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ORIGINAL ARTICLE

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Choosing a home: how the scouts in a honey bee swarm perceive the completion of their group decision making

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Abstract This study considers the mystery of how the scout bees in a honey bee swarm know when they have completed their group decision making regarding the swarm's new nest site. More specifically, we investigated how the scouts sense when it is appropriate for them to begin producing the worker piping signals that stimulate their swarm-mates to prepare for the flight to their new home. We tested two hypotheses: "consensus sensing," the scouts noting when all the bees performing waggle dances are advertising just one site; and "quorum sensing," the scouts noting when one site is being visited by a sufficiently large number of scouts. Our test involved monitoring four swarms as they discovered, recruited to, and chose between two nest boxes and their scouts started producing piping signals. We found that a consensus among the dancers was neither necessary nor sufficient for the start of worker piping, which indicates that the consensus sensing hypothesis is false. We also found that a buildup of 10–15 or more bees at one of the nest boxes was consistently associated with the start of worker piping, which indicates that the quorum sensing hypothesis may be true. In considering why the scout bees rely on reaching a quorum rather than a consensus as their cue of when to start preparing for liftoff, we suggest that quorum sensing may provide a better balance between accuracy and speed in decision making. In short, the bees appear to begin preparations for liftoff as soon as enough of the scout bees, but not all of them, have approved of one of the potential nest sites.

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Introduction

Although one ordinarily thinks of decision making as a process performed by individuals, sophisticated acts of decision making are also performed by groups, most notably those groups that have evolved a high level of functional organization, such as colonies of army ants, honey bees, and other social insects (reviewed by Bourke and Franks 1995; Camazine et al. 2001). The decision-making problems faced by animal groups include choosing where to forage (Beckers et al. 1990; Seeley 1995; Biesmeijer and Ermers 1999; Detrain et al. 1999), when and where to move (Kummer 1971; Franks and Fletcher 1983; Prins 1996; Boinski and Garber 2000), which route to take to a given destination (Goss et al. 1989; Strickland et al. 1992), when and how to build a communal nest (O'Donnell and Jeanne 1990; Franks et al. 1992; Jeanne 1996; Pratt 1998; Theraulaz et al. 1999), when to become active (Cole and Trampus 1999), and whether or not to attack another group (Hölldobler 1982; Adams 1990; Boehm 1992).

Nest-site choice by a honey bee swarm is an impressive example of group decision making. Swarming usually occurs in the spring when a colony outgrows its hive and divides itself by swarming (the biology of swarming is reviewed in Michener 1974 and Winston 1987). The mother queen and approximately half the worker bees leave the parental nest to establish a new colony, while a newly reared daughter queen and the remaining workers stay behind to perpetuate the old colony. The swarm bees leave en masse, forming a cloud of bees just outside the parental hive, but within about 20 min they coalesce into a cluster at an interim site, usually a nearby tree branch. From here they choose their future nest site. Several hundred scout bees fly from the swarm cluster and search out tree cavities and other potential dwelling places. The dozen or so scouts that find suitable cavities report these locations by means of waggle dances on the surface of the swarm, and other scouts decode the dances, visit the sites themselves, and may dance in turn. A process of recruitment and selection ensues in which one site comes to dominate in visitation and dancing, and the swarm takes flight again and moves to the selected cavity.

One part of the decision-making process that remains mysterious is how the scouts sense when a decision has been reached. Scouts apparently do sense this, and change their behavior, beginning to produce a vibrational signal (the wings-together form of worker piping) an hour or so before the swarm takes flight to move to the chosen nesting cavity. This signal stimulates the other bees in the swarm to warm their flight muscles to a flight-ready temperature ($\geq$35°C) in preparation for the move to the new home (Heinrich 1981; Seeley and Tautz 2001; Seeley et al. 2003). However, we do not know how the scouts sense when a decision has been made and thus when to begin this flight-preparatory piping. Solving this mystery was the objective of our research.

