Behav Ecol Sociobiol (1999) 45: 19–31

ORIGINAL ARTICLE

Thomas D. Seeley · Susannah C. Buhrman

Group decision making in swarms of honey bees

Received: 26 February 1998 / Accepted after revision: 16 May 1998

Abstract This study renews the analysis of honey bee swarms as decision-making units. We repeated Lindauer's observations of swarms choosing future home sites but used modern videorecording and bee-labelling techniques to produce a finer-grained description of the decision-making process than was possible 40 years ago. Our results both confirm Lindauer's findings and reveal several new features of the decision-making process. Viewing the process at the group level, we found: (1) the scout bees in a swarm find potential nest sites in all directions and at distances of up to several kilometers; (2) initially, the scouts advertise a dozen or more sites with their dances on the swarm, but eventually they advertise just one site; (3) within about an hour of the appearance of unanimity among the dancers, the swarm lifts off to fly to the chosen site; (4) there is a crescendo of dancing just before liftoff, and (5) the chosen site is not necessarily the one that is first advertised on the swarm. Viewing the process at the individual level, we found: (1) the dances of individual scout bees tend to taper off and eventually cease, so that many dancers drop out each day; (2) some scout bees switch their allegiance from one site to another, and (3) the principal means of consensus building among the dancing bees is for bees that dance initially for a non-chosen site to cease their dancing altogether, not to switch their dancing to the chosen site. We hypothesize that scout bees are programmed to gradually quit dancing and that this reduces the possibility of the decision-making process coming to a standstill with groups of unyielding dancers deadlocked over two or more sites. We point out that a swarm's overall strategy of decision making is a "weighted additive strategy." This strategy is the most accurate but also the most demanding in terms of information processing, because it takes account of all of the information relevant to a decision problem. Despite being composed of small-brained bees, swarms are able to use the weighted additive strategy by distributing among many bees both the task of evaluating the alternative sites and the task of identifying the best of these sites.

Key words *Apis mellifera* · Communication · Dance language · Decision making · Swarming

Introduction

One of the most spectacular examples of an animal group functioning as an adaptive unit is a swarm of honey bees choosing its future home. This phenomenon occurs in the late spring and early summer when a colony outgrows its hive and proceeds to divide itself by swarming. The mother queen and approximately half the worker bees leave the parental hive to establish a new colony, while a daughter queen and the remaining workers stay behind to perpetuate the old colony. The swarm bees leave en masse, quickly forming a cloud of bees just outside the parental hive, but within about 20 min they coalesce into a beard-like cluster at an interim site (usually a nearby tree branch) where they choose their future dwelling place. The nest site selection process starts with several hundred scout bees flying from the swarm cluster to search for tree cavities and other potential nest sites. The scouts then return to the cluster, report their findings by means of waggle dances, and decide which one of the dozen or so possible nest sites that they have discovered should be the swarm's new home. Once the scouts have completed their deliberations, they stimulate the other members of the swarm to launch into flight and then steer them to the chosen site (the biology of swarming is reviewed in Michener 1974; Seeley 1982; Winston 1987).

T.D. Seeley (✉)
e-mail: tds5@cornell.edu, Tel.: +1-607-2544301
Fax: +1-607-2544308

S.C. Buhrman
Section of Neurobiology and Behavior, Cornell University
Ithaca, NY 14853, USA

Previous investigations of the functional organization of honey bee swarms have focused on the mechanisms of cluster formation at the interim site (Ambrose 1976), thermoregulation in the swarm cluster (Heinrich 1981, 1993), evaluation of potential home sites (Seeley 1977, 1985; Witherell 1985), and movement to the chosen site (Lindauer 1955; Seeley et al. 1979). To date, there is just one study, by Lindauer (1955, 1961), which has examined how the scout bees collectively choose the swarm's new home. Lindauer reported that a scout bee can communicate the location of a potential nest site to other scouts on the swarm cluster by means of the waggle dance, and that the "enthusiasm" of a dancer depends on the quality of the site being advertised. He also observed that initially, the scouts dance for a number of different sites, but that eventually they all dance for just one site. Shortly thereafter, the swarm lifts off and flies to this site. Lindauer suggested that the dancers achieve a consensus by influencing one another, for he observed bees that ceased to dance for one site and later danced for another site after being recruited to it. However, the precise mechanisms of the decision-making process in honey bee swarms remain unclear even though they have been the subject of much discussion (Lindauer 1955, 1961, 1975; von Frisch 1967; Wilson 1971; Griffin 1981, 1992; Dawkins 1982; Markl 1985).

This study resumes the analysis of group decision-making in honey bee swarms. One thing that favors this analysis is that the decision-making process is an external one: it occurs on the surface of the swarm cluster where it is easily observed. The swarm's surface is where the scout bees produce the waggle dances which advertise the sites they favor. As Lindauer (1955, 1961) discovered, one can monitor the building of a consensus among a swarm's scouts by watching their dances. The technology of videorecording was not available to Lindauer, however, so he could not make a complete record of the scout bees' dances. It seemed to us, therefore, that a sensible first step in probing further the bees' decision-making process would be to utilize videorecording techniques to make a complete record of the scout bees' dances and thereby obtain a detailed picture of the basic phenomenon under investigation. We did this with three swarms, each of which consisted entirely of bees labelled for individual identification. With each bee so labelled, it was possible to follow each bee's history of dancing throughout the decision-making process. Hence our videorecords yielded not only a synoptic view of this process at the level of the whole swarm, but also insights into how this group decision making arises from the behavior of individual bees.

Methods

General plan of study

Our overall plan was simple: (1) videorecord all the dances performed on each of three swarms composed of individually identifiable bees; (2) determine for each dance the time of its performance, the location (direction and distance) of the nest site it indicated, the number of waggle runs in the dance, and the identity of the bee that performed the dance; (3) synthesize this mass of information by making a series of plots, one for every 2 h of data collection, showing the number of bees that danced for each nest site. We suspected that these plots, combined with information about when each individual performed her dances, would help us understand how the dancing bees reach an agreement about the location of their future home.

We examined the decision-making process in just three swarms because the extraction and analysis of the information from the videorecords for each swarm was extremely time consuming. Although each swarm gave rise to only 12–16 h of videorecords, the subsequent analysis of these videorecords and of the huge data set they yielded required more than 250 h of painstaking work per swarm.

Study sites

Of the three swarms studied, two (swarms 1 and 3) were observed at the Liddell Field Station of Cornell University, in Ithaca, New York (42°26′ N, 76°30′ W), and one (swarm 2) was observed at the Cranberry Lake Biological Station (44°09′ N, 74°48′ W) in the Adirondack State Park, Saint Lawrence County, in northern New York State. The landscape around the Liddell Field Station consists of fields, many tracts of woods, and residential areas, whereas that around Cranberry Lake consists of bogs, vast expanses of woods, and lakes. The woods at both sites are unmanaged and contain many old trees with cavities, so undoubtedly there were numerous potential nest sites for the bees.

Swarm preparation

All three swarms were artificial swarms composed of one queen bee and several thousand worker bees labelled for individual identification. Each swarm was prepared as follows. First, we removed the queen bee from a thriving colony, placed her in a small (2 × 3 × 8 cm) queen cage, and suspended this cage inside a large (14 × 26 × 35 cm) swarm cage which eventually would hold the entire swarm. Next, using a large funnel, we shook approximately 1000 worker bees (from the same colony that provided the queen) into each of four medium-size (10 × 10 × 25 cm) holding cages. The bees were then shaken from the holding cages into plastic bags, with about 25 bees per bag, and these were placed in a 3–4 °C refrigerator. Once the bees in a bag were immobilized by the cold, they were spread on a block of reusable "ice" where they remained immobile while we glued a bee tag (Opalithplättchen, Graze, Endersbach, Germany) to each bee's thorax and applied a paint mark to her abdomen (see Seeley 1995, p. 80, for additional details). When all the bees from a plastic bag had been labelled, we transferred them from the ice to the swarm cage in which we had previously placed their queen. Here the worker bees warmed up, clustered around their queen, and drank from a sugar water feeder mounted atop the cage. After all the bees in a swarm had been labelled, each swarm was fed lavishly with concentrated sugar solution by brushing it on the sides of the swarm cage. This enabled the bees to become engorged with food, as is characteristic of bees in swarms (Combs 1972).

