-Packard 97 calculator. Sun azimuth was added to the recorded dance angle to yield the bearing to the food source. Dance tempo recordings were converted to units of seconds per dance circuit. Within a series of tempo measurements for a single bee's dances, obviously inconsistent values were discarded, and the remainder averaged. This average was then related to distance, using our calibration curve. Finally, the pollen color was noted, and an appropriate symbol plotted from the bearing, distance, and pollen color information. Because pollen-bearing bees perform most of their recruitment before depositing their pollen loads in the comb for storage ( $91.7 \pm 9.3\%$  of the total duration of dancing is performed before unloading pollen;  $N = 10$  dancers), bees dancing without pollen would usually, but not always, be bees that had foraged exclusively for nectar. In most cases pollens were identified only by color, and microscopic determination of the source plants has not been done. We do know, however, that the pollen designated yellow-grey in Fig. 4 came from *Rubus* spp., since we found bees foraging on *Rubus* and gathering yellow-grey pollen in the locations indicated by dancers bearing yellow-grey pollen. Similar confirmations were made on birdsfoot trefoil (*Lotus corniculatus*) and alfalfa (*Medicago sativa*) during other observation periods, and these increase our confidence in the accuracy of our mapping techniques.

#### Error analysis

There is some scatter inherent in the dance language of honeybees, and some introduced by approximations and errors in our recording techniques. To assess the total scatter, dances to a known feeding station were recorded and plotted using the techniques outlined above. This work was done in January 1981, at the Archbold Biological Station, Lake Placid, Florida, USA, with a different colony of bees than was used in the rest of the study. The bees were trained to a feeder 1250 m from the colony. Because of intercolony differences in dance tempo this distance corresponded to a different dance tempo than we had found for the other colony used, and in construction of the plots of dances to this feeder we made the assumption that the



tempo–distance curve was parallel to that which we had previously calibrated. This is a fairly robust assumption, and small differences in the calibration curve’s slope would affect the conclusion of our scatter analysis only little. The scatter in the inferred location from recruitment dances to this known single point is shown in Fig. 2A.

The absolute magnitude of plotting error for a given angular error increases with increasing distance. Fig. 2B depicts the expected distribution of errors in the 1871 points on the forage maps that would result from the superposition of the angular scatter in Fig. 2A and the distance distribution of points inferred in the Arnot Forest study. Fig. 2C depicts the frequency distribution of observed error in the indication of distance in Fig. 2A. Overall, 90% of the plotted points fall within 500 m of the feeder’s true location. A careful examination of the forage maps confirmed that the indicated locations make sense in terms of the topography and the presence of clearings, plantings, and watercourses in the surrounding area.

Activity measurements

During each day of observation we made 10 hourly measurements of the level of recruitment, flight, and pollen collection activity. We recorded the following items: five counts of bees leaving the colony through the entrance tunnel in 30 s, five counts of bees performing recruitment dances in the hive (both inside and outside of the sampling grid), and two counts of bees returning to the colony with each color of pollen in 1 min.

Surrounding colonies, bee tree hunting

During the summer and fall of 1978 we censused the population of feral bee colonies inhabiting the Arnot Forest. Using a modification of bee-lining techniques (Edgell 1949), we fed captured foraging bees scented 2 mol/L sucrose syrup and then released them to return to their colony. Usually some bees would eventually return to the comb feeder, recruiting nestmates as well. Once bees were well oriented to the feeder, they would leave in a beeline homeward, and we would record a vanishing bearing for these bees; this was approximately the direction to the colony. Distance to the colony could be estimated from the minimum round-trip time of individually marked bees.

To census the colonies within the Arnot Forest, we systematically initiated beelines from open areas spaced throughout the forest, usually <1 km apart. Often in a single patch of flowers we initiated beelines from several different colonies. Once the beelines were established, foragers at the feeder were again trapped, and carried along one of the beelines to another clearing. Here the bees were again released, and their vanishing bearings noted. By repeating such moves, the tree which the colony inhabited could be located. In areas of uninterrupted forest this technique was diffi-

TABLE 1. Correlations between (1) sums over 9 d of 10 hourly counts per day of incoming bees bearing each color of pollen and (2) number of dancers recorded during the 9-d period bearing that color of pollen. Pearson’s *r* as an estimator of this parameter requires no assumptions, and is appropriate to indicate the degree of linear relationship. Spearman’s *r<sub>s</sub>*, a distribution-free estimator, is used to evaluate the significance because neither variable is expected to be normally distributed, as hypothesis tests with Pearson’s *r* require.

| Observation period | Pearson’s product-moment correlation coefficient ( <i>r</i> ) | Spearman’s rank correlation coefficient ( <i>r<sub>s</sub></i> ) | Significance level (for <i>r<sub>s</sub></i> ) | Number of pollen colors |
|--------------------|---------------------------------------------------------------|------------------------------------------------------------------|------------------------------------------------|-------------------------|
| 12–20 June         | .997                                                          | .943                                                             | <.005                                          | 6                       |
| 9–17 July          | .763                                                          | .904                                                             | <.001                                          | 10                      |
| 28 July–5 August   | .671                                                          | .745                                                             | <.010                                          | 10                      |
| 19–27 August       | .966                                                          | .942                                                             | <.001                                          | 13                      |

cult and time consuming, and we relied instead on triangulation: locating the colony from intersecting vanishing bearings from widely spaced locations in the forest.

