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Research article

House-hunting by honey bee swarms: collective decisions and individual behaviors

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Summary. Thousands of individuals in a house-hunting honey bee swarm make a collective decision for one among many nest sites discovered. We recorded the dances on swarms in a forested area, where one swarm's search encompassed about 150 km^2 and many different sites. We then analyzed swarms in a desert area with only nest sites that we provided and monitored, to study how the swarm winnows multiple finds to a single site over the course of a few days. Most bees did not visit any site, very few visited more than one. Apparently choices were made with little or no direct comparison, through the interaction of two mechanisms: positive feedback through recruitment leading to growth in the number of scouts visiting good nest sites, and attrition reducing activity and recruitment for non-chosen sites. Individual differences between bees substantially affected these dynamics. Scouts varied considerably in amount of dancing and persistence, but most that danced did so vigorously after their first few visits, and then dropped out, ceasing their dancing though continuing to visit the nest site. Dances were nearly twice as long as reported for nectar and pollen. Scouts followed dances of others, and occasionally visited alternative sites, but rarely switched their dancing. When unanimity is reached, the bees must recognize that a decision has been made, break up the swarm cluster, and fly to the nest site. Buzz-running (Schwirrlaufen) probably plays a role here, but we observed less buzz-running than previously reported, and this occurred even early in the process; it might function as a chain-reaction effect triggering the end of the house-hunting process. Our results suggest that the choice among nest sites relies less on direct comparison of nest sites, and more on inherent processes of positive feedback and attrition by dancers dropping out.

Key words: Apis mellifera, honey bee, swarm, communication, house-hunting, decision-making.

Introduction

Natural history of house-hunting by honey bees

The choice among alternative nest sites by a swarm of honey bees (*Apis mellifera*) is a striking example of collective decision making (Lindauer, 1957, 1961). When a colony of honey bees divides, several thousand workers and the colony's queen leave the colony as a swarm. The swarm settles and scout bees fly throughout the surrounding countryside searching for new nest-site cavities. When a scout returns to the swarm after inspecting a high-quality cavity, she performs waggle dances which encode the distance and direction to the site. Since a swarm has many scouts, many potential nest sites may be discovered, and dances for several sites may be performed simultaneously on the surface of the swarm cluster. However, in time, the bees reach a consensus, and only dances for a single site are seen. Shortly thereafter the cluster abruptly breaks and the bees fly to the chosen site.

Former studies

Evaluation of nest sites

The first answers regarding how a swarm finds and evaluates nest sites were provided by Lindauer (1951, 1953, 1955). These were followed by Seeley and Morse (1978) and Seeley (1977) testing the properties of nest sites that were evaluated by bees, and how the volume of the nest cavity is measured by scout bees. These studies show that scout bees evaluate many properties of nest sites, including volume, exposure, entrance size, and height from the ground, and show consistent preferences in these properties.

Who the scouts are

Lindauer (1955) also investigated which bees participate in house-hunting as scouts, and reported that they were often

bees which had been nectar foragers in the colony prior to swarming. Gilley (1998) reported that scouts were older on average than non-scouting bees on the swarm, but somewhat younger on average than foragers in the pre-swarming colony. Seeley et al. (1979) estimated that about 5% of the bees in the swarm scout for nest sites, but only about one third of the scouts that visit a site dance for it.

How a decision is reached

Lindauer (1961) summarized his findings in the following hypothesis: "the better the qualities a nesting place exhibits, the livelier and longer will be the messengers' dance after the inspection. In this way new messengers are recruited in the cluster for this place, and then they too solicit by means of the same lively dances. If those scouting bees which at first had only inferior or average dwellings to announce are persuaded by the livelier dances of their colleagues to inspect the other nesting place, then nothing more stands in the way of an agreement. They can now make a comparison between their own and the new nesting place, and they will solicit in the cluster for the better of the two."

Lindauer's hypothesis has two components. First, there is recruitment for good sites, in which scouts recruit more scouts who in turn recruit more, potentially leading to exponential increases in scout numbers. Second, there is comparison of alternative sites by individual scouts, in which scouts that have evaluated nest sites follow dances for others, visit them, and recruit for the one they find superior. In subsequent discussions invoking Lindauer's work, Gould and Gould (1994) emphasized the comparison aspect, and Griffin (1981, 1984, 1992) discussed its cognitive implications.

How the decision is perceived

To a human observer, the emergence of a consensus is apparent as the number of different sites advertised by dances on the swarm diminishes, until all reference the same site. Some time after this occurs, the bees seem to sense that a decision has been made, and many scouts begin to perform "Schwirrlaufen" (Lindauer, 1955) or buzz-running on the nest sites, which apparently signals the bees at the nest site to return to the swarm (Lindauer, 1955; Seeley et al., 1979). The mechanism that informs scouts that a decision has been reached remains unknown; it may involve perceiving unanimity in the dances, or buildup of scouts at the nest box to critical densities, or other cues on either the swarm cluster or nest boxes.

How takeoff is triggered

Probably, few bees participate in the decision-making process. These bees then need to activate the entire colony from a quiescent cluster to an airborne swarm. Lindauer (1955) described bees buzz-running and burrowing through the swarm cluster and butting into other bees as the critical signal, which causes the swarm to break its cluster and fly, but there are other components as well. Near the time of takeoff, bees in the swarm emit a piping noise (Esch, 1967) that may also activate the bees.

How flying swarms orient

The flying swarm consists largely of bees which have never been to the nest site, and most have probably not followed dances indicating it, so the mechanism by which the swarm is steered remains a challenging, and unanswered question. Lindauer (1955) hypothesized that once airborne, the swarm is directed toward the chosen nest site by scouts who streak rapidly through the airborne swarm cloud in the appropriate direction. Seeley et al. (1979) observed bees flying through the swarm cluster which may have been "streakers," and Avitabile et al. (1975) suggested that pheromones might also be used by scout bees to lead the swarm. However, no experimental work has been done to test these hypotheses.

Objectives

A full understanding of this complex process will require answers to a series of questions about different stages in the process: How do the bees find and evaluate nest sites? How do they as a group choose and reach agreement among alternative nest sites which are discovered, and how does the group know when a collective decision has been reached? How do the bees switch from being a quiet cluster to a moving swarm in flight, and how do they orient as a group while moving to the chosen nest site whose location is unknown to a majority of the bees? In this study we describe the overall patterns of house-hunting in a forested area, and then examine the individual behaviors of bees within the swarm which underlie the patterns of collective behavior. The data from the study are particularly relevant to the questions of how the decision among nests sites is reached and perceived, and how swarm takeoff is triggered.

Methods

General methods

We collected data on 8 swarms (named for relevant events and surroundings, Table 1). We observed both collective behaviors (buildup of scouting and dancing, overall spatial and temporal patterns of finds, focusing on one from many sites) and individual behaviors (nest box visitation, dancing, and other behaviors of marked scouts). These categories are considered separately in the results, along with some methodological details of the individual experiments. General methods are presented here. Throughout, numbers in the form m ± sd denote means and standard deviations. Degrees of freedom of test statistics are denoted by subscripts.