How might the scouts sense when a decision has been made? One hypothesis, which has been frequently stated (Lindauer 1955; Seeley and Buhrman 1999; Visscher and Camazine 1999), is what we call the “consensus sensing hypothesis”: the scouts note when all the bees performing waggle dances are advertising just one site.[1] In support of this hypothesis is the observation that swarms generally move to their new dwelling only after the dancers have reached a unanimous agreement. However, Lindauer (1955) reported that 2 out of the 19 swarms that he studied lifted off when there were two coalitions of dancers advertising different sites. This suggests that unanimity among the dancing scouts may not be necessary for the scouts to sense that a decision has been made, though it is also possible that these two liftoffs were simply anomalies. Lindauer’s (1955) report of an occasional liftoff with dissent, plus our own observations of scout bees becoming numerous at chosen nest sites, led us to a second hypothesis. This is the “quorum sensing hypothesis,” related to quorum sensing in bacteria (Shapiro and Dworkin 1997), and studied already in ants (Pratt et al. 2002). In the quorum sensing hypothesis, the scouts note when a site is being visited by a sufficiently large number of scouts. Shortly before a honey bee swarm lifts off to fly to its future home site, there are usually numerous scouts at the chosen nest cavity, with ten or more outside and probably even more inside (Seeley et al. 1979; Visscher and Camazine 1999; Seeley and Buhrman 2001). It should be noted that the consensus sensing hypothesis proposes that the scouts sense a critical variable at the swarm cluster, while the quorum sensing hypothesis proposes that they sense a critical variable at the nest site.

To test the two hypotheses, we recorded events at the swarm cluster and at each of two nest boxes simultaneously as a swarm discovered and chose between the nest boxes and started preparing for liftoff. Because it is the scouts that initiate the preparations for liftoff, and the shift to piping behavior reliably occurs shortly before swarm liftoff, it seems reasonable to assume that this shift in behavior indicates that the scouts have sensed that a decision has been reached. Our aim was to observe whether worker piping (i.e. preparation for liftoff) began as soon as numerous scouts were visiting one of the nest sites (even if many dances were still occurring for alternative sites), as predicted by the quorum sensing hypothesis, or whether liftoff preparations began only after a consensus in dancing had been reached (often long after scout numbers had built up at the favored nest site), as predicted by the consensus sensing hypothesis. The first result would contradict the consensus sensing hypothesis while the second would contradict the quorum sensing hypothesis.

Methods

Study site

The work was conducted at the Shoals Marine Laboratory on Appledore Island, Maine (42°58′N, 70°37′W). This 39-ha island is nearly treeless and bears only a few buildings, hence it has few natural nest sites for honey bees. Here we could set out our nest boxes and be confident that they would receive attention from the scout bees of our swarms.

Swarm preparation

All our swarms were artificial swarms prepared from colonies kept on the mainland. These colonies were headed by “Buckfast” queens (Adam 1987). In making an artificial swarm, we first located a colony’s queen and put her in a small cage (3.2×10×1.6 cm). Then, using a large funnel, we shook 1.0 kg of worker bees (some 7,500 bees, Mitchell 1970) from the frames of this colony’s hive into a swarm cage (15×25×35 cm) made of wood with wire-screen sides. We also placed the caged queen inside the swarm cage. The caged bees were then ferried to Appledore and kept in the shade for 48–72 h (until copious wax scales appeared beneath the swarm cage). During this time, we fed the bees ad libitum with a sucrose solution (1:1 by volume, granulated sucrose:water). Finally we opened the swarm cage and fastened the queen (still in her own little cage) to a swarm mount (see Apparatus), and shook the workers onto the base of the mount. Within an hour, the workers clustered around the queen and behaved like a natural swarm. Prepared this way, workers eventually choose a nest site, take off, and start to move together to their new home. However, because in most cases we kept the queen caged at the swarm mount, the workers were not able to complete their move and returned to the swarm mount to recluster around their queen.