Swarms 1 and 3 each contained 4000 newly labelled worker bees and each swarm was made from a different colony. Swarm 2, however, contained the remaining bees from swarm 1 plus 1000 newly labelled bees from the same colony that provided the bees for swarm 1. Table 1 shows the colony of origin, date of preparation, and dates of observation for each swarm.

Swarm mount and videorecording

To determine accurately the location of the site indicated by each dance, we needed to (1) arrange for the scout bees to perform their

Table 1 Specifications of the swarms used in this study. The sizes of swarms 1 and 3 were determined by subtracting from 4000 (the number of bees labelled) the number of bees found dead in the swarm cage after installing the swarm on the mount. The size of swarm 2 was determined by counting the bees in the swarm after observing it

Swarm	Origin of bees	Period of preparation	Period of observation	Swarm size	Number of bees that danced	Percent of bees that danced
1	Colony A	16–18 June 1997	19–21 June 1997	3252 bees	73	2.2
2	Colony A	3 July 1997	7–11 July 1997	2357 bees	47	2.0
3	Colony B	16–19 July 1997	19–22 July 1997	3649 bees	149	4.1

dances on a planar surface set perpendicular to the videocamera, so that we could accurately read the angle of each dance's waggle runs, and (2) prevent the dancing bees from seeing the sun or blue sky, so that we could prevent light-dependent "misdirection" in the scouts' dances (von Frisch 1967, pp. 196–204). To meet the first need, we installed each swarm on the mount shown in Fig. 1, which is similar to the swarm mount designed by Anja Weidenmüller (unpublished data). The queen remained in the small queen cage and this was inserted in the opening in the board beneath the feeder bottles. The workers could contact the queen only via the surface of the queen cage facing the movable screen. As a result, when the swarm bees were shaken from the swarm cage they formed a compact cluster over the queen cage. The distance of the screen from the board was adjusted so that the outermost layer of bees in the swarm was standing on the outer surface of the screen. Returning scouts landed on the screen and performed their dances while walking on it.

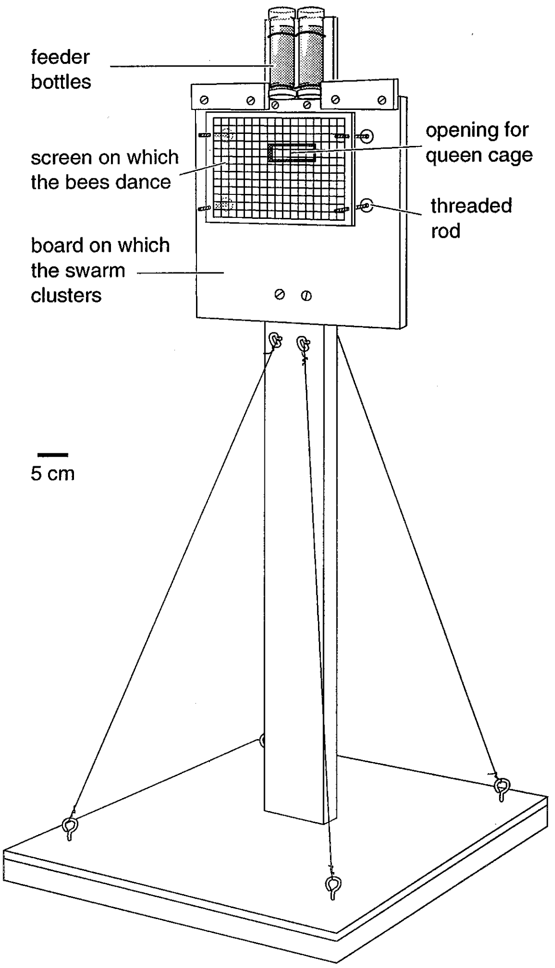


Fig. 1 Swarm mount used for videorecording the dances of the scout bees

To meet the second need, the bees on the swarm mount were placed inside a small (122 × 122 × 175 cm) three-sided hut that was positioned outside a laboratory building, approximately 1 m away, with the open side of the hut facing a window. This configuration of bees, hut, and building prevented the bees dancing on the swarm cluster from seeing any celestial cues, but at the same time allowed the scouts to fly freely from the cluster. The swarm was illuminated for videorecording by two 20-W fluorescent lamps mounted vertically inside the hut.

The dances of the scout bees were recorded with a videocamera (Panasonic WV-F250B) with docking videocassette recorder (Panasonic AG-7450) equipped with a time code generator (Panasonic AG-F745). The camera was set up inside the laboratory building where it was aimed at the swarm through an open window. The camera lens was adjusted so that the camera field of view encompassed the entire screen of the swarm mount, hence the entire surface on which dances were performed. Each day, the videocamera was turned on before the dancing began and was left on until after the last dance was completed. Because the numbers of the bee tags used to label the bees were indistinct in the playbacks of our videotapes, we recorded the identity of each dancer by stationing ourselves beside the swarm throughout the observations, pointing to each dancing bee, and announcing her identity so that it was recorded on the audio channel of the videotape. The time of day was recorded automatically on the videotape.

To eliminate the need to forage, and thereby ensure that all the dances performed on the swarm were for potential nest sites, the bees were constantly fed sugar solution by means of two feeder bottles on the swarm mount.

Video transcription

Videotapes were analyzed using a videocassette player with variable-speed playback (JVC BR-S525U). For each dance, we noted (1) the time of day at the start of the dance, (2) the identity of the dancing bee, (3) the angle of dancing, (4) the waggle run duration, and (5) the total number of waggle runs produced in the dance.

The angle of dancing was determined for each dance by measuring the angles of five separate waggle runs and then calculating the mean of these five measurements. If the dance consisted of fewer than five waggle runs, then the five measurements were spread as equally as possible over the available waggle runs. The angle of each waggle run was measured using a large protractor similar to the one described by von Frisch (1967, p. 26). It consisted of a circular Plexiglas plate with parallel lines 2 cm apart and a peripheral scale drawn upon it, which rotated over a square Plexiglas plate that was mounted in front of the screen of the videomonitor. At the top of the square plate, vertically aligned with the center of the circular disk, an index line was marked. To measure the angle of a waggle run, the circular plate was rotated until the direction of the waggle run (the direction that the dancing bee's head pointed while waggling) was aligned with the parallel lines drawn on the circular plate. The angle of the waggle run, relative to vertical, was then read from the peripheral scale by reference to the index line.

The waggle run duration was determined for each dance by measuring the durations of five separate waggle runs and then calculating the mean of these five measurements. If the dance consisted of fewer than five waggle runs, then the five measurements were spread as evenly as possible over the available waggle runs. The duration of each waggle run was measured with a stopwatch while playing the videotape at normal speed.

Data analysis

For each dance, we determined the direction and distance of the potential nest site indicated by the dance. The direction was determined by computing the sun azimuth at the time of each dance using a program for the Hewlett-Packard 41C calculator, and then adding the sun azimuth to the angle of dancing. The distance was determined by converting the waggle run duration to a distance using a calibration curve made from data published by von Frisch (1967, Table 13).

For each swarm, we made a master table in which we listed in chronological order every dance performed on the swarm. This table also listed for each dance, the location (direction and distance) of the site it indicated. There were obvious clusters of the sites indicated by the dances, with each cluster corresponding to a potential nest site. We labelled each such cluster of dances (i.e., potential nest site) with an alphabetical letter, assigning letters in the order in which the sites were first reported on the swarm. In this way we were able to associate each dance with a particular site. We then determined for every 2-h block of observations (corresponding to a single videotape), which sites were advertised by which bees. Then for each site that was advertised in the 2-h block, we determined how many different bees danced for it and how many total waggle runs were produced by these bees.

Finally, for each swarm we assembled a notebook containing one page for each bee in the swarm that performed at least one dance. On each page we placed, in chronological order, all of our records of dancing by a particular bee, thereby creating a compact summary of this bee's contribution to the swarm's decision-making process.