Artificial swarms, swarm stand

We prepared artificial swarms (Lindauer 1955, Morse and Boch 1971) from honey bee colonies by shaking bees from their combs into a screened cage. We placed the colony's queen in a small cage with several worker bees, and suspended this inside the larger cage, where the bees clustered around it. To estimate the population of each swarm, we removed a sample of bees, then counted and weighed them to extrapolate the number of bees in the known weight of the whole swarm. We fed the swarm a concentrated sugar solution over the next 3 to 4 days.

Table 1. Swarms observed in the study

Swarm Name	Layout	Location	Swarm population	Swarm set up	First dance	Swarm takeoff
Cranberry Lake	Forest natural cavities	Cranberry Lake, NY	7240	24 Jun 92 18:00	25 Jun 16:04	26 Jun 13:34
Blackberry	Forest natural cavities	Cranberry Lake, NY	2355	5 Jul 92 18:30	6 Jul 16:24	8 Jul 12:07
Adirondack	Forest natural cavities	Cranberry Lake, NY	4295	12 Jul 92 10:15	12 Jul 13:00	15 Jul 14:09
Ithaca	Forest natural cavities	Ithaca, NY	3500	24 Jul 92 17:30	25 Jul 11:50	27 Jul 08:35
Ocotillo	2 nest boxes: N (140 m) S (240 m)	Cactus City, CA	4135	4 Dec 95 14:00	5 Dec 08:52	6 Dec 11:02
Crailsheim	3 nest boxes: E (175 m) W (203 m) NE (280 m)	Cactus City, CA	3856	9 Dec 95 15:00	10 Dec 07:35	10 Dec 12:20
Cholla	2 nest boxes E (174 m), W (146 m)	Cactus City, CA	4000	12 Dec 95 14:15	13 Dec 08:42	13 Dec 12:38
Times	2 nest boxes: E (174 m) W (146 m)	Cactus City, CA	5630	18 Feb 97 17:00	19 Feb 08:00	19 Feb 14:22

At the start of each experiment we attached the queen cage to the center of the flat vertical surface of our swarm stand, and shook the bees out of the large cage; they then formed a flattened cluster around the caged queen. The swarm stand consisted of a 53 × 58 × 2 cm board mounted vertically on a stake approximately 1.5 m off the ground. So the bees would use just gravity as a reference for their dances, we mounted a hood of translucent white plastic above and on the sides of this board to prevent the bees from directly viewing the sun and most of the sky. On the swarm stand, the bees were continuously fed sugar syrup from a 1.3-cm-diameter tubular trough 15 cm long mounted below the queen cage. This tube bent and passed through a hole in the swarm board, and was kept filled through an opening behind the board.

Artificial swarms prepared by this method behave like normal swarms (Lindauer, 1955; Morse and Boch, 1971; Avitabile et al., 1975). Scout bees seek new nest sites, and advertise the sites with waggle dances on the swarm.

Videotaping and transcription

We made color VHS videotape recordings of activity on the swarms. In some experiments the bees of interest were individually marked, but the video resolution could not distinguish among marked bees. Therefore, at intervals of one minute or less, an observer at the swarm pointed to each marked bee and announced its name for the audio portion of the videotape. We mounted a clock on the face of the swarm stand, next to the bees, within the field of view of the video camera to provide timing. A string with a plumb bob hung in view of the camera to provide an accurate vertical reference.

We transcribed the tapes, listening to comments of the observers at the swarm, and tracking the verbally identified bees forward and backward to yield a complete record of all activities of each marked bee. For our graphical presentations, we represent the behavior of each bee for each minute. We classified minutes with multiple behaviors according to the hierarchy: dancing, dance following, DVAV, walking, resting, off swarm.

Marking of bees

To individually identify bees of interest, we marked them either with colored, numbered tags glued to the thorax, or colored paint (Frisch, 1967) dabbed on the thorax or abdomen, depending on the experiment. When marking at the swarm, we grasped a bee by her wings, marked her and returned her to the swarm. The marked bees usually resumed their previous activity without apparent disturbance. When marking at nest sites, we caught the bee in a small insect net (usually as she exited the nest box), marked her through the mesh of the net, and then released her.

Mapping nest site dancing

Study site – New York forest

To describe the broad pattern of a honey bee swarm's choice among nest sites, we first observed the house-hunting process in a forested area, working on the grounds of Cranberry Lake Biological Station (44°09′N, 74°48′W) in upstate New York. This site is surrounded by deciduous forests and lakes for more than 20 km, and this habitat provides an abundance of potential nest sites in tree cavities. We observed 3 swarms in this habitat, and one swarm in a rural area near Ithaca, NY (Table 1). The patterns we saw on all these swarms were similar, but here we present detailed analysis of only the Cranberry Lake swarm.

Analysis of dancing sites

We made a continuous video recording of the Cranberry Lake swarm during daylight hours from the time the swarm was set up until it left on the second day. We analyzed the video record by measuring and averaging the durations and the angles (relative to the plumb string) of multiple waggle runs of each scouts' dances, and recording the number of waggle runs for as long she continued dancing (usually until she left the swarm, but sometimes a bee would disappear into the swarm cluster and end her record). We refer to each period of continuous observation as a dance segment. We converted the duration of the waggle-run to distance

to the nest sites based on data in Frisch (1967, Table 13 and Fig. 64), and calculated directions from the dance angles as described in Visscher and Seeley (1982).

Controlled nest site experiments

Study site – Cactus City, California

To study the house-hunting process at both ends – the swarm and the nest sites – and manipulate the system experimentally, we utilized an area nearly devoid of good nest sites, located in the "Cactus City" area (at 33°40′N, 115°55′W) of desert approximately 20 km east of Indio, California. Trees here are too small to provide nesting cavities, there are almost no human structures, and the soil is too sandy to contain large underground cavities. As a result, bees reliably scout and move to sites we provide.

As nesting sites, we provided empty Langstroth-size beehive bodies (with attached plywood tops and bottoms) with an internal volume of 40.8 l and a round entrance hole 4.1 cm in diameter approximately in the middle of the smallest side. These boxes had previously been occupied and contained residues of wax and propolis. Visscher et al. (1985) had shown that previously occupied cavities are especially attractive, and our nest boxes were readily accepted as nesting sites when placed in the shaded crotches of palo verde trees (usually about 1.5 m from the ground). We observed 4 swarms in Cactus City (Table 1), but present detailed analyses of two: the Ocotillo swarm where our most detailed data are on the scouts at the nest sites, and the Cholla swarm where we obtained detailed records on the swarm for all scouts which danced for nest sites.

Results

Collective behaviors

Overall pattern

The nest site finds in house-hunting by a swarm in a forested area is illustrated in Figure 1. In this forest the bees found and recruited to a large number of nest sites, ranging in distance from 554 to 9520 m.

The distances over which this swarm (and the Blackberry and Adirondack swarms, which were similar) found and advertised nest sites were larger than those reported in Lindauer's 1955 studies. Figure 2 shows the distribution of distances in the dance information during the first part of nest site selection, until the time at which there was nearly a consensus on one site (we considered just this period to avoid biasing the distribution with the many dances that occurred for the chosen site at the end of the decision-making process). For comparison, this same information is presented for the 5 swarms house-hunting in an urban area for which Lindauer (1955) reported dance information (again omitting the final periods).