Apparatus

Swarms were placed on a swarm mount that has been described previously (see Fig. 1 in Seeley and Buhrman 1999). This mount consists of a vertical board, on which the swarm clusters, and a wire

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[1] In naming our hypotheses, we have chosen the words “consensus” and “quorum” based on their definitions in the *Oxford English Dictionary*. Consensus: agreement in opinion; the collective unanimous opinion of a number of persons. Quorum: a fixed number of members of any body, society, etc., whose presence is necessary for the proper or valid transaction of business.

screen (of 8-mesh hardware cloth with several passageways for the bees cut into it) mounted vertically over the swarm's surface so that the outermost layer of the swarm is on the outside of the screen. This apparatus facilitated video recording the scout bees' dances, which was done to determine when the dances became unanimous for one of the nest boxes. Our video equipment consisted of an S-VHS camera (Panasonic WV-F250B) and videocassette recorder (Panasonic AG-7450) equipped with a time-code generator (Panasonic AG-F745). The videotapes were analyzed using a videocassette player with variable-speed playback (JVC BR-S525U).

To record worker piping within the swarm cluster, we mounted two small, 5-mm-diameter, custom-made microphones (flat frequency response from 20 to 6000 Hz), one on each side of the swarm, on the rods supporting the screen of the swarm mount. This positioned each microphone deep inside the swarm cluster. The two microphones were connected to an amplifier whose two channel output was recorded with a stereo digital minidisc recorder (Sony MZ-R37SP).

To record the ambient temperature near the swarm cluster, we used a copper-constantan thermocouple probe and a digital thermometer (Bailey Bat-12). The probe was mounted on the swarm mount, 2 cm below the board on which the swarm was clustered.

The two nest boxes used in this study were specially designed and constructed to enable us to count the scout bees at a potential nest cavity, both outside and inside the cavity. Each was cube-shaped, built of 2.0-cm-thick plywood, and sized to provide a 27-l nesting cavity. Each had one entrance opening, a 2.0-cm-diameter hole centered on one side wall, and had one of its side walls left open. And each was bolted to the side of an observation hut, with the open side aligned with a matching opening in the wall of the hut. A sheet of 3.2-mm-thick glass provided a window-wall between the nest box and observation hut. Each observation hut (244×113×113 cm) was constructed of wood with lightproof joints and had its inner walls painted flat black. Thus it provided a dark viewing chamber from which we could scan the interior of the attached nest box for scout bees. The entrance hole of the nest box admitted sufficient light for observing the bees.

Experimental layout and data collection

We began each trial by placing a swarm on the mount located on the covered porch of Bartel's Hall and giving the bees sugar water ad libitum from two feeder bottles. We had already positioned the two nest boxes in locations that were the same distance (250 m), but in different directions (angular separation of 58°), from the swarm. One was near Broad Cove while the other was 240 m away, in the vicinity of Devil's Glen (we used sites 2 and 5 shown in Fig. 2 of Seeley and Buhrman 2001). To help the scouts locate the nest boxes at the start of a trial, we inserted in the entrance opening of each nest box a pheromonal swarm lure (Ecogen, Langhorne, Pa.) suspended from a wire. Once the bees were settled on the swarm mount, an observer was stationed at each nest box to record when it was discovered by a scout bee and to be present for the start of data collection.

Immediately upon observing a scout bee at either nest box, we took several steps to begin data collection. First, the pheromone lure was pulled from the newly found nest box and stored in an odor-proof glass jar. Second, the observer at each nest box began following a standard protocol for measuring the number of scout bees at his or her nest box. Every 5 min, the person would make four separate counts of the maximum number of bees seen simultaneously at the nest box over a 30-s period, with two counts based on the bees seen inside the nest box and two counts based on the bees seen outside. When the number of bees inside or outside rose above ten, precise counts were impossible, and the observer noted the number of bees as a range (e.g. 20–25 bees). Third, the observer at the swarm cluster turned on the video camera, so that the dances of the scouts would be recorded from their start, and he began following a standard protocol for measuring the level of worker piping within the swarm. Every 5 min, he would make an audio recording, lasting at least 60 s, using the stereo microphones mounted inside the swarm cluster. He would also begin recording at 5-min intervals the ambient temperature of the swarm cluster.