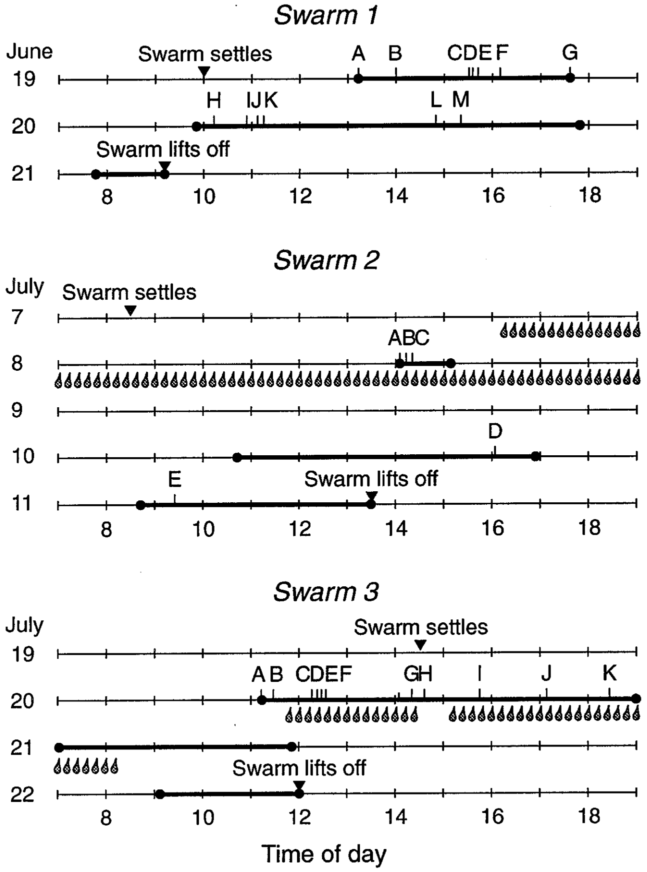


Fig. 2 Daily time lines for each swarm showing some of the major events in the decision-making process: when the swarm settled and began the decision-making process, when each of the alternative nest sites was first reported on the swarm (indicated by *uppercase letters*; see Figs. 3–5), and finally when the swarm finished its decision making and lifted off (*raindrop symbols* denote periods of rainy weather when there was no flight from the swarm; *bold lines* denote the periods of dancing on the swarm)

Results

Group-level view

Figure 2 shows for each swarm a set of daily time lines along which are marked some of the key points in the decision-making process: when the swarm settled into a cluster, when the scouts started and stopped dancing each day, when each of the potential nest sites was first reported, and when the swarm finally lifted off. In each case, the time when dances were performed was spread over 3 days and totalled some 12–16 h. Given this similarity in the total dance time for the three swarms, we are able to depict in Figs. 3–5 the record of dancing on each swarm by means of a standard, eight-panel diagram. Each panel shows for an approximately 2-h period, the number of bees that danced for each potential nest site and the total number of waggle runs that the dancing bees performed for each site.

We can see in Figs. 3–5 that the general course of the decision making was similar for all three swarms. During the first half of the decision-making process (i.e., in the first four panels), the scout bees reported the majority of the potential nest sites that each swarm would consider: 11 out of 13 sites in swarm 1, 3 out of 5 sites in swarm 2, and 11 out of 11 sites in swarm 3. We can also see that during the first half of the process, the dancing bees did not advertise any one of the alternative sites more strongly than any other. But then, during the second half of the decision-making process, one of the sites that had been advertised during the first half suddenly (in swarms 1 and 2) or gradually (in swarm 3) began to be advertised more strongly than all the others. Indeed, during the last hour or so of the decision making, the site that had emerged as the front-runner became the object of all the dances performed on the swarm: by the end there was unanimity among the dancing bees.

Examination of Figs. 3–5 reveals several other consistent features in the decision-making process besides the conspicuous transition from diversity to uniformity in the sites advertised by the dances. One such similarity is the crescendo in dancing at the end of the decision making. If, for each swarm, one compares the last panel with the seven prior panels in terms of number of dancing bees, dances, and number of waggle runs, one sees that the last panel has by far the highest number of each. A second pattern shown by each swarm is the way in which the site that was ultimately chosen was not the site that was first advertised on the swarm. In swarm 1

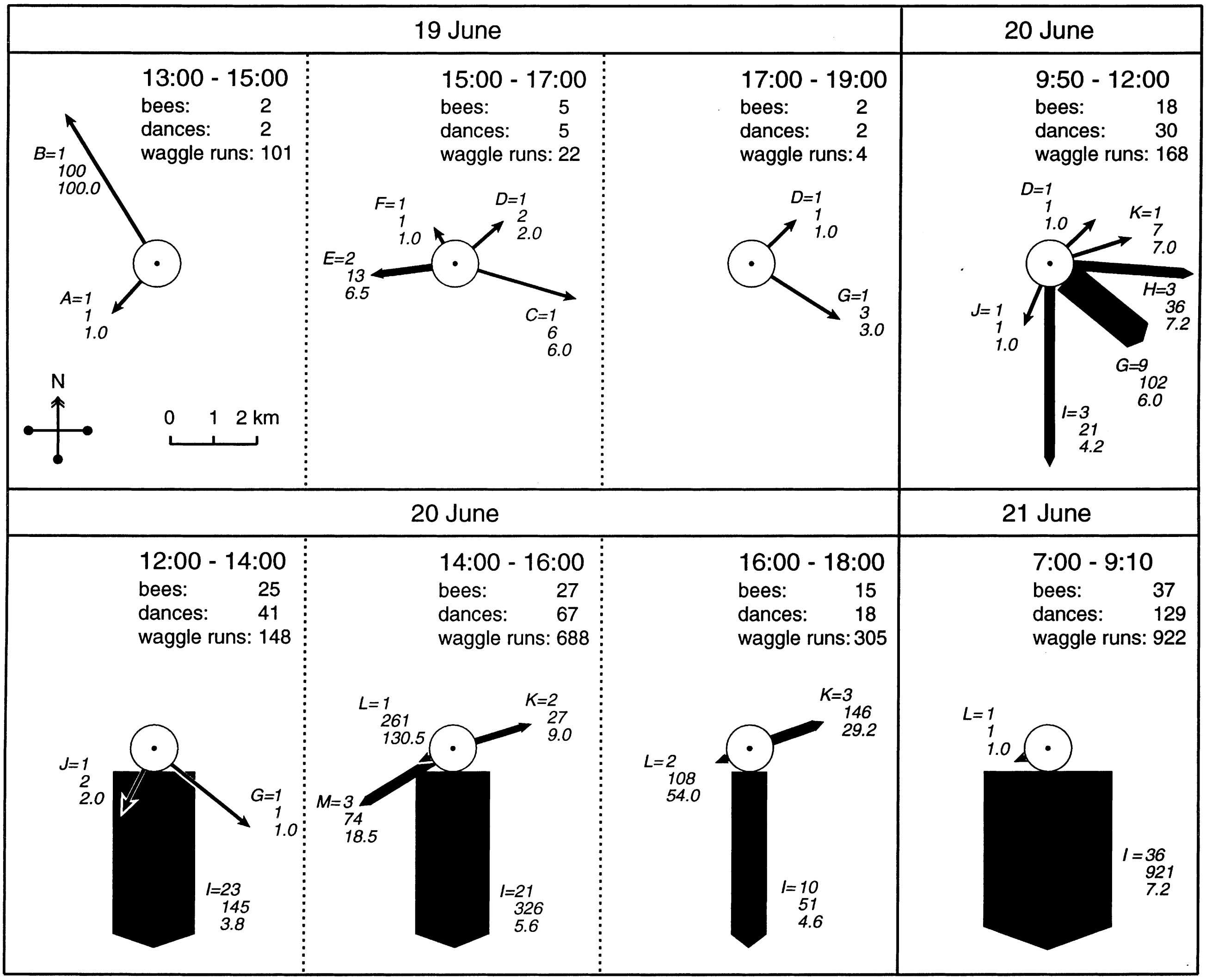


Fig. 3 History of swarm 1's decision-making process from the time that the first potential nest site was advertised on the swarm (shortly after 1300 hours on 19 June, see Fig. 2) until it lifted off to fly to its new home (at 0910 hours on 21 June). The *circle within each of the panels* represents the location of the swarm; *each arrow pointing out from the circle* indicates the distance and direction of a potential nest site; the *width of each arrow* denotes the number of different bees that danced for the site in the time period shown. The *set of numbers at the tip of each arrow denotes three things*: *top* the number of bees that danced for the site; *middle* the number of waggle runs performed for the site; *bottom* the mean number of waggle runs per dance for the site. The *numbers after "bees", "dances," and "waggle runs"* within each panel denote the total number of each (summed over all the potential nest sites) for the time period shown

the chosen site was the 9th out of 13 sites in order of discovery, in swarm 2 it was the 2nd out of 5 sites, and in swarm 3 it was the 7th out of 11 sites. A third pattern shared by all the swarms is that many potential nest sites are advertised only weakly and briefly on the swarm, that is, by just one to three bees and often in just one or two panels (hence for at most 2–4 h). This was the case for sites A, B, C, D, E, F, H, J, K, L, and M in swarm 1; for sites A, C, and D in swarm 2; and for sites C, E, F, H, I, J, and K in swarm 3. A fourth common pattern is that the potential nest sites were distributed randomly with respect to direction. For all three swarms the bearings of the potential nest sites have a distribution that cannot be distinguished from a uniform distribution ($P > 0.05$ for each swarm, Rayleigh test). And fifth, in all three swarms, most of the potential nest sites were located far from the swarm cluster. The mean swarm-to-site distance was 1808 m for swarm 1, 2240 m for swarm 2, and 1718 m for swarm 3. Thus we see that the three swarms showed numerous similarities in the way they chose their nest sites.