The changing distribution of advertised nest sites during the selection process in this swarm is illustrated in Figure 3. The period graphed is from the first dance until a consensus emerged for the site approximately 2 km to the SSE (the heaviest vector in diagram 3). For each of three intervals the distribution is plotted in the form of Lindauer's (1951,1955) vector diagrams. However, Lindauer plotted only sites advertised by newly-marked dancers (which probably exaggerates changes in the distribution of sites), whereas we included all dances. Figure 3 also shows the time course and number of circuits of each dance segment (defined as a period of continuous dance observation from the time the scout started to dance until she either stopped dancing or was lost to view). Note the shape of the cumulative amount of dancing (i.e. the profile of the left edge dance segments series), which shows the effect of positive feedback in the steepening of the curve, and a stairstep-like rise. Scatter in dances and the possibility

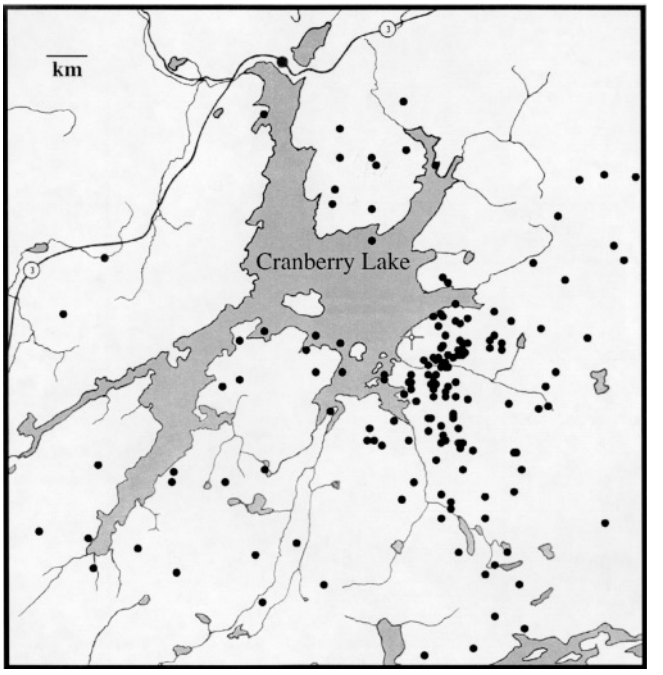

Figure 1. The overall pattern of house-hunting by the Cranberry Lake swarm, which was set up in a forested region of the Adirondack Mountains in New York. The dots represent nest locations inferred from dances of scouts on the swarm, and the location of the swarm is noted by a cross near the southeast shore of the lake. Note that bees scouted over an immense area, even across several km of water to the north shore but apparently not across the broader expanse of water to the northwest shore

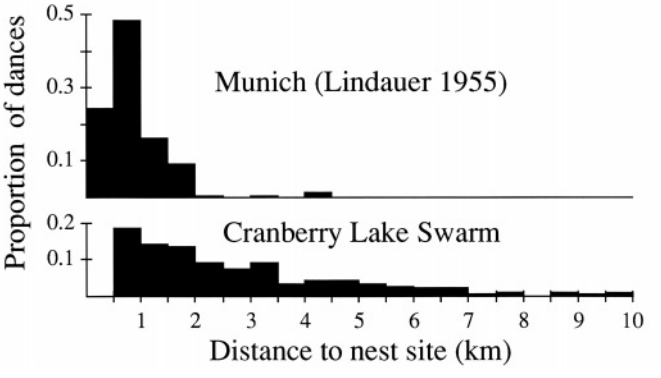

Figure 2. Distances inferred from dances for the Cranberry Lake swarm, and for 5 swarms observed by Lindauer

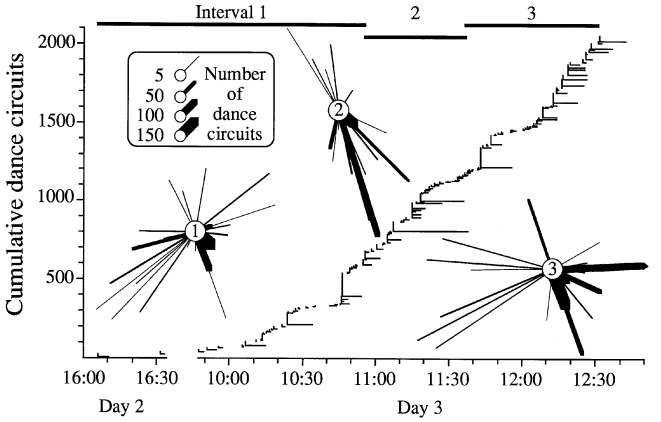

Figure 3. Dance segments in the Cranberry Lake swarm. Each "L"-shaped symbol represents one dance segment. The horizontal portion shows when the dances were performed. The vertical portion indicates the number of dance circuits. The vector diagrams summarize the distribution of dancing during 3 intervals in the house-hunting process (shown at the top) with equal numbers of dance segments. The orientation and length of each vector correspond to the direction and distance to the site, and the width is proportional to the number of dance segments advertising that site. The vector lengths shown in the legend correspond to a distance of one km. Sites with a single dance circuit are omitted in the vector diagrams

of sites near each other in a forest introduce uncertainty over which "sites" to lump or split, so the number of sites in the vector diagrams should be interpreted with caution. They do show the shifting emphasis in the locations of the swarm's scouting over time, and the beginning of reduction in the number of sites, which reduced sharply after time period 3 until swarm takeoff.

The swarm as an information center

Like a honey bee colony in an established nest, a swarm of bees serves as an information center in which the findings of many scouts are advertised in a central location. Figure 4 shows the location of dances on the surface of the Cholla swarm during 3 successive portions of the nest site selection process. Analyses of dance patterns in the Ocotillo and Crailsheim swarms showed similar patterns. Dances on the swarm cluster were initially (Fig. 4A, lower left quadrant) concentrated in a restricted "dance floor" (Visscher and Seeley, 1982; Seeley and Towne, 1992; Seeley, 1994), but this concentration reduced later, when dances spread out over much of the cluster (Fig. 4C). For efficient communication, one might hypothesize that the dances would not only be concentrated on a particular portion of the swarm, but also that dances for each site would be spatially segregated on the dance floor. However, this appeared not to be the case. There was a broad overlap in the location of dances for the 2 nest sites. Except in Figure 4B where the mean horizontal location of the dances for the East site was somewhat to the left (east) of those for the West site ($t_{35} = 2.66$, $P = 0.01$), there was no significant spatial segregation of dances for the 2 sites.