The census appears to have been exhaustive. Bees from all nine colonies located in either of the two ways described above were captured at  $2.7 \pm 0.7$  locations in the forest, and this redundancy reassured us that there were not colonies in the forest whose members we did not capture. The four precisely located bee trees confirmed the accuracy of the triangulation technique; in these cases triangulation indicated a point within 200 m of the bee tree. The locations of the nine feral colonies in the study site are indicated in Fig. 1.

Scale hive techniques

In 1979, we recorded the daily changes in mass of a hive of bees in a wooded area 30 km from the Arnot Forest from 27 May to 6 October. Because the phenologies of major nectar sources are similar throughout this region and fairly consistent year to year, these data are useful in interpretation of the Arnot Forest results, and provide an appropriate independent measure of the variability in forage available throughout a summer. Each evening at 2100 the mass of the hive, the mean temperatures for the hours 0600–1200 and 1200–1800 (estimated from continuous thermograph recordings), and the weather (wind, sun, and rain) for the day were recorded. The bulk of each daily mass change represents nectar gathered or honey consumed.

RESULTS

Foraging and dance activity correlations

There were close correlations (Table 1) between number of foragers returning with pollen of a given

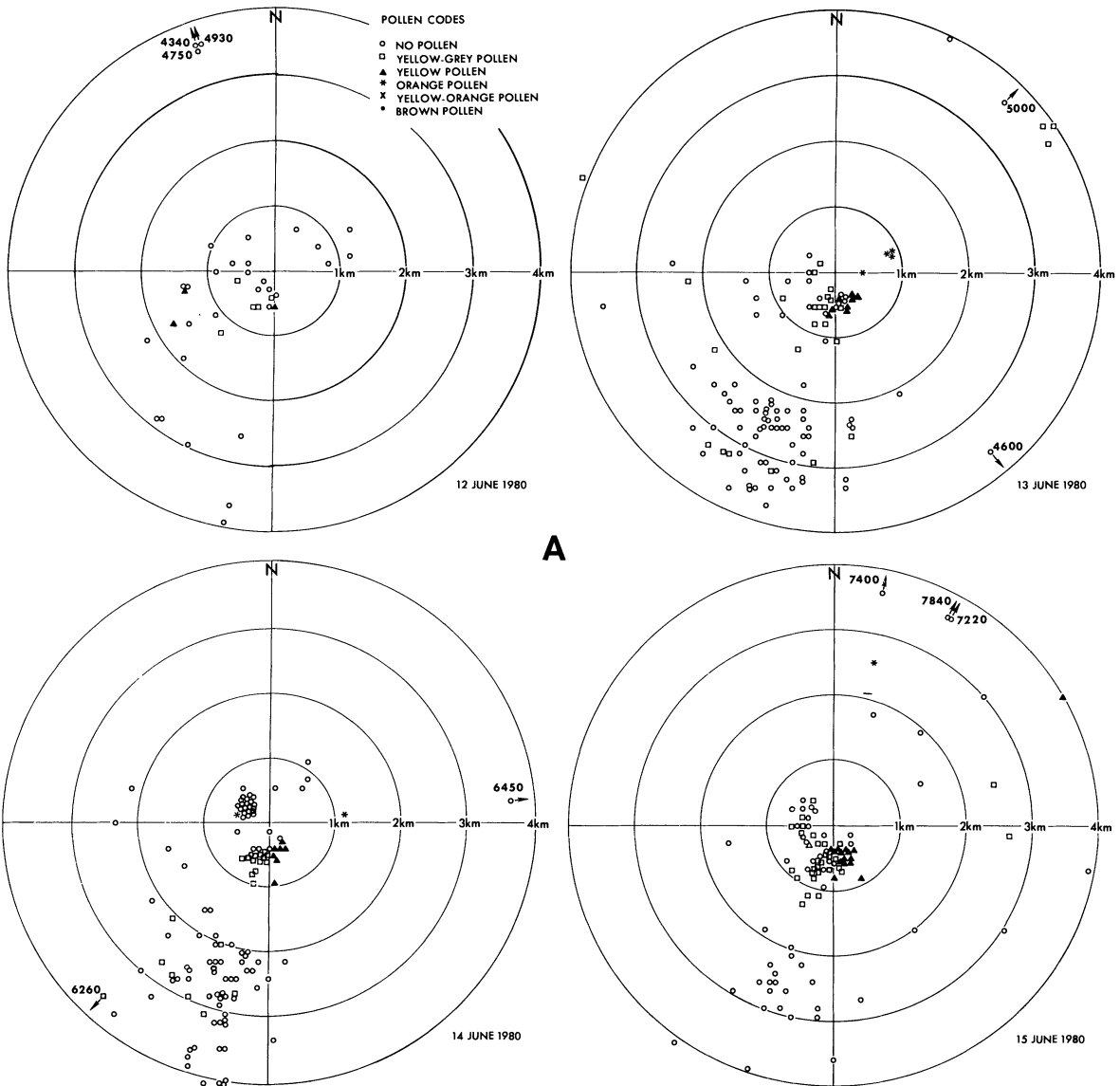


FIG. 3. Maps of the foraging locations inferred from honeybee recruitment dances. Different symbols code the colors of pollen, if any, borne by the dancing bee. Locations beyond the edge of each map are indicated by arrows next to the