Meteorological data were recorded automatically by a weather station on Appledore Island that is operated by the National Oceanographic and Atmospheric Agency.

Data analysis

The video recordings were analyzed to determine the number of waggle runs performed for each nest box over 20-min intervals before liftoff. The nearly 60° difference in direction to the two nest boxes made it possible to tell which nest box was represented by each dance. We made our counts of the waggle runs by reviewing each video recording and, whenever a bee began to dance, noting the time (indicated on the video record) and the location (specified using a system of quadrats on the video monitor) at which this bee began to dance, and then counting the waggle runs contained in this bee's dance. By noting the starting time and starting location of each dance, we avoided double counting the waggle runs contained in any dance, even though sometimes 10 or more dances were performed simultaneously.

The audio recordings were analyzed to get estimates of the percent time that worker piping was heard, at 5-min intervals before liftoff. From each 60-s audio recording that we had made, we took three 20-s intervals, and for each of these intervals we counted the number of 1-s subintervals (*N*) in which worker piping was audible. From these counts we calculated the percent time that piping was audible during each 20-s interval (*N* /20×100). Finally, using the three measurements for each sampling period, we calculated the mean value of the percent time that piping was heard.

Results

Swarm 1

This swarm was placed on the swarm mount at 1800 hours on 23 June 2002. Two days later, at 1620 hours, a scout bee discovered the Broad Cove nest box and spent the next 62 min there inspecting it excitedly. This bee, however, performed no dances for this nest box on this day, perhaps because she discovered it rather late in the day.

Figure 1 depicts the results obtained the next day (26 June). The Broad Cove nest box was visited by a scout bee starting at 0900 hours, but no dances were performed for this site until 1101 hours. By 1120 hours, several scout bees were visiting both the Broad Cove and the Devil's Glen nest boxes and strong dances were being performed for both sites. By 1150 hours, there was noticeable piping at the swarm cluster. The start of this piping came shortly after the number of scouts at the Devil's Glen nest box had risen to approximately 15 total (about 12 inside and 3 outside), the number of scouts at the Broad Cove nest box was at most 2 total, and nearly all the dancing had been for the Devil's Glen nest box. (For the 20-min period of 1126–1146 hours, 137 waggle runs were produced for the Devil's Glen nest box but only 4 for the Broad Cove nest box). From 1146 to 1406 hours, when the swarm lifted off and started to move to the Devil's Glen nest box, the number of scouts at the Devil's Glen nest box remained fairly steady at about 10–15 total, the number of scouts at the Broad Cove nest box remained low except for a brief