Nest site observations

In our simplified experimental situation, we observed much the same temporal pattern that we saw in the Cranberry Lake swarm, but were able to add observations of scouting at the nest sites. With the Ocotillo swarm, we paint-marked scouts with different colors at each of two nest sites, and distinctively marked a small number of bees observed recruiting

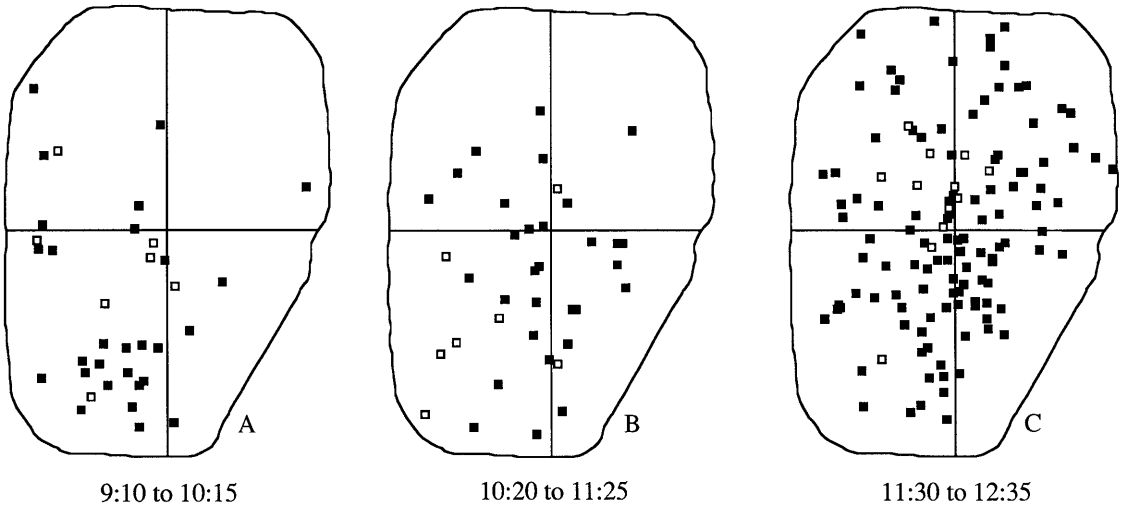

Figure 4. Dance locations on the surface of the Cholla swarm for 3 divisions of the entire house-hunting process. Filled and open squares indicate dances to the West and East sites, respectively. Initially (A) there is a compact "information center" in the lower left quadrant, which later spreads out to cover the entire swarm (B and C). The dimensions of the vertical and horizontal axes in the figure are 30 cm and 22 cm, respectively

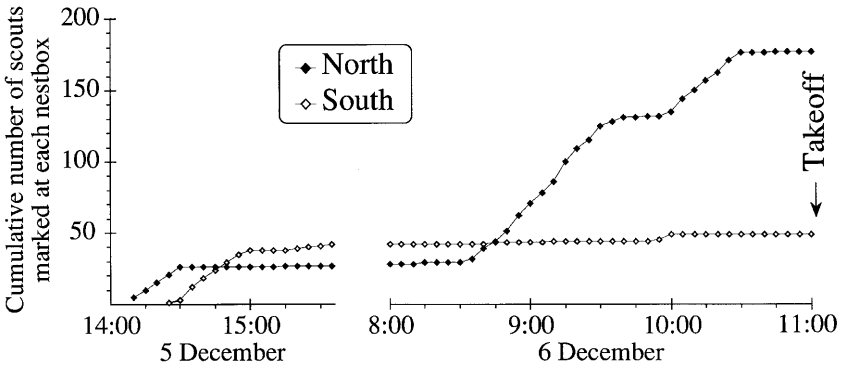

Figure 5. Buildup of scouts at the North and South nest boxes in the Ocotillo swarm. The stairstep pattern reflects waves of recruitment which finally lead to takeoff of the swarm toward the North site

vigorously on the swarm. With the Cholla swarm, we marked every dancer when we first observed her dancing, using individually numbered tags. In both of these experiments, we observed events at the swarm and at two nest boxes throughout the discovery and decision-making process.

Figure 5 shows how the buildup of individual scouts at two nest boxes in the Ocotillo swarm mirrored the accelerating dancing of the Cranberry Lake swarm. Since scouts visited the sites repeatedly after they were marked, the buildup in visitation was even greater than the number of scouting individuals shown here. In Figure 5 the North site was found first, but recruitment of new scouts at the nest site was somewhat more intense for the South site the first day, with 38 bees at the South and 26 at North box marked by 15:00. However, the rates of recruitment for these first cohorts of recruits were quite similar for the two sites. On the second day, recruitment began first at the North site, and then increased (in two waves) until swarm takeoff. There were flat areas on the curve of the North site, and throughout most of the second day on the South site, corresponding to periods in which no new recruits arrived. Note that one of these occurred at the North site just before takeoff.

Buildup of dances at the swarm

With the Cholla swarm, we obtained simultaneous measures of dancing on the swarm cluster, scouting at the nest boxes, and detailed individual information on all bees that danced for either nest site. These observations allowed us to relate the behaviors at the swarm to those at the nest sites, and to see how the individual behaviors (below) related to the collective patterns.

Figure 6A shows the buildup of scouts at the two nest sites slightly differently than Figure 5 since here we recorded the total number of scouts rather than the newly recruited scouts. In parallel with this information, we see the amount of dancing during any one time interval for each site (Fig. 6B, C) and the cumulative buildup of dancing for each site (Fig. 6D). As before, cumulative dancing shows a stairstep pattern. This pattern is strikingly similar for the two sites, but offset in time, as illustrated in the inset in Figure 6D, showing the cumulative dancing curves for the two sites superimposed from their respective beginnings at the time of the first dance for each site.

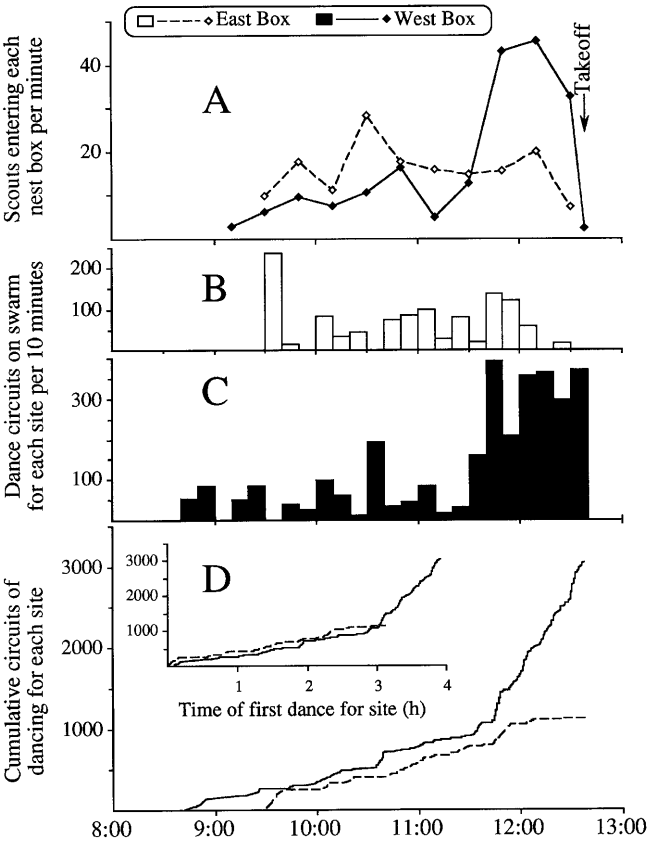

Figure 6. Dynamics of recruitment in the Cholla swarm. A) Scouting activity at the two nest boxes. Note that at the ultimately successful West site scouting builds up but the scouts disappear from the nest site shortly before takeoff. B,C) Amount of dancing for East (B) and West (C) nest boxes over time. D) Buildup of dancing by the scouts for the two nest sites. The inset superimposes the timelines by shifting time of first dance of each site to time 0, and shows that the pattern of buildup from the time of discovery of each site is very similar

Individual behaviors

The collective behavior of the swarm has its origins in individual actions of the bees. To understand these actions and interactions, we marked bees with individually-identifiable marks and recorded their behaviors on the swarm cluster and at the nest sites.