color and number of dancers observed with that color of pollen. This supports the validity of describing the foraging patterns of a colony based only on reading its recruitment dances. If a substantial proportion of the food sources in use by a colony were not being recruited to, we would not expect the correlations to be so close, except in the unlikely event that the distribution of pollen colors was the same among sources with and without recruitment.

#### Forage maps

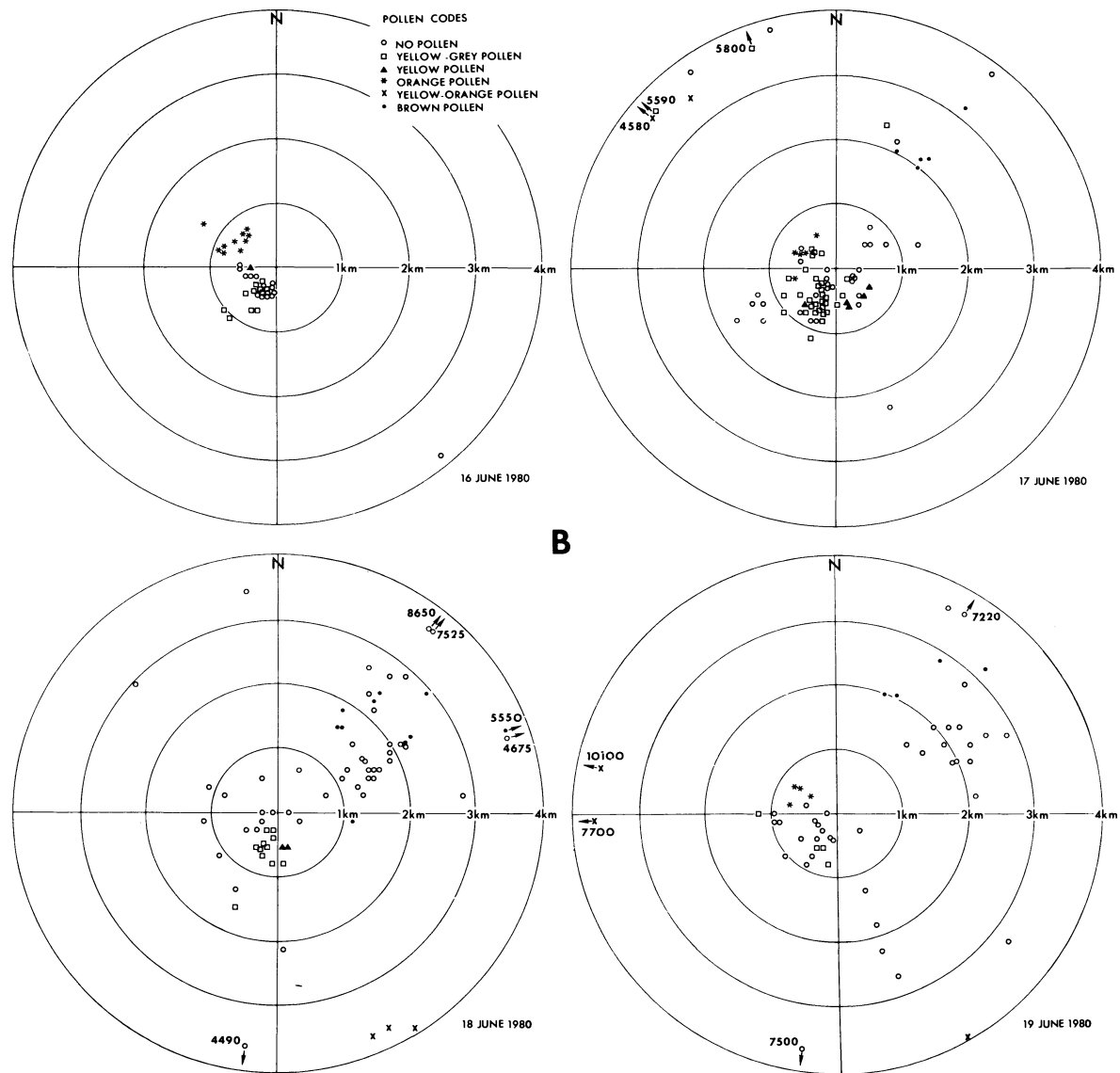
Thirty-four forage maps were constructed for 36 d of observation, divided into four 9-d periods. (The days 20 June and 29 July were entirely rainy, and the bees did not forage.) Overall, 1871 forage locations were

plotted (637, 517, 345, 372, respectively, for the four periods). Eight of these maps, from 12–19 June 1980, are presented in Fig. 3.