There was, however, one important aspect of the decision-making process that was not shared by the three swarms. Only in swarm 3 did there appear to be a real "debate" among the dancing bees. As is shown in Figs. 3 and 4, on both swarms 1 and 2 just one potential nest site was advertised strongly – that is, by more than ten bees in a 2-h period – and this was the site that was ultimately chosen. In swarm 1 this was site I and in swarm 2 it was site B. The only serious rivals to these chosen sites were site G in swarm 1, and site E in swarm 2. But in swarm 1, the dancing for site G faded quickly once site I began to be advertised, between 0950 and

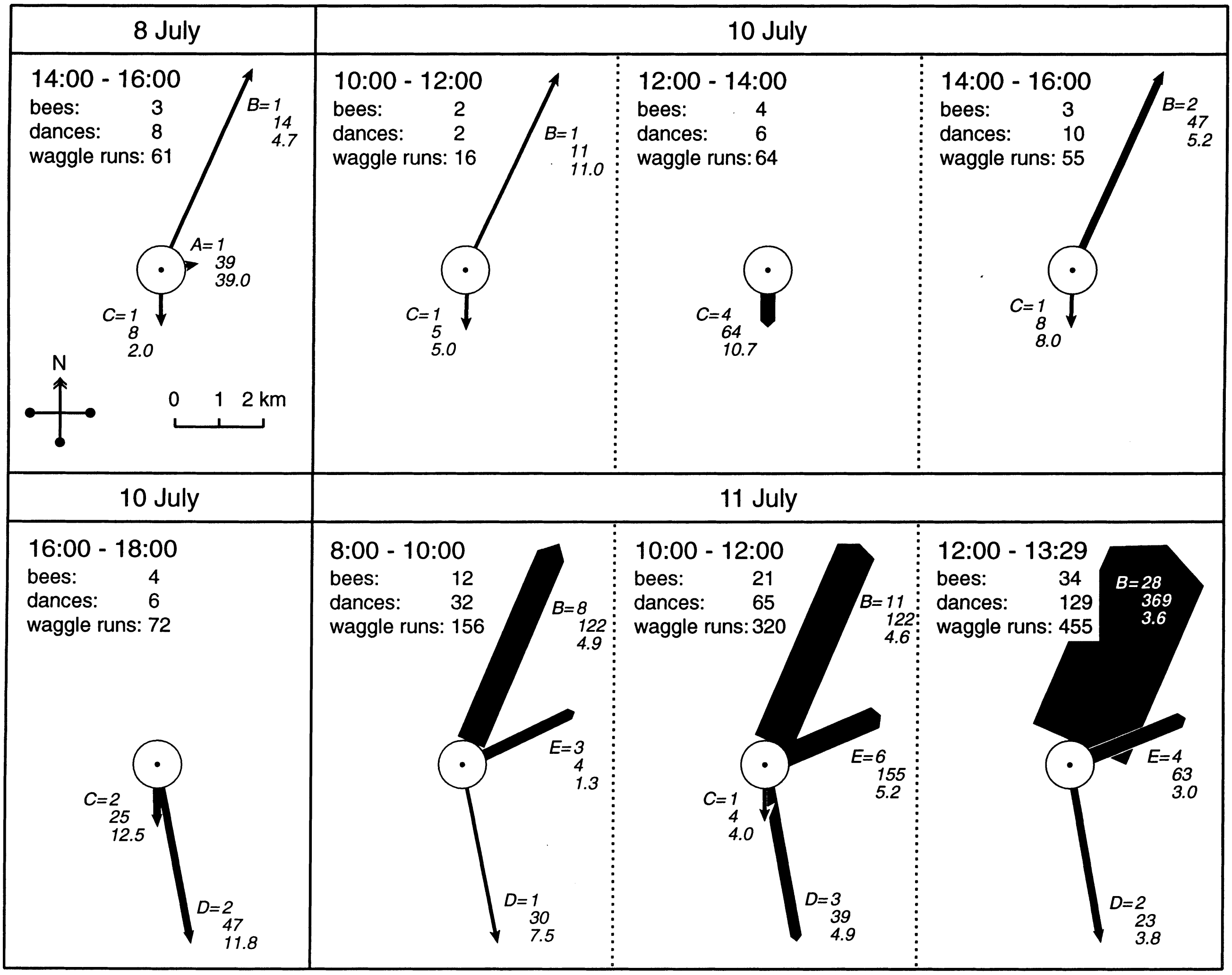


Fig. 4 As in Fig. 3, but for swarm 2

1200 hours on 20 June. And in swarm 2, the dancing for site E seems to have begun too late to overcome the lead held by site B. Site E began to be advertised only on the morning of the final day of the decision-making process, at which time eight bees were already engaged in advertising site B. Although site E stimulated several bees to produce vigorous dances for it over the next 3 h, these bees were never able to reduce the lead held by the site B scouts, and eventually the site E scouts ceased dancing. Thus, in both of the first two swarms there was little disagreement among the dancing bees as to which site should be their new home even though numerous alternatives were presented by the scout bees. Hence for these two swarms it seems that the dancing bees rather easily achieved the broad agreement that marks the end of the decision-making process.

The decision making proceeded with greater complexity in swarm 3 (Fig. 5). In this case, the scout bees found three sites – sites A, B, and G – which elicited strong dancing by several bees over periods lasting several hours, and so were represented by hundreds or thousands of waggle runs. While watching this swarm, we thought at first that site A would be the chosen site, for during the first 2 h of dancing it gained a strong lead among the dancers. But the advertising of site A faded after several hours. Meanwhile the dancing for sites B and G became stronger and stronger. By the end of the first day (20 July), it was clear these two sites were the leading candidates, though it was not clear which site would ultimately be chosen. Between 1700 and 1900 hours site B led site G in terms of both dancers (13 vs 9) and waggle runs (920 vs 765), but there was no doubt that the scout bees were still far from an agreement. The second day (21 July) began with both sites continuing to receive strong, nearly equal advertising by the dancers, but over the course of the morning the dancing for site G strengthened while that for site B weakened. If rain had not shut off the debate at the end of the morning, it seems likely that all the dances would have been for site G by sometime in the afternoon on 21 July. As it was, the bees that danced on the morning of 22 July were unanimous in advertising site G and at 1158 hours, the swarm lifted off and flew in the direction of site G.