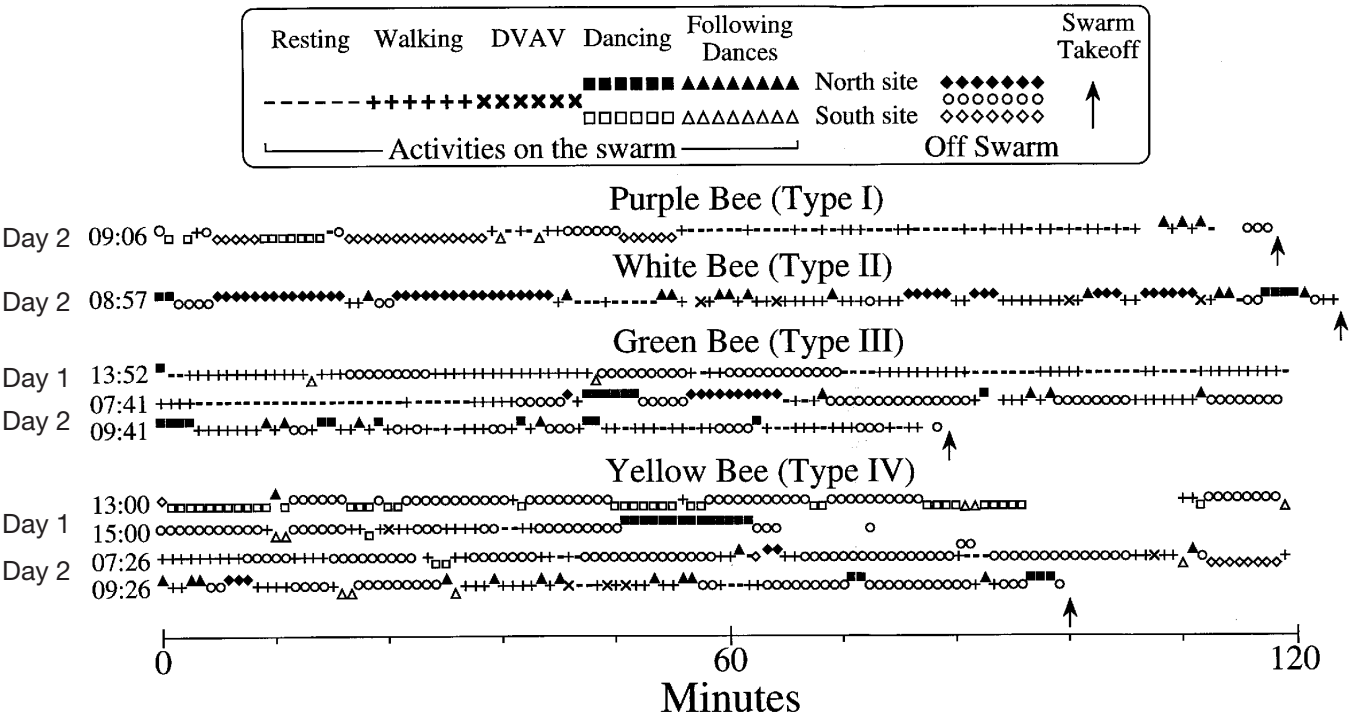

Figure 7. Timelines for 4 individual bees from the Ocotillo swarm, showing the predominant activity of each bee for each minute of observation.Symbols representing dancing for, following dances for, or visiting the North and South nest site are offset above and below the line, respectively

Figure 7 presents timelines for 4 individual bees from the Ocotillo swarm. In this and all figures referring to individual behaviors, symbols and bars are filled for the site finally chosen, and open for the alternative site. Also, the symbols for the two nest sites are displaced above and below each bee's timeline. "Off swarm" records are shown as circles placed on the time line when the bee was off the swarm (presumably at one of the nest sites) but was not observed. (Since bees enter and leave the boxes rapidly, and spend most of their time inside the box out of view, their visits are sometimes missed.) In the Ocotillo swarm the home site search spanned 2 days.

Dancing behavior

The bees presented in Figure 7 exhibited patterns of behavior which we saw repeatedly. Although individual differences between bees form a continuum, we found it useful to define 4 general patterns. The first was typified by the purple-marked bee. She was marked as a vigorous dancer for the South site on day 2 (we do not know her behavior on day 1). She danced for a short period of time after being marked, followed dances for the South site, and was observed making several visits there. Shortly before the swarm took off to the North site, she followed dances for the North site, and then left the swarm (presumably for one of sites, though we could not record which one). This bee initially danced vigorously, but subsequently did not dance at all.

The white-marked bee showed a second type of behavior. She was also marked early in day 2, danced for North and then stopped dancing but continued to follow North dances and to visit the North site. She finally danced for it again just before the swarm took off.

The third type of behavior pattern can be seen in the records of the green-marked bee. She was one of the early dancers for the North site. She danced for this site, and then spent the rest of day 1 alternately on and off the swarm. Note that she often followed dances for a few minutes, and left the swarm immediately. On day 2 she began to dance more frequently, interspersed with dance-following and flights off the swarm, for the rest of the day until swarm takeoff.

The yellow-marked bee showed a fourth type of behavior. She was the first vigorous dancer observed on this swarm, initially danced for the South box, then briefly followed a dancer for the North box, then sporadically danced for South, but finally switched to dancing for North late in day 1. On day 2 she again danced for South, but later switched to North. She visited and followed dances for both sites.

To obtain a more complete picture of the individual behavior of scout bees, we marked all 75 scouts that danced on the Cholla swarm and followed their activities from the time they first danced and were marked until the swarm departed. For these bees we obtained minute by minute data of their behaviors similar to that of the 4 bees in Figure 7. This complete behavioral record allowed us to estimate the frequency of the 4 behavioral patterns (for detailed individual timelines for all bees, see Visscher and Camazine, 1999a). As shown in

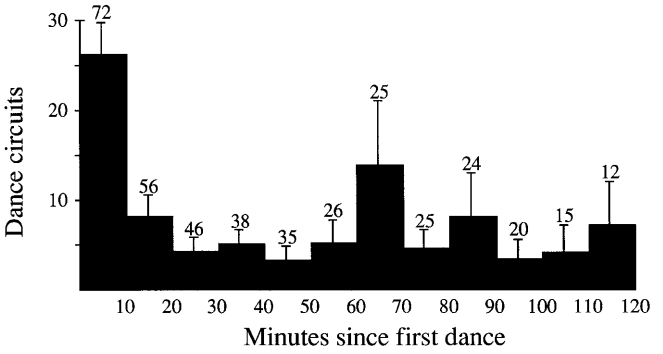

Figure 8. The mean number of circuits of dancing performed by nest site scouts during successive 10-minute intervals after each scout's first dance. The pattern is that bees perform most of their dancing at first, and then largely drop out. The numbers above the bars are the number of individuals' records for each interval; these diminish at higher intervals because some bees began dancing nearer to the time of swarm takeoff than others, and so had shorter records

Figure 8, most bees danced for a relatively short period and then stopped dancing (like the Purple bee in Fig. 7; we refer to this as Type I behavior). A few danced initially, then stopped dancing, but danced again near the time of swarm takeoff (e.g., White in Fig. 7, Type II). Many bees danced throughout the process (e.g., Green in Fig. 7, Type III). Only a few visited alternative sites to the one for which they had danced, (e.g., Yellow in Fig. 7, Type IV). The relative frequencies of behavioral Types I to IV, respectively, among the 75 marked dancers in the Cholla swarm were 0.32, 0.09, 0.28, and 0.07. (These do not sum to 1 since 15 of the dancers could not be categorized because they began dancing shortly before takeoff. Three additional dancers perished or lost their tags, and so have incomplete records. They were omitted here and other analyses where their truncated records might bias results).