These maps reveal that the overall pattern of a colony's foraging is a rapidly changing mosaic of food source patches. A day-by-day commentary follows, accompanied by the mean and median distance recorded for each day.

*12 June.*—There are relatively few points because the colony was observed for fewer than the 9 h recorded other days (mean distance = 1542 m; median = 1120 m).

*13 June.*—Here the patterns of forage are well established. Most foraging occurs in the open areas



appropriate pollen symbol and a number indicating the distance in metres from the colony to that food source. (A) 12–15 June 1980. (B) 13–19 June 1980.

(Fig. 1) SSW of the hive near the colony, and in a valley bottom and ridge to the SSW at 2.5–3.5 km. The NNW patches visited on 12 June are not represented, and two new patches to the NE are present (mean distance = 2031 m; median = 2030 m).

14 June.—None of the distant NE sites evident on 13 June was seen. A new patch near the hive to the NW has become important (mean distance = 1806 m; median = 2030 m).

15 June.—The food sources to the SSW are less dominant; several dances for sites between 7.2 and 7.8 km are present to the NNE (mean distance = 1478 m; median = 680 m).

16 June.—The weather this day was cool with intermittent rain, so the bees foraged relatively little

and only fairly close to the colony. The source of orange pollen to the NW, which had received only one dance before, became a major source (mean distance = 666 m; median = 510 m).

17 June.—The source to the SSW, which had figured strongly before the contraction of foraging range with poor weather on 16 June, does not reappear. Several sources to the NE, both near and far, and distant sources to the NW, appear for the first time (mean distance = 1971 m; median = 1560 m).

18 June.—The orange pollen source near the colony to the NW has disappeared, as have the distant sources to the NW. A new patch of yellow-orange pollen sources has appeared at 3.7 km to the SE (mean distance = 1836 m; median = 1540 m).

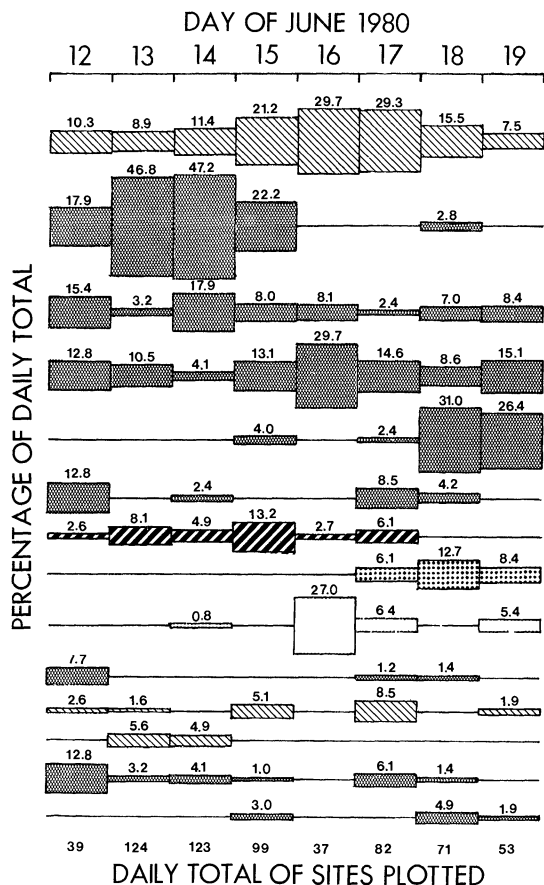


FIG. 4. Summary of the turnover of food source patches from day to day. Each line represents a patch of forage of a given pollen color. The width of the lines (and the numbers above them) denote the percentage each patch represents of the total number of sites plotted each day. Only those patches comprising at least 1% of the record for the 9 d are presented.

**19 June.**—This plot resembles the 18 June plot. The yellow pollen source at 0.5 km to the SE is absent, and new sources at intermediate distances to the SE have appeared. Note the very distant (7.7 and 10.1 km) yellow-orange patches to the W, and the reappearance of orange sources to the NW near the colony (mean distance = 1971 m; median = 1560 m).

**20 June.**—No bees foraged, as it was cold and rainy all day.

On the forage maps there are obvious groupings of points with the same color of pollen (or none). These are often so tightly clustered that they must denote a distinct patch of flowers, or a single flowering tree, with scatter introduced by the errors inherent in the dance language and our system of recording. In other cases the points are spread out over quite a large area, suggesting a food source patch that is more widely dispersed (such as the grouping of points 2–4 km in

the SW, present 12–15 June). We summarized the changes in food patches from day to day by defining a region and color of pollen that seemed to correspond to a distinct patch, and then describing the change in the relative abundance of recruitment to that patch and others from day to day. We must emphasize that these estimates of turnover are conservative, since we defined the food source patches broadly and erred on the side of lumping rather than splitting. Fig. 4 presents these results for sources comprising at least 1% of the recruitment recorded 12–19 June 1980.