This synoptic view of the history of the scout bees' dances on three swarms leaves us with a clear picture of

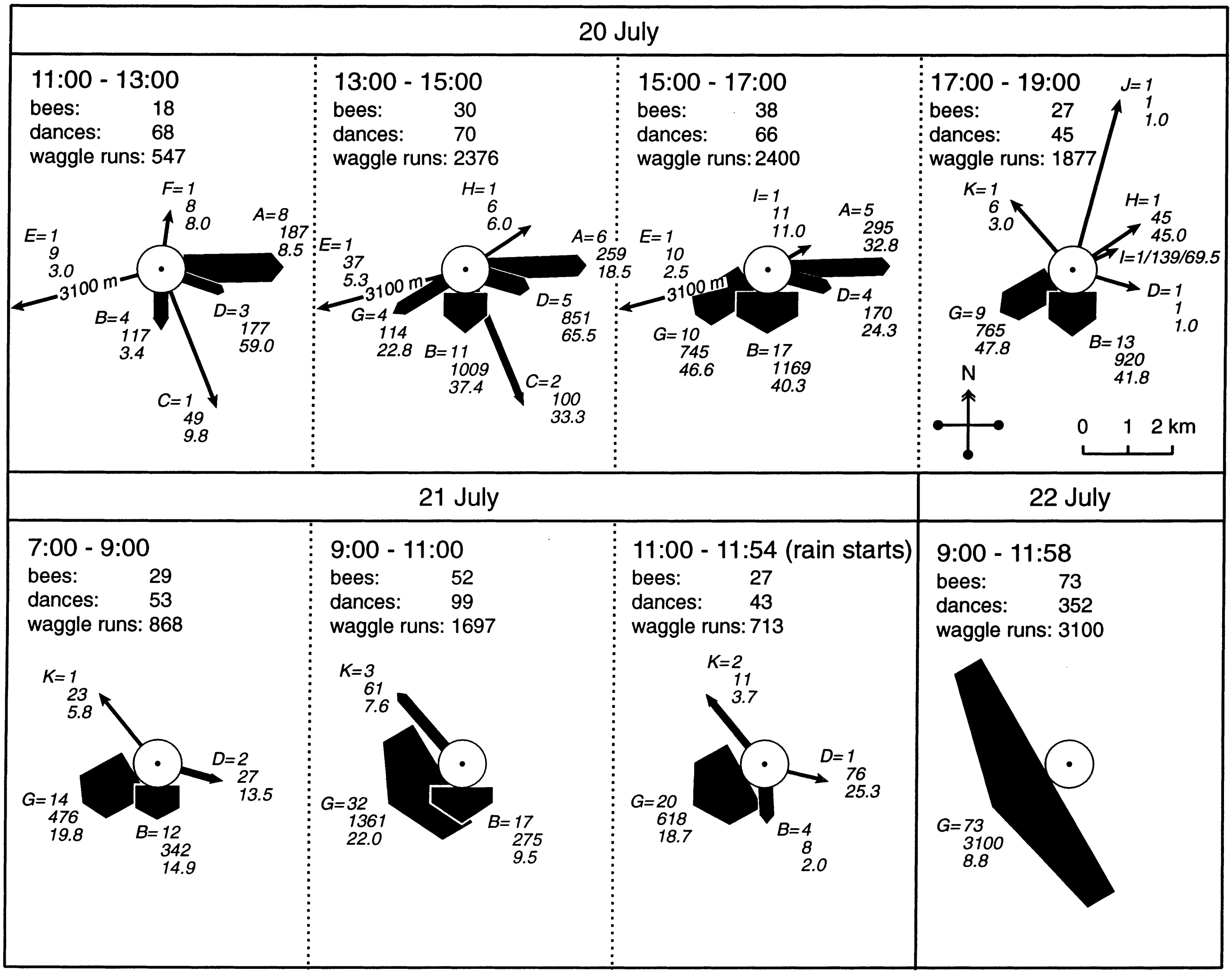


Fig. 5 As in Fig. 3, but for swarm 3

the way that the bee's decision-making process starts with dances on the swarm advertising a variety of potential nest sites, and then ends with all the dances advertising just one site. Sometimes, the building of a consensus among the dancing bees proceeds simply, as in swarms 1 and 2, when just one of the potential sites elicits strong dancing. Other times, the consensus building appears to be more complex, as in swarm 3, when each of several sites elicits much dancing. If we assume that achieving unanimity among the dancing bees lies at the heart of the decision-making process, then the key question before us now is this: how exactly do the dancing bees achieve a unanimous agreement about their future home site? To solve this puzzle, we must turn to examining the decision-making process at the level of individual bees.

Individual-level view

How many bees participate in the dancing?

In Table 1 we indicate for each of our three swarms, the number of different individuals that performed at least one dance. This number varied between 47 and 149, representing 2.0–4.1% of the bees in a swarm. Thus the dancing bees in a swarm form a fairly large group in absolute terms, but only a small group in relation to the total population of a swarm.

How many alternative sites does each dancing bee advertise?

As is shown in Table 2, in each of the three swarms, a large majority (76–86%) of the bees that performed dances did so for just one of the several potential nest sites that was reported on their swarm. A small minority (11–22%) of the dancers danced for two sites. And only a tiny percentage (2–3%) danced for three or more sites. Since only a rather small fraction of the dancers ever dance for multiple sites, the process of consensus-building among the dancers must *not* involve a large fraction of the bees switching from dancing for one site to dancing for a second site.

Table 2 Distribution of the number of potential nest sites advertised by individual bees

Number of sites danced for by a bee	Swarm 1		Swarm 2		Swarm 3	
	Number of bees	%	Number of bees	%	Number of bees	%
1	63	86.2	39	83.0	113	75.9
2	8	11.0	7	14.9	33	22.1
3	1	1.4	1	2.1	3	2.0
4	1	1.4	0	0.0	0	0.0
Total	73	100.0	47	100.0	149	100.0

What is the dropout rate of the dancers?

To address this question, we first assigned each dancing bee in a swarm to one of three cohorts according to the day on which the bee *began* to dance. Then we determined how many bees in the first cohort danced again on the 2nd or 3rd days, and how many bees in the second cohort danced again on the 3rd day. The fates of the three cohorts in each swarm are shown in Fig. 6. Here we see that many bees cease dancing (drop out) from one day to the next. In swarm 1, for instance, less than half of the bees that first danced on day 1 (cohort I) danced on day 2 or on day 3, and only about a third of the bees that first danced on day 2 (cohort II) danced on day 3. Such high dropout rates were also found in the other two swarms. These findings reveal that in our swarms, an important part of the process by which dancer consensus was achieved was a high dropout rate by the dancers. In particular, the high dropout rate of the early dancers (the bees in cohorts I and II) may explain why many of the alternatives to the ultimately chosen site were advertised early in the decision-making process but not later on. If the small number of proponents of these alternative sites all stopped dancing before they had recruited other bees, then these alternative sites would be dropped from the debate.