The individual records in the Cholla swarm provide some other insights into the collective decision for the West site by the swarm. Although the nest boxes were nearly identical, and situated at similar distances from the swarm, the scout bees that visited the ultimately successful West site danced more than did the East-box scouts for the East box (Fig. 9, also Fig. 6B, C, D). To compare these statistically, we analyzed the amount of dancing by bees to the two sites during the period before consensus had clearly emerged, when there were similar numbers of scouts representing each site. This also avoids truncation of the data on bees which first danced shortly before takeoff, when there would be relatively few minutes of observation in which they could dance. The 12 dancers to the West site performed an average of 111 ± 103 dance circuits, while the 13 dancers to the East site averaged 77 ± 21 ($t_{23} = 0.94$, $P = 0.35$, NS).

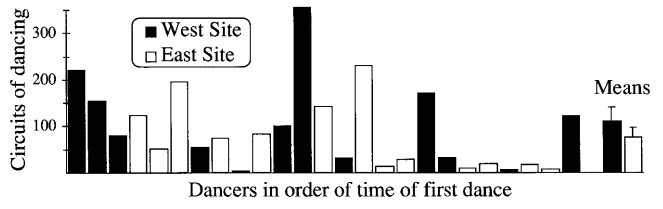

Figure 9. The amount of dancing performed by individual scouts for the East and West nest boxes on the Cholla swarm, and the mean ± SE number of circuits of dancing for East- and West-site dancers. The figure excludes scouts that began dancing after 11 : 40 (when recruitment for the West site began its sharp rise; see text)

Dance following

Most bees that danced for nest sites also followed dances of other scouts, for both their own site and alternative sites, and interspersed this following with their own dances. In the Cholla swarm, of the 46 dancers that danced prior to 30 minutes before swarm takeoff (and thus had considerable opportunity to follow other dances) 89% followed other dancers. Forty-one percent of these 46 followed dances that were for the same site these scouts had danced for, 13% only for the alternative site, and 35% followed dances for both sites. These percentages are close to those expected if scout bees simply followed dances randomly in proportion to their frequency on the swarm (Visscher and Camazine, 1999b).

Scouting nest sites

Bees repeatedly visited nest sites, even when they no longer performed dances for the sites they had visited (i.e. type I and II behavior). During these visits we observed their behavior as similar to that described by Seeley (1977), with most of their time spent inside the cavity, out of our view. Throughout the process, bees on the outside of the box, especially at the entrance, and bees on the inside, seen through the nest entrance, performed buzz-running when other scouts were present (see below).

As noted above, some bees followed dances for both sites, and occasionally they visited both sites. In the Cholla swarm, 6.7% (5 of 75) of the marked recruiters visited both sites. In the Ocotillo swarm, where we marked all scouts whether they danced or not, 9.2% (16 of 174) visited both sites. Most of these were bees which had visited the South site, which was finally rejected, and then visited the North site later in the process (when nearly all of the dancing was for North). Only 2.9% (5 of 174) were North site scouts observed to also visit the South site.

Buzz-running

In the Cholla swarm, we observed buzz-running prior to swarm takeoff as reported by Lindauer (1955), (but less than seen by Seeley et al. (1979) with a larger swarm). Most of these buzz-runners (7 of 10) were bees marked earlier as dancers. However, buzz-running was also performed by unmarked bees, even in experiments where all nest site scouts were marked, rather than just dancers. In our observations, buzz-running generally began first on the nest site, and in many cases rather little buzz-running occurred on the swarm prior to swarm takeoff. During liftoff, and after most

bees had flown from the swarm stand, buzz-runners were particularly active on the queen cage.

DVAV

On the swarm cluster, we frequently saw a bee hold another bee while performing dorso-ventral abdominal vibrations (DVAV). This behavior was frequently associated with dancing, either preceding or following bouts of dancing. As with buzz-running, while DVAV was frequently performed by bees which had danced for a site, it was not restricted either to dancers or to bees which had visited nest sites, since we saw it performed by unmarked bees in all experiments.

Consensus-site vs. "losing" site bees

As a consensus developed on the swarm for one site, there were very few dances occurring for the "losing" site. The scouts which had danced for that site became relatively inactive, especially as takeoff neared, though some continued to follow dances, then occurring almost exclusively for the consensus site. On the Cholla swarm, the proportion of bees marked for the losing nest box which were moving on the surface of the swarm in the last 5 minutes before swarm takeoff (12 of 17 moved) was significantly less than the proportion of bees marked for the winning nest box which were active (38 of 40 moved; $P = 0.048$, binomial test). (However, a larger proportion of the winning site bees had been recently marked, which might bias this comparison.) There was not, however, a discernible difference in the takeoff behavior of the two groups: when most of the swarm had lifted off there were a large number of marked bees among the bees performing buzz-running on the swarm stand and the queen cage, but these included bees marked for both sites.

Discussion

House-hunting versus forager allocation

The collective decision-making process of house-hunting by honey bee swarms exemplifies the insect colony as an information center. The colony functions as an information center also in the allocation of its foragers (Visscher and Seeley, 1982; review by Seeley, 1995), but in house-hunting this function is even more refined. The only thing a nest-site scout brings back to the swarm is information, and this information is critical for the swarm to make an appropriate collective decision of enormous consequence for the colony's survival and reproduction.

This process is different from and more complex than the selection of nectar or pollen foraging resources in several key ways. The most important difference is that only one site can be selected as a home, whereas in foraging many sites can be used simultaneously, and there is no need for an individual forager to find the best site, but only one which is adequate. In addition to mechanisms for reaching unanimity, the bees must have a mechanism for knowing that a unanimous decision has been reached. Nothing like this occurs in foraging: the mechanisms of foraging regulation result in advertisement of multiple sites, and the presence of dances for a foraging site is apparently evidence enough that it is worth a recruit's attention. Finally, once the bees know that a unanimous decision has been made, there must be a signal that triggers take off. Again, this does not occur in foraging. While there is evidence of mechanisms that activate foragers, and recruit more bees to food-storage tasks, foraging remains essentially an individual enterprise guided by shared information. In contrast, the movement of a swarm to a new home site is one of the most dramatic whole-group activities seen in animal societies. The shared information in house-hunting is primary, and individuals have no other enterprise than gathering and communicating information.