These measurements can be further summarized by estimating the mean length of use of a food source patch, using techniques derived from renewal theory (D. S. Robson, *personal communication*, Drake 1967; see Visscher 1982 for more detail). Our data present two complications for this analysis. On the one hand, lumping of actually distinct patches distorts the mean-use-interval estimate upward. On the other hand, we may overestimate the number of short intervals, since random sampling may not have recorded bees recruiting to a given patch on a given day; this problem is pronounced for minor patches, which may show up as a single observation, although in use at a low level for several days. We scored records in which patch use was interrupted for a single day, but resumed within the 9-d period of observation, as continuous. Records with interruptions of two or more days were scored as separate use intervals. We performed the analysis twice: first including all patches, even single observations, which probably underestimates the mean use interval length, and second including only patches that comprised at least 1% of the record for the period, which probably yields an overestimate. The mean lengths of use of a food source patch by the colony (not by individual bees), estimated in the first and second ways above, respectively, were: 12–19 June, 4.0 and 17.2 d; 9–17 July, 5.8 and 13.6 d; 28 July–5 August, 2.4 and 3.6 d; 19–27 August, 3.0 and 8.2 d.

To estimate the number of food source patches worked each day by a colony, we calculated for each of the 36 d of observation the number of food source patches needed to account for 90% of the colony's recruitment activity (and by inference, foraging activity; see Table 1). This yielded  $8.0 \pm 2.4$ ,  $7.9 \pm 2.8$ ,  $5.9 \pm 2.6$ , and  $16.3 \pm 3.1$  patches/d for the four 9-d observation periods, respectively, and  $9.7 \pm 4.9$  patches/d upon averaging over all 36 d of observation. It is evident that, on any given day, the vast majority of a colony's foragers are distributed over a small number of food source patches.

The distances over which the observation colony foraged are remarkably large. Pooling data from all 36 d of observation yields the following statistics on foraging distance:  $2260 \pm 1890$  m (mean  $\pm$  1 SD); range 50–10 100 m; 50th percentile (median), 1650 m; 90th percentile, 5000 m; 95th percentile, 6000 m; 99th percentile, 7700 m.