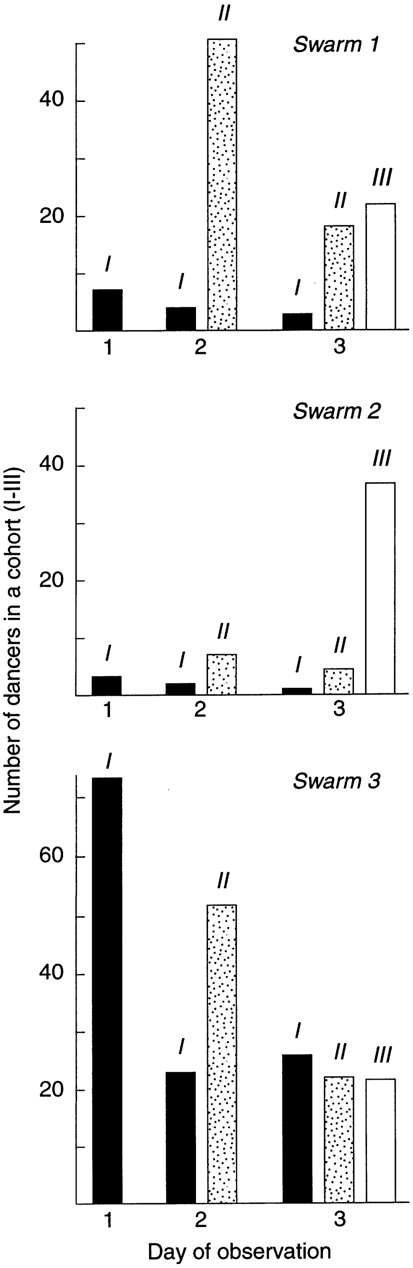
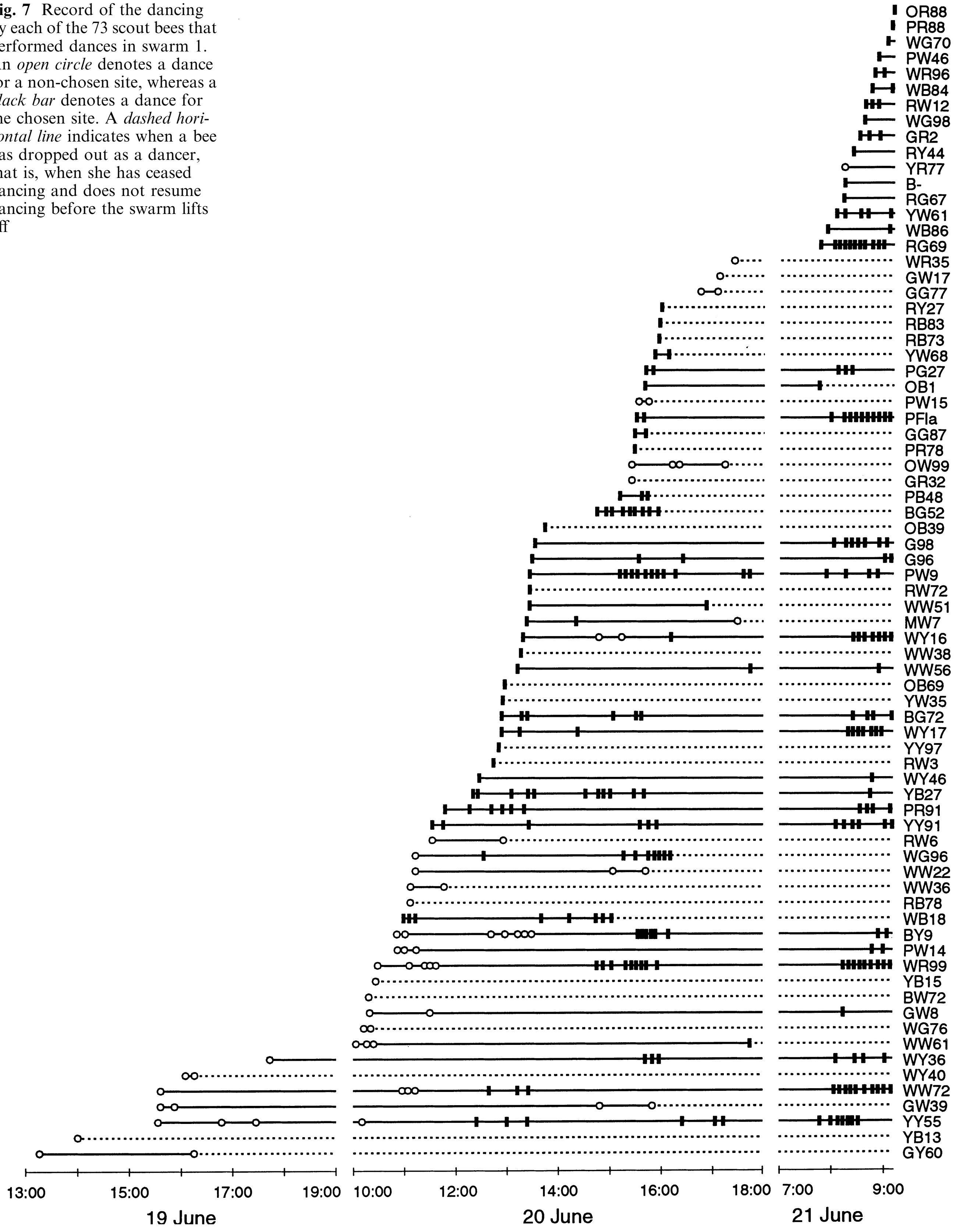


Fig. 6 Plots for each swarm of the number of bees that began dancing on each of the 3 days when decision making was observed, and how many bees in each of these cohorts again danced on subsequent days

How important is ceasing dancing compared to switching dancing in the building of a consensus among the dancers?

To achieve consensus among the dancing bees, all of the bees that dance for a potential nest site other than the ultimately chosen site must, at some point, stop dancing for the non-chosen sites. This requires each bee that dances for a non-chosen site do one of two things: *cease* her dancing altogether or *switch* her dancing from the non-chosen to the chosen site. To determine the relative importance of these two processes, we plotted the dancing history of each dancer in each swarm, noting whether each dance was for a non-chosen site or the chosen site. Figure. 7, for example, shows the plot for the 73 dancers in swarm 1. Using these plots, we divided the bees into two groups, those that danced initially for a non-chosen site, and those that danced initially for the chosen site. Then for each group we determined what fraction of the bees fell into each of three categories: (1)

Fig. 7 Record of the dancing by each of the 73 scout bees that performed dances in swarm 1. An *open circle* denotes a dance for a non-chosen site, whereas a *black bar* denotes a dance for the chosen site. A *dashed horizontal line* indicates when a bee has dropped out as a dancer, that is, when she has ceased dancing and does not resume dancing before the swarm lifts off



bees that continued dancing for their initial site type (chosen or non-chosen) until the end of the decision making, (2) bees that switched to the other site type by the end, and (3) bees that ceased dancing by the end. We defined "the end" as the period of 1 h before liftoff. If a bee did not dance during this final hour she was put in category 3. If a bee did dance during this final hour she was put in category 1 or 2 depending on whether her final dance was for the same or different site type (chosen or non-chosen) as her first dance.

The results of this analysis are shown in Table 3. Most importantly, among the bees that initially danced for a non-chosen site, in all three swarms, the large majority (67–80%) ceased dancing by the end, only a small minority (20–33%) switched their dancing to the chosen site, and none continued dancing for a non-chosen site until the end. We see a different pattern among the bees that initially danced for the chosen site. Here less than half of the bees (19–48%) ceased dancing by the end, none switched dancing to a non-chosen site, and more than half (52–80%) continued dancing for the chosen site until the end. Thus we have a curious result: the process of building a consensus among the dancing bees relies more upon bees ceasing to dance than upon bees switching their dances to the chosen site.

Why do bees stop dancing for the non-chosen sites?

One possible explanation for the gradual disappearance of bees dancing for the non-chosen sites is that there is high mortality among the scout bees. These bees fly hither and yon, crawl into dark cavities, and perform other seemingly dangerous activities, so it is reasonable to suspect that the scouts' mortality is high. If the mortality rate among dancers for non-chosen sites is higher than their "birth" rate, that is, the rate at which these bees recruit others to dance for the non-chosen sites, then this group of dancers – and their dances – will literally die out. However, we found the mortality rate of scout bees to be low. We censused the bees in swarm 2 at the end of their 5-day decision-making period and found that only 3 of the 47 bees (6.3%) that we had observed dancing on this swarm were missing. Similar results were obtained from two more swarms, each of which had a 2-day decision-making period: 2 out of 27 dancers (7.4%), and 3 out of 40 dancers (7.5%) were missing at the end (unpublished results from the study of Gilley, in press). Thus it seems clear that high mortality among scout bees is not the reason for the gradual disappearance on swarms of dances for the non-chosen sites.

This conclusion implies that the dances for non-chosen sites ultimately fade away because the bees that perform them decide either to cease dancing altogether or to switch to dancing for the chosen site. What might cause these bees to make this decision? The cause(s) could be *external* or *internal*, or both. External influences might include such things as encountering on the swarm a bee dancing extremely enthusiastically for the chosen site, or experiencing an absence of other bees at a potential nest site (indicating that this site is not succeeding in the competition for the attention of the scout bees). Internal influences might include a neurophysiological process which causes every nest site scout to gradually lose her motivation to dance for a site, even one that is high in quality. Such a process could foster consensus building among dancers. Automatic fading of each bee's dancing would lower the odds of the decision making coming to a standstill with groups of unyielding dancers deadlocked over two or more sites. Also, it might help the dancers reach unanimity more quickly than they would otherwise, for endowing each bee with an automatic tendency to lose interest in any given site would make each bee a highly flexible participant in the decision-making process.