The findings of this study provide a much more detailed description than was previously available of the repertoire and relative frequency of individual behaviors that lead to the group-level decision for a home site by a swarm of honey bees. Most of what we previously knew of individual behavior, for instance, was based on the records of the 3 bees shown in the figures of Lindauer's (1955) paper. What we have found casts new light on how the decision-making process occurs. We discuss these implications in separate sections below, following a discussion of the spatial scale of the process.

Spatial scale

The spatial scale of this process is impressive, and mirrors that of a colony's foraging (Visscher and Seeley, 1982). In searching for nest sites, a swarm of bees surveys an area of more than a hundred square kilometers (a circle enclosing 95% of the nest site finds in Figure 1 has an area of 147.8 km^2, and one enclosing 50% 13.9 km^2). Within this area, it is unknown how completely the bees search. The task is a daunting one: to find cavities in trees, structures, or the ground that are visible to searching bees only as openings the size of knotholes. Given the limited visual resolution of bee eyes, to find all such cavities would involve close-up inspection of the surface of all the trees in a forest! Complete or not, the bees' search is remarkably effective, and even in an area as nearly devoid of nest cavities as our Cactus City site, scouts occasionally returned with news of cavities in the surrounding mountains kilometers away.

As shown in Figure 3, the search distances of the Cranberry Lake swarm were greater than reported by Lindauer (1955); this may reflect a lower density but fairly uniform distribution of high-quality sites in the wooded area we studied, compared with a relatively high density of good nest cavities in buildings of war-damaged Munich in Lindauer's studies. The sites finally chosen by Lindauer's swarms, and by 13 swarms observed by Seeley and Morse (1977) had a median distance of about 900 m, and few swarms selected sites beyond 1500 m or closer than 300 m. The Cranberry Lake swarm chose a site at about 1950 m. Lindauer (1955)

hypothesized that bees preferred more distant nest sites over very close ones, but Seeley and Morse's (1977) study did not confirm this hypothesis. If nearby nest sites are preferred, it is surprising that scouts search and dance intensively for very distant nest sites. The most likely explanation is that the long distance searches increase the likelihood of finding superior cavities.

Temporal scale

Most of our swarms discovered and moved to nest sites quite quickly, sometimes on the same day as the first discovery of the site, and usually within 2 days. These times are not aberrantly short. Among Lindauer's (1955) 19 swarms, 13 moved within two days, 3 moved within 4 days, and 1 failed to move at all (for 2 there were no data). Griffin (1992) speculated that it is adaptive for the house-hunting process to proceed at a leisurely pace, allowing the bees to evaluate alternative nest sites, and to compare them under a range of conditions. However, our results do not support this idea; the swarms probably move as soon as they are able to complete the decision-making process.

Dances on swarms, as noted by Lindauer (1955), last considerably longer than dances for forage sites. On those return trips to the swarm in which they danced, the scouting bees of the Cholla swarm averaged 29.7 ± 33.0 (n = 142) dance circuits per trip. These times are significantly longer than Seeley (1994, Table 1) reported for forager bees recruiting to an especially rich sugar syrup feeder [n = 60, 11.4 ± 2.0 circuits per trip, $t_{200} = 4.29$, $P \ll 0.0001$), or than Camazine (unpublished data) found for pollen foragers recruiting to floral sources during the spring and summer in Ithaca, New York (n = 122,18.9 ± 24.2, $t_{262} = 2.60$, $P < 0.003$).

How a decision is reached

The process of reaching a unanimous decision comprises three aspects. First, there must be communication of finds, so that sites become familiar to a number of bees. Second, there must be some mechanism by which recruitment and visitation to non-chosen sites ceases. Third, there must be recognition of when the process is complete.

Spatial patterns and information centers

The spatial distribution of dances (Fig. 4) suggests that within the swarm cluster, information exchange is concentrated in a particular area, but spreads out over the swarm as time goes on. This pattern might be explained on both mechanistic and functional levels. The clustering of dances early in the process could result from individual bees returning to the same area of the swarm from which they departed, and in which they observed dances. Such a mechanism might allow scouts to improve their search by refining their information on nest site location through observing further dances. Also, at early stages of the process, when relatively few scouts have found nest sites to advertise, a small information center would make it easier for these scouts to recruit others than if the potential recruits were widely scattered. The spread of the sites of information transfer later in the process might, mechanistically, be a result of an accumulation of variance in bees returning to the same place on the swarm. Functionally, such a pattern might contribute to more efficient information transfer because of space limitations on the swarm as the number of dancers increases over time. It would also spread information about a site of growing consensus to scouts outside the initial information center in other areas of the swarm. The spread of dances more widely over the swarm, once a consensus has been reached, might also function to communicate to non-scout bees that a decision has been made and that takeoff is imminent.

Two models of how decisions might be reached

In its decision-making process a swarm begins with no recruitment dances, then dances build up, usually for several sites, and finally the dances for one site begin to predominate at the expense of the others until all or nearly all dances on the swarm indicate a single site. For this unanimity to be reached, two things need to happen. First, as suggested by Lindauer (1957), there must be positive feedback through recruitment for sites, so that the numbers of scouts visiting them and dancing for them increases. Second, there must be attrition: somehow scouts must stop dancing for "losing" sites. Lindauer presented more than one version of how this attrition occurs. One process of attrition is comparison: "those scout bees which at first had announced the inferior nesting places are won over by the more lively dances of their competitors and as a result themselves inspect this home – so that they can compare the two – then they naturally choose the better one" (Lindauer, 1957). However, Lindauer also suggested that some scouts drop out of the recruitment process and pass the decision to the next cohort of scouts: "the scout bees do not remain stubborn about their first decision, but after a shorter or longer time, they become silent and leave the further decision to the new scouts" (Lindauer, 1955).

These are two quite different formulations of the decision-making process: In the first, individual bees compare sites, and switch to the better one; that is, bees change their minds. In the second, bees merely drop out after performing a greater or lesser amount of recruitment, and the subsequent dynamics of the process are determined solely through sites competing for the attention of future scouts through gaining an edge in the positive feedback system of recruitment.

Lindauer's description of the house-hunting process has resulted in subsequent authors seizing on the house-hunting process as a particularly telling example of cognitive processes in insects, and these authors have generally emphasized the comparison aspect. Gould and Gould (1994), for example, wrote that a bee will "investigate the competition. If one of the alternatives is clearly better, the scout will switch allegiance and begin dancing for the new site…Over the course of several days a consensus builds among the scouts, and finally the swarm departs for its new home … Multiple cues at

competing sites are weighed in an ongoing process that resembles more the way humans evaluate real estate than any simple task-related behavior" However, Griffin (1992) was more cautious, pointing out that "Lindauer was only able to observe [nest-site comparison and switching] in a handful of cases, and it is not clear how large a role this [comparison] plays in the process of reaching a group decision."

Evaluating the two models

Our results suggest that direct comparison of sites is relatively rare in house-hunting. In the Cholla swarm no bees ever danced for both sites, though at least 5 bees did visit both, and 16 followed dances for both sites. In the Ocotillo swarm, where we could detect visits to both sites by bees that did not dance, we saw more comparison, with 6.3% of bees which had scouted the losing site switching over to the winning site, and 2.9% switching in the other direction. In some other swarms we have observed some switching of dances between sites, but its relative rarity suggests that comparison plays a minor role, if any, in the decision-making process.