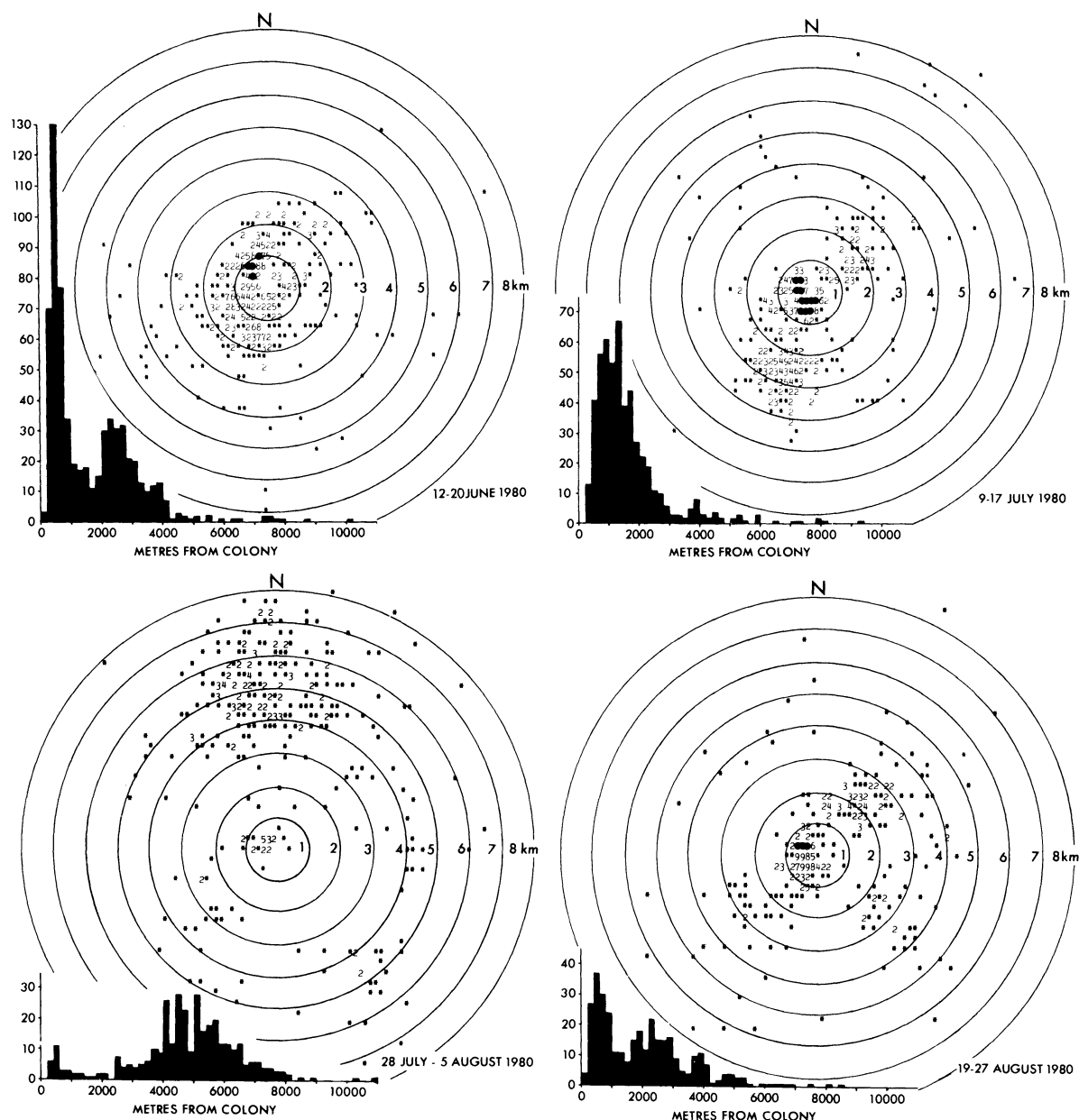


FIG. 5. Maps of the locations recruited to for four 9-d periods during the summer of 1980. Numbers on the plots represent overlap of that number of single points; black circles indicate 10 or more overlapping points. Accompanying each plot is a histogram of the distance distribution of sites for that period.

There was a great deal of variability in the patterns of foraging distance at different times during the summer. Fig. 5 presents composite maps of all the recruitment dances recorded during each of the four 9-d observation periods. Also included in this figure are histograms of the distance distributions for the plotted points. Each distribution differs from all others ( $P < .01$ , Mann-Whitney  $U$  test) except the pair 9-17 July and 19-27 August ( $P = .18$ ).

In addition to the day-to-day and week-to-week

variations in position of food source patches, the overall richness of forage is also quite variable. We measured this variability in two ways. First is the variation in the rate of foragers returning to our observation hive with pollen and nectar. These results, presented in Fig. 6, probably reflect both the number and richness of flowers, which affect the number of bees deployed in gathering food, and the distance and dispersion of flowers, which affect handling time and thus the number of trips a forager makes in a day. A second indi-

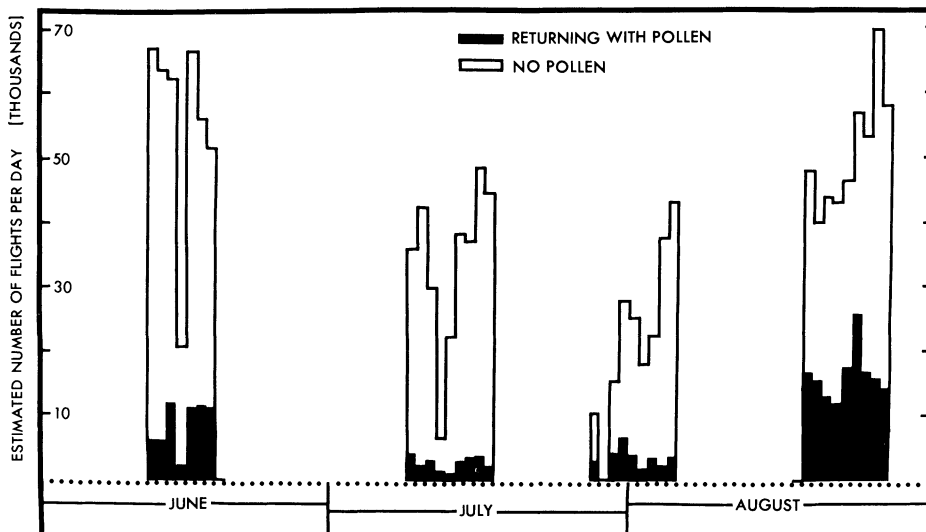


FIG. 6. Variation in foraging activity during four periods throughout the summer of 1980. Number of flights is estimated from the sum of 10 hourly counts of the number of bees returning from flights. Because the foraging day was often longer than 10 h, this estimate is somewhat low. The length of each day's bar, as drawn, represents the sum of bees returning with and without pollen.

cator of variability is the day-to-day pattern of mass changes in a hive on a scale, depicted in Fig. 7. Notice in this figure that if the histogram were smoothed, removing the day-to-day effects of bad weather, the foraging season would be characterized by a baseline where nectar collection balances the colony's energy use, punctuated by "honey flows" when certain particularly rewarding flowers bloom, and colonies gather substantial surpluses of food.

#### DISCUSSION

The principal significance of the present study is that it helps us perceive the foraging strategy of honeybee colonies. An understanding of this strategy requires combining the present findings on colonial labor patterns with earlier findings on the mechanisms of recruitment communication in honeybee colonies. Thus this study both extends our knowledge of honeybee foraging and gives new meaning to prior findings. A further value of the present study is that it graphically illustrates some of the benefits which can result from cooperation in food collection.

Four main patterns characterized the foraging of the colony in this study: (1) strong variation across the summer in intensity of foraging, (2) regular foraging at sources several kilometres from the nest, (3) frequent (at least daily) adjustment of forager allocation to food source patches, and (4) use of relatively few food source patches at any one time, each for only a few days.