Our observations do not provide evidence for or against the existence of external influences on the bees' tendency to stop dancing, but they do provide some evidence supporting the hypothesis that scout bees have an internally driven tendency to stop dancing for a site. Some of this evidence is presented in Fig. 8, where we show the dance records of all 20 bees in swarm 3 that performed more than five dances in a single day for a single nest site. For most of these bees, we see that their earlier dances contained more waggle runs than their later dances. When a regression line was fitted to each bee's dance data, we found that for 17 of the 20 bees, the slope of the regression line was negative (the 3 exceptions are OW28, MY69, and MW50). Statistical analyses revealed that for 12 out of these 17 bees, the negative slope of the regression line was significantly different from zero ($P < 0.05$) (the 5 exceptions are bees RR69, MR23, OG25, PG99, and MB23). It should be noted that the bees whose regression lines have significantly negative slopes include both bees that danced for non-chosen sites A, B, and D (bees OR11, MY48, OW61,

Table 3 The fates of bees that danced initially for a non-chosen or chosen nest site

	Swarm 1	Swarm 2	Swarm 3
Bees that danced initially for a non-chosen site	26 bees	15 bees	72 bees
(1) Continued dancing for such a site until end	0%	0%	0%
(2) Switched dancing to the chosen site by end	27%	20%	33%
(3) Ceased dancing by end	73%	80%	67%
Bees that danced initially for the chosen site	47 bees	32 bees	77 bees
(1) Continued dancing for this site until end	60%	81%	52%
(2) Switched dancing to a non-chosen site by end	0%	0%	0%
(3) Ceased dancing by end	40%	19%	48%

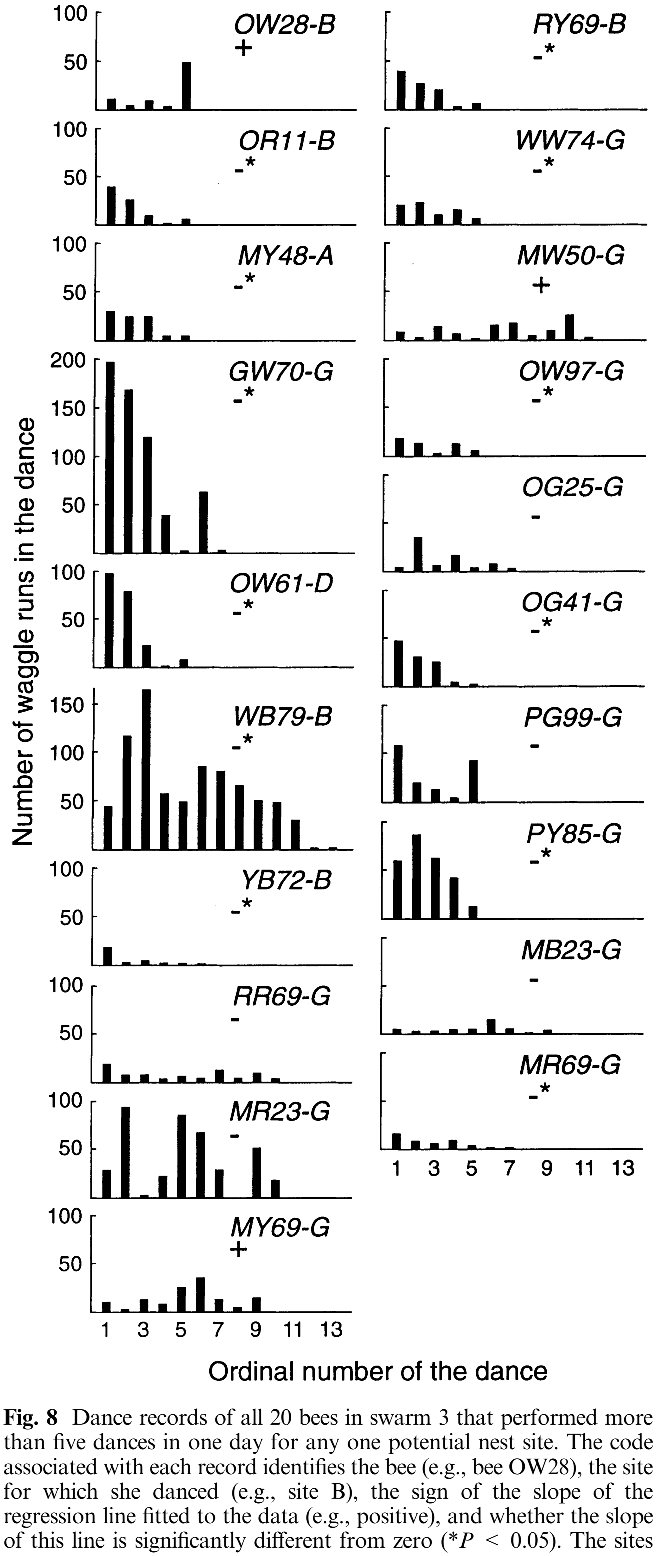


Fig. 8 Dance records of all 20 bees in swarm 3 that performed more than five dances in one day for any one potential nest site. The code associated with each record identifies the bee (e.g., bee OW28), the site for which she danced (e.g., site B), the sign of the slope of the regression line fitted to the data (e.g., positive), and whether the slope of this line is significantly different from zero (*$P < 0.05$). The sites are labelled in this figure just as they are in Fig. 5

WB79, YB72, RY69) and bees that danced for the chosen site G (bees GW70, WW74, OW97, OG41, PY85, MR69). This result is consistent with the results reported in Table 3, which show that a sizable fraction of the dancers ceased dancing by the end, and that this is true for both bees that danced initially for a non-chosen site (67–80%) and bees that danced initially for the chosen site (19–48%). The fact that we see a strong drop in the number of waggle runs per dance, even among bees dancing for the chosen site – a site that is high in quality, is attracting many bees, and seems to provide only positive external influences to scout bees – suggests that the bees' tendency to stop dancing arises from an internal influence.

Discussion

The mechanisms of decision making

The aim of this study was to renew the analysis of honey bee swarms as decision-making units. To do this we have repeated Lindauer's (1955, 1961) broad observations of swarms performing the decision-making process. We have, however, taken advantage of modern videorecording and bee-labelling techniques to describe this process in finer detail than was possible when Lindauer conducted his study, some 40 years ago. Given that we and Lindauer observed the same biological phenomenon but used different methods of observation, it seems appropriate to begin this discussion by comparing our results with those of Lindauer.

Our findings match closely those of Lindauer. With respect to patterns in the overall process of decision-making, we found, as did Lindauer, that (1) the scout bees locate sites in all directions and at distances of up to several kilometers from the swarm; (2) initially, the scout bees advertise a dozen or more potential nest sites but eventually they advertise just one site; (3) within an hour or so of the appearance of unanimity among the dancers, the swarm lifts off; (4) there is a crescendo of dancing just before liftoff; (5) the chosen site is not necessarily the one that is first advertised on the swarm, and (6) in some swarms, the decision making is fairly simple with only one site ever receiving strong advertising (our swarms 1 and 2; his Eck and Rotdorn swarms), while in other swarms, the decision making is complex, with multiple sites simultaneously receiving strong advertising (our swarm 3; his Propylaën, Zwillings, and Balkon swarms). With respect to patterns in the behavior of individual bees, we found, as did Lindauer, that (1) there is a high dropout rate among the dancers, and (2) some bees will switch their allegiance from one site to another. The close match between what we and Lindauer observed is reassuring. In particular, it tells us that we did not witness sociological oddities despite our use of artificial swarms (Lindauer used natural swarms), and it reassures us that Lindauer's famous description of the decision-making process is correct despite his use of simple recording techniques that yielded only partial records.

Our findings also closely match those of Gilley (in press) with respect to the fraction of bees in a swarm that perform dances. The mean percentage of dancing bees in our three (artificial) swarms was 2.8%, while that in Gilley's five (natural) swarms was 6.3%. In both our study and Gilley's, the swarms were small, containing some 2000–3600 bees. Despite this fact, and despite the fact that the fraction of dancers in each swarm was small, we and Gilley both observed at least several dozen dancing bees in each of our swarms. Thus it is clear that typically there is a sizable number of individuals involved in a swarm's decision making: 50–100 or even more bees.

Although many of our results merely confirm and quantify phenomena that have been previously reported, some of our results provide new and important insights into the mechanisms of the decision-making process. One such result is the discovery that only a small minority of the dancers ever dance for more than one site (Table 2). This implies that the process of consensus building among the dancers does not involve a large fraction of the dancers switching the site that they advertise. A second important result, closely related to the first, is the discovery that the principal means of consensus building among the dancers is for dancers advertising the non-chosen sites to cease their dancing (Table 3). In other words, most bees that dance initially for a site other than the ultimately chosen site terminate their dancing for this site by ceasing their dancing altogether, not by switching their dancing to the chosen site. Moreover, we made the curious discovery that nearly half of the bees that dance initially for the *chosen* site cease dancing before the end of the decision-making process. This finding indicates that the tendency of dancers to cease dancing is not simply a result of bees visiting undesirable sites (presumably the chosen site is a highly desirable site), and instead may be a reflection of an internal mechanism which causes all nest site scouts to eventually lose interest in dancing for any given site. Such a mechanism could be important because it would guarantee that all the participants in the decision-making process are flexible, and hence unlikely to produce a dangerous deadlock.