The alternative model, of positive feedback and dropout, is more strongly supported by our observations. In Figures 3, 5 and 6D the stairstepped exponential rise in recruitment (either as scouting or dancing) reflects this feedback, and the individual records show that by far the most common kind of behavior among scout bees is to recruit for a relatively short period and then fall silent, generally without visiting the alternative site (see also Lindauer, 1955; Fig. 20). The stairstepped shape of the buildup curves suggest that a scout recruits a new cohort of scouts for a site, which in turn inspect the site and then recruit the next, larger cohort.

How do alternative sites compete in a positive feedback/dropout model?

A simple positive feedback and attrition system will function effectively if the parameters underlying the exponential rise in recruitment for alternative sites are slightly different, so that one has a chance to pull ahead onto a steep area of the curve, after which it will quickly and automatically come to dominate, especially if there are mechanisms of attrition for losing sites. The section above discusses what appears to be the principle mechanism of attrition, the dropout of dancers. There are a number of sources for differences in the recruitment dynamics to two sites, which fall broadly into random events and quality differences in the two sites.

Random differences

Bees are quite variable in their dancing intensity for the same site, and thus a site which happens to attract a vigorously-dancing scout will receive many recruits, even if the alternative site is of equal quality. Especially in the early stages of recruitment to our nest boxes, we noted that a single individual could have a dramatic impact on visitation to a site. For example, two of the West-box recruiters of the Cholla swarm danced quite vigorously with many bees following. Very soon after these bees stopped dancing, many bees arrived at the West nest box (Fig. 6A). Another source of random differences is time of discovery. A site that is discovered first may have several cycles of recruitment by the time another site of equal quality is discovered, thereby building up to an overwhelming majority before the second site can attract enough recruits to compete.

Quality differences

Bees grade their dancing to sites depending on the perceived quality of the sites. Lindauer (1955) mentions differences in both the duration and vigor of dances, and these differences are obvious on our swarms as well. In nectar foraging, it seems that the duration of dances is the important variable affecting dancing (Seeley, 1995). Lindauer (1957) suggests that scouts might be able to read site quality from dances and be "won over by the more lively dances of their competitors." To us, there appears to be striking differences in the vigor of dancing, and it merits further research whether the bees perceive differences in dance vigor aside from differences in dance duration (which are correlated, so a critical test will involve prematurely terminating high-vigor dances).

Distance from the swarm to the nest box could also affect dancing buildup, even if there were no differences in quality grading or discovery time for more distant sites, because differences in travel time could lengthen an individual bee's dancing and scouting cycle, decreasing recruitment to more distant sites. This could underlie the trend toward selection of nearby sites reported by Seeley and Morse (1977).

Why did the West site win in the Cholla swarm?

The Cholla swarm, where we have our most detailed information, illustrates a number of the above differences in recruitment buildup that may explain why the West site was selected. First, the West site was slightly closer to the swarm (146 vs. 174 m). Second, the West site was found first. As shown in Figure 6D inset, the buildup of dances for both the West and East sites followed a very similar course, but the West site was ahead in time, so that it reached the rapidly steepening part of the positive feedback recruitment curve earlier. Perhaps dances for the West site so vastly outnumbered those for the East site that recruitment to the East site ceased. Finally, the bees may have perceived quality differences between the East and West sites. Among the scouts which first danced during the initial period of site selection (up to about 11:40), when both sites were being recruited to, more of those for the West site showed the Type III pattern of continuing to dance throughout the search interval. Scouts for the West site also performed more dance circuits (though not significantly so), and these biases in dancing during the early part of the process may have strongly influenced the ultimate success of that site. It is not possible to say which of the above factors led to the choice for the West box, and all probably played some role.

How the decision is perceived

It turns out that in the perception that a decision has been reached it is neither necessary nor sufficient that unanimity has been reached. Lindauer (1955) reports two cases among his 19 swarms in which the bees took off without unanimity in the dances and tried to depart in two different directions. In our observations, we saw occasional dances for distant sites other than our nest boxes, and in three of our swarms, these dances continued at a low level up until swarm takeoff. In contrast, we have also seen situations (e.g., the Times swarm) in which only one site is ever advertised, so that unanimity is achieved from the first dance, but takeoff nonetheless awaits other developments.

In some way, then, the swarm decides that is it time to take off. To a human observer, the obvious criterion is that many dances are occurring, all for the same site. But do the bees census the dances and respond to the unanimity? The above arguments suggest that this is probably not the case, and that some other mechanism is responsible. Since there are shifts in behavior as takeoff nears, such as the resumption of dancing by Type II bees that had danced earlier but then became quiet, there must be some information available that takeoff is nearing. Similarly, the scouts for the winning West nest site in the Cholla swarm, and those which switched from East to West, were more active near swarm takeoff than those for the losing East nest site, who were nearly motionless on the swarm, often under other bees. Although these activity differences might be influenced by the fact that more of the West site bees had only recently begun dancing during this time interval, they also suggest that the bees might be responding to the developing decision in favor of the site with which they are familiar.

Aside from increasing unanimity, we observed an increase in buzz-running by scout bees at the nest site as takeoff approached. This is consistent with the possibility that scouts somehow assess the amount of scouting at the nest site, which in turn plays a role in concluding the decision.

How takeoff is triggered

The trigger for take off could occur without the need for a "switch" in which bees directly assess a change in the status of the house-hunting process and change behavior qualitatively. Take off may instead be triggered, as in a chain reaction, when a critical level of some activity is achieved. A likely candidate is buzz-running activity which is observed at low levels throughout the decision-making process, but reaches a crescendo near the time of take off.

Lindauer (1955) described buzz-running on the swarm as the principal signal for takeoff. However, in many of the swarms we observed it was rather uncommon. For example, we observed only 10 buzz-runners on the Cholla swarm prior to the beginning of swarm takeoff. Yet, buzz-running was always common on the swarm stand among the bees remaining after most of the bees had taken off. Also, we observed a high proportion of known (marked) nest site scouts remaining behind on the cage containing the queen after takeoff, suggesting that the scouts do play a special role in the takeoff process.

As takeoff nears, we noticed that bees on the swarm begin to make a high pitched piping vibration, as mentioned by Lindauer (1955) and Seeley et al. (1979). The origin of this sound is not known; it may be produced by buzz-running bees or by other bees in the swarm cluster stimulated by buzz-runners or other takeoff triggers. The vibration itself may play a role in triggering takeoff; playback experiments might help shed light on its role.

Conclusions

This study has deepened the detail of our knowledge about the events during house-hunting by honey bee swarms. Observations of individual bees confirm some patterns reported previously, such as the tendency of scouts to dance and then stop. Our results show that other aspects of swarm decision making probably work differently than formerly hypothesized. For example, nest-site comparison by individuals, which seemed characteristic, appears to be uncommon. Simultaneous observations of events at the nest site and the swarm cluster suggest a process of positive feedback and dropout, in which behavioral variability among individual scouts and stochastic events can play a large role.

Thus the wisdom of the swarm in reaching a unanimous decision on a single nest site resembles not a committee where individuals compare and choose nest sites and persuade others to their choice, but rather a self-organized system where simple rules for individual behavior lead to growing recruitment from some sites and dropout at others until a clear collective decision is reached.

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