The strong day-to-day or week-to-week variations in foraging activity shown in Fig. 6 are evidently rooted in the variation in foraging opportunity reflected in

Fig. 7. For example, the low flight activity at the end of July 1980 (Fig. 6) reflects a dearth of forage at that time in the study area; despite excellent weather, little recruitment occurred. This dearth is typical for our region (Fig. 7). Because the availability of forage appears to change weekly or even daily (as indicated by mass changes in the scale hive), and because it takes a colony 30–40 d for a change in the brood rearing activity to influence the size of the forager force (21 d development time plus 10–20 d of preliminary in-hive labor), colonies cannot track changes in foraging opportunity by adjusting their rate of brood rearing. Colonies do have some ability to respond to changes in foraging opportunities by accelerating or decelerating the workers' rate of passage through the age-labor schedule (Sekiguchi and Sakagami 1966); however, their main strategy is to maintain a large standing force of foragers. During times of rich forage, foragers are active in the fields; during times of poor forage many remain inside the nest, conserving their flight energy and the energetic capital they themselves represent. These reserve foragers are alerted to improved foraging conditions by recruitment dances performed by the still active foragers, who collect what little forage is available and monitor the foraging conditions (von Frisch 1967). Reserve foragers were apparent during periods of nectar dearth, forming tight masses of bees hanging quietly in peripheral regions of the observation hive.

As we have seen, the foraging radius of a honeybee colony is surprisingly large. Prior studies, conducted in agricultural areas, had suggested that the median

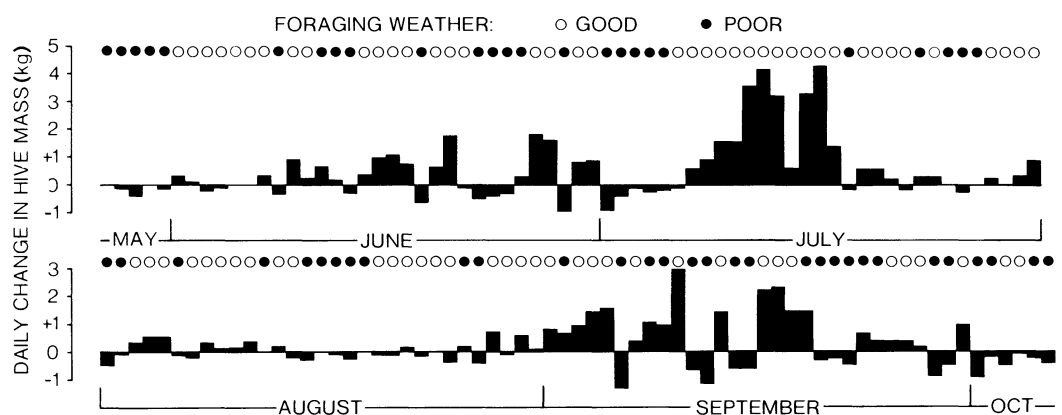


FIG. 7. Daily change in mass of a hive of honeybees. "Good" foraging weather was defined here as a mean temperature above 14°C during the hours 0600–1800 and no rain during the day.

foraging radius of honeybee colonies was only a few hundred metres (reviewed by Ribbands 1953, Free 1970, Michener 1974). On the other hand, Gary et al. (1972) reported significant forager populations from apiaries 3700 m distant, and Knaffl (1953) observed vigorous recruitment to feeding stations 8000 m distant and food collection out to 10 100 m from a hive. Both studies indicate that the potential foraging range of a colony is large. Our study suggests that substantial foraging over large distances may be commonplace in nature. The circle enclosing 95% of the foraging sites for our observation colony has a radius of 6000 m and an area of 113 km<sup>2</sup>.

The adaptive significance of such a large foraging range is not entirely clear. On the one hand, as Hamilton and Watt (1970) argue for central-place foragers in general, it may be essential to providing an adequate resource base for a honeybee colony with its large biomass and energy budget. Michener's (1974) observation of a positive relationship between colony biomass and foraging radius for the social bees in general supports this idea. On the other hand, the large foraging radius may not be energetically essential to a colony, but nevertheless advantageous to it, since the larger the foraging range of a colony, the larger the sample of food source patches among which it may choose to forage. This wider choice could raise the average richness of the food source patches which a colony works and so raise the colony's feeding efficiency. Probably there is a minimum foraging range which colonies require for an adequate resource base, but they go beyond this for enhanced efficiency in food collection.

The scale on which a honeybee colony is able to forage results in a great deal of overlap between the potential foraging areas of the feral colonies we found inhabiting the Arnot Forest. Assuming that the observed density of 0.5 colonies/km<sup>2</sup> holds outside the

Arnot Forest, and given that the 95% envelope for our observation colony's foraging activity encloses 113 km<sup>2</sup>, then within its foraging area there were  $\approx 50$  other colonies. (Analysis of 17th-century Russian estate records by Galton [1971] yielded a value of  $0.51 \pm 0.37$  honeybee colonies/km<sup>2</sup> in several forests closely inspected for wild honeybee colonies.) In this context, the spacing between adjacent colonies becomes essentially irrelevant as a means of minimizing the overlap of colonies' foraging areas. This is consistent with the observations of Seeley and Morse (1977) that honeybee swarms do not prefer new homesites far from the parent nest, as preliminary observations by Lindauer (1955) suggested they might. Likewise, proximity of a colony's nest to open areas in the forest seems unimportant. Although location close to large agricultural fields has been shown to increase honey yields from beekeepers' colonies (Ribbands 1953), there is probably little overall advantage to a forest-dwelling colony in nesting at the edge of a meadow which bears rich food for only a short time, as it is well within the range of other colonies, and much of the colony's foraging will occur elsewhere.