Of course, this study leaves unsettled many questions about the mechanisms of the decision-making process. Besides the puzzle of what causes bees to stop dancing, there is the puzzle of how bees go about switching their dancing from one site to another. Even though the bees that change their dance targets are only a small fraction of the dancers, they do contribute to the consensus-building process and so we need to understand their behavior. What causes them to switch their dancing and is this related to what causes most bees to stop their dancing? When switching, how do they sample the dances on the swarm? And do they tend to switch to the site that will become the chosen site? Another question is whether honey bee swarms possess mechanisms that produce "diversity" (alternative generation) and "conformity" (alternative selection) phases in the decision-making process, as human groups often do (Aldag and Fuller 1993). The three swarms that we studied did appear to work by first finding a variety of possible nest sites from which to choose, and then later selecting the most desirable site. But whether bees possess specific mechanisms for creating such phases – i.e., whether such phases are really part of the functional organization of the bees' decision-making process – is unknown.

Perhaps the most fundamental question that remains about a swarm's mechanisms of decision making is whether building a consensus among the dancing bees is the essence of the decision-making process. Is achieving dancer unanimity what really matters or is it merely correlated with some other phenomenon – such as getting many scout bees assembled at one of the sites – that actually indicates to the bees that a decision has been made? In this study, we observed for three swarms that the liftoff of a swarm always followed the appearance of unanimity among the dancers, which is consistent with the assumption that dancer unanimity is crucial. Likewise, Lindauer (1955, 1961) observed that swarm liftoff occurred only after the appearance of dancer unanimity in 17 of the 19 swarms that he studied, which further supports this assumption. However, Lindauer also observed 2 swarms, his Balkon and Moosacher swarms, which lifted off when their dancers were still split between two opposing factions promoting two distinct nest sites. In the Balkon swarm, for example, one site was 600 m to the northwest and the other site was 800 m to the southwest and after liftoff there appeared to be an aerial tug-of-war as the two groups of scouts tried to steer the swarm in different directions. Although the behavior of these 2 swarms is rare, the fact that such behavior exists at all runs contrary to the idea that achieving unanimity among the dancers is tantamount to completing the decision-making process. We feel, however, that before any firm conclusion should be drawn on this matter, it needs to be investigated with further experiments.

The strategy of decision making

We now step back from the mechanistic details of how swarms make decisions to consider their overall strategy of decision making. Decision making is, in essence, a process whereby one course of action is chosen from a number of alternatives. This process involves generating a set of alternatives, evaluating them, and finally selecting one of the alternatives. Payne et al. (1993) point out that there are many ways for a decision-making unit (be it an individual or a group) to evaluate and choose among alternatives. One is to use a *satisficing strategy:* evaluate the alternatives sequentially and choose the first one that exceeds an acceptance threshold. Another is to use an *elimination-by-aspects strategy:* determine the most important attribute, set an acceptance threshold for it, evaluate each alternative for this attribute, and reject all the alternatives that fall below the acceptance threshold for this attribute; repeat with the remaining alternatives but now using the second most important attribute, and so on. And still another is to use a *weighted additive strategy:* evaluate each alternative in light of all the relevant attributes, weight each attribute according to its importance, sum the weighted attributes for each alternative, and finally choose the alternative whose total valuation is the highest.

Of the various decision-making strategies, the weighted additive strategy is the most accurate but it is also the most demanding because it requires processing all of the information relevant to a problem. Thus, although the weighted additive strategy can potentially yield the highest payoffs to a decision maker, often it is not used because it demands high computational capabilities. It is especially likely to be rejected in favor of one of the simpler strategies when a decision maker must consider numerous alternatives and each alternative must be evaluated with respect to numerous attributes (Simon 1990). This is precisely the decision-making situation faced by a honey bee swarm. The present study and that of Lindauer (1955, 1961) have shown us that a swarm typically considers a dozen or more alternative nest sites. And various prior studies (reviewed by Seeley 1985; Witherell 1985) have shown us that a swarm evaluates each alternative nest site with respect to at least six distinct attributes with different weightings: cavity volume, entrance height, entrance area, entrance direction, entrance position relative to the cavity floor, and presence of combs from a previous colony. Nevertheless, all the evidence at hand suggests that the additive weighted strategy is the one used by a swarm of bees to decide where to live.

How is it possible that a honey bee swarm, composed of small-brained bees, can pursue the most sophisticated strategy of decision making? We have seen that the typical scout bee performs dances for (and so perhaps evaluates) just one of the many alternative nest sites, hence the work of evaluating the alternative sites appears to be broadly distributed among the many scout bees. In addition, we have seen that there is no omniscient supervisory bee that compiles all the evaluations and selects the best site. Instead, it is the highly distributed process of friendly competition among the scout bees that identifies the best site. Hence the cognitive effort that each scout bee must make is evidently quite small relative to the information processing done by the entire swarm. We suggest, therefore, that even though a swarm is composed of tiny-brained bees it is able to use the additive weighted strategy of decision making because it distributes among many bees the task of evaluating numerous potential sites and the task of selecting one particular site for its new home.

Acknowledgements The research reported here was supported by the U.S. National Science Foundation (grant IBN96-30159) and by the U.S. Department of Agriculture (Hatch grant NYC-191407). We are deeply grateful to David C. Gilley for helping label the bees and reviewing the manuscript, and to Dr. Robin Kimmerer for providing space and facilities at the Cranberry Lake Biological Station.

References

Aldag RJ, Fuller SR (1993) Beyond fiasco: a reappraisal of the groupthink phenomenon and a new model of group decision processes. Pyschol Bull 113:533–552

Ambrose JT (1976) Swarms in transit. Bee World 57:101–109

Combs GF (1972) The engorgement of swarming worker honeybees. J Apic Res 11:121–128

Dawkins R (1982) The extended phenotype. Oxford University Press, Oxford

Frisch K von (1967) The dance language and orientation of bees. Harvard University Press, Cambridge, Mass

Gilley DC (in press) The identity of the nest-site scouts in honey bee swarms. Apidologie

Griffin DR (1981) The question of animal awareness. Rockefeller University Press, New York

Griffin DR (1992) Animal minds. University of Chicago Press, Chicago

Heinrich B (1981) The mechanisms and energetics of honeybee swarm temperature regulation. J Exp Biol 91:25–55

Heinrich B (1993) The hot-blooded insects: strategies and mechanisms of thermoregulation. Harvard University Press, Cambridge, Mass

Lindauer M (1955) Schwarmbienen auf Wohnungssuche. Z Vergl Physiol 37:263–324

Lindauer M (1961) Communication among social bees. Harvard University Press, Cambridge, Mass

Lindauer M (1975) Verständigung im Bienenstaat. Fischer, Stuttgart

Markl H (1985) Manipulation, modulation, information, cognition: some of the riddles of communication. In: Hölldobler B, Lindauer M (eds) Experimental behavioral ecology and sociobiology. Fischer, Stuttgart, pp 163–194

Michener CD (1974) The social behavior of the bees. Harvard University Press, Cambridge, Mass

Payne JW, Bettman JR, Johnson EJ (1993) The adaptive decision maker. Cambridge University Press, Cambridge, UK

Seeley TD (1977) Measurement of nest-cavity volume by the honey bee (*Apis mellifera*). Behav Ecol Sociobiol 2:201–227

Seeley TD (1982) How honeybees find a home. Sci Am 247:158–168

Seeley TD (1985) Honeybee ecology. Princeton University Press, Princeton, NJ

Seeley TD (1995) The wisdom of the hive. Harvard University Press, Cambridge, Mass

Seeley TD, Morse RA, Visscher PK (1979) The natural history of the flight of honey bee swarms. Psyche 86:103–113

Simon HA (1990) Invariants of human behavior. Annu Rev Psychol 4:1–19

Wilson EO (1971) The insect societies. Harvard University Press, Cambridge, Mass

Winston ML (1987) The biology of the honey bee. Harvard University Press, Cambridge, Mass

Witherell PC (1985) A review of the scientific literature relating to honey bee bait hives and swarm attractants. Am Bee J 125:823–829

Communicated by R.F.A. Moritz