The most thought-provoking finding of this study is, as indicated in Figs. 3 and 4, that honeybee colonies seem to constantly readjust their allocation of foragers to the various food source patches. Moreover, the small number of patches worked each day, the large areas around a nest without significant foraging each day, and the short span of a colony's attention to a given food source patch, together suggest that colonies organize their foraging so that on any given day a colony's foragers are focussed on the few, highest-quality food source patches which the colony has found. An alternative hypothesis is that the colony had found only a few food source patches, worked all that it could find, and changed patches when it found new ones or old ones were exhausted. Several observations con-

tradict this null hypothesis and support the choice hypothesis. First, when bad weather arose on 16 June 1980, the colony began foraging on the previously little-worked pollen patch 700–1000 m NW of the hive (Fig. 3; also represented by the ninth line from the top in Fig. 4). It seems unlikely that this patch suddenly began to produce food with the onset of cold, rainy weather. Rather, the bad weather probably rendered the distant patches unprofitable (dangerous to fly to or without food), so the bees turned to what had been a relatively low-quality patch (when good weather resumed, this source was again abandoned). Secondly, during all four periods of observation, the relative importance of certain patches diminished and then subsequently expanded, suggesting that these patches were available throughout the interval but were used less when other patches became temporarily richer, and then returned to as the other patches faded. See, for example, the records of foraging activity for the patches represented by the lines third and fourth from the top in Fig. 4. Third, we observed patches of flowers (*Apocynum androsaemifolium*, *Lotus corniculatus*, *Rubus* spp.) near the hive which we knew honeybees to work at other times, and which were being visited by nectar feeders (*Bombus* spp., various butterflies), but which were not in use by our colony. Fourth, during times of rich nectar production only a few bees from a colony will forage at an artificial feeder provided them, whereas when the natural forage declines many bees from the same colony will forage vigorously at the same feeder (P. K. Visscher and T. D. Seeley, *personal observation*, von Frisch 1967).

Prior experimental studies further support the hypothesis that honeybee colonies select the few most profitable among known sources. Boch (1956) and Butler et al. (1943) both demonstrated that a honeybee colony offered two food sources in various combinations of richness and distance from the hive can evaluate the relative profitability of the two, allocate its foraging labor accordingly, and shift its forager force from one to the other within hours of a reversal of their relative profitability. Furthermore, prior studies (reviewed by von Frisch 1967, Heinrich 1978) have unravelled the mechanisms underlying this ability to allocate foragers to the best of the various known forage patches. In essence, this occurs because every time a forager returns with a load she is informed (based on the quality of her forage) whether or not to continue foraging at her current work site; most foragers find new work sites by following recruitment dances, and the intensity of dances advertising a work site is proportional to the site's profitability relative to all the other known sites.

The following points now seem clear about the adaptive significance of the honeybee's dance language recruitment system, at least for colonies living under the conditions found in our study area. First, unlike many species of ants (Oster and Wilson 1978),

individual bees do not require the direct assistance of recruits to harvest their food, because nectar and pollen occur in small, easily retrieved units. Second, recruits do not help overpower competitors, as they could at rich clumped sources (Johnson and Hubbell 1974), because most food sources are thinly dispersed and so are not easily defended (for example, a patch of goldenrod). Rather, the dance language recruitment system (combined with a division of labor among foragers between scouts and recruits) probably helps minimize the average cost per forager of finding and tracking high-quality food sources, especially when such food sources are patchy and widely dispersed.

In insect societies without recruitment communication, like those of bumblebees (Heinrich 1979), each individual is limited in choosing a work site to the information she herself collects. Thus she must strike a compromise between searching (inexpensively) a small area and probably not encountering a rich food source vs. searching (more expensively) a large area and so possibly discovering a high-quality food source. Furthermore, each bumblebee forager must periodically devote time to monitoring alternative food sources in order to track changes in forage opportunity. In contrast, within a honeybee colony, each individual is guided in her choice of a work site by the summed information on food sources gathered by all of the colony's foragers. This pool of information, as we have seen, can reflect the monitoring of known food sources and the discovery of new ones over an area of 100 or more square kilometres. Moreover, once an individual has chosen a food source, recruitment communication still helps her to track the best known food. Whenever a scout bee discovers a new rich food source, or the relative quality of two known sources changes, individual foragers are redirected to better work sites without their having constantly to make personal comparisons between current and possible alternative food sources. In short, through recruitment communication, a honeybee colony operates as an information center in which the reconnaissance of foragers is pooled and processed to focus the colony's efforts on the best forage sites found about the nest.

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