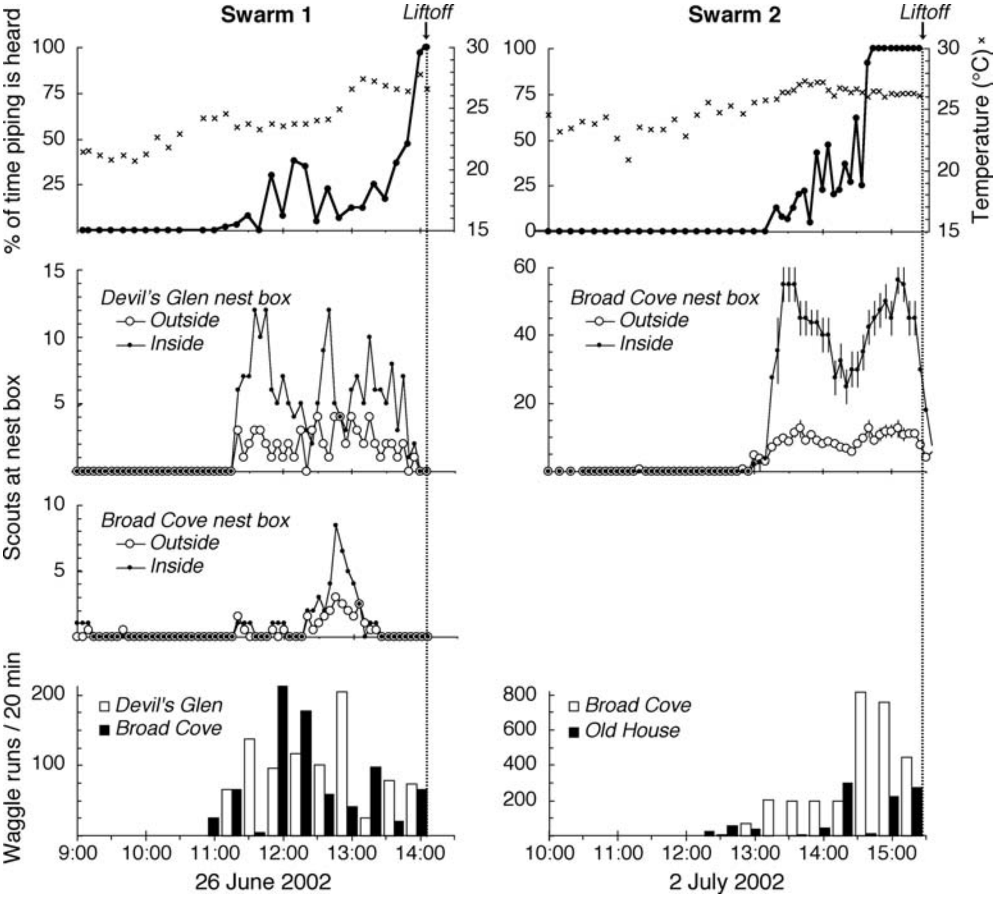

Fig. 1 Results from monitoring two swarms as their scout bees chose between two potential nest sites and then began preparing for liftoff (indicated by the start of worker piping). At the swarm, we recorded the intensity of worker piping every 5 min and the number of waggle runs that were produced for each site in 20-min intervals before liftoff. At the potential nest sites, we recorded the number of scout bees outside and inside each site every 5 min, except when one of the sites was an unidentified location in an old house

time around 1300 hours when it rose to about 10 total, and the piping persisted at a moderate level until the last half hour before liftoff, when it rose to a high level. Curiously, this swarm completed its decision making and performed a liftoff without having a prolonged period of unanimous dancing for the chosen site.

In summary, in this swarm the liftoff preparations (worker piping) began at a time when the number of bees at the ultimately chosen nest box had risen to 10–15 and when the dancing had been, for about 20 min, virtually unanimous for the ultimately chosen nest box. Liftoff occurred without unanimity among the dancers.

Swarm 2

This swarm was placed on the swarm mount at 1900 hours on 29 June 2002. On 2 July, at 1241 hours, a scout bee discovered the Broad Cove nest box and at 1256 hours the dancing for this nest box began. Somewhat earlier, at 1207 hours, dancing had also begun for an unidentified site in a southerly direction, hence nearly 180° from our nest boxes, probably in one of the old houses on the south shore of the island.

Figure 1 depicts the results for the remainder of the day, until liftoff at 1526 hours. The number of scout bees at the Broad Cove nest box rose rapidly following its discovery. Likewise, the first sounds of piping workers were heard soon after the number of scouts at the Broad Cove nest box had begun to grow. The Devil's Glen nest box was never discovered, so the counts of scouts there remained at zero. The dancing was, naturally, unanimous for the Broad Cove nest box, except when some dances were also performed for the Old House site. It should be noted that in this swarm, like in swarm 1, liftoff was not preceded by a period of unanimous dancing for the chosen site, though the dancing had been primarily for the Broad Cove site. Shortly after liftoff, the swarm moved in the direction of the Broad Cove nest box.

In summary, in this swarm as in the previous one, liftoff preparations (worker piping) began at a time when the number of bees at the ultimately chosen nest box had become considerable (30–40 bees in this case), and when the dancing was unanimous for the ultimately chosen nest box. And, as with the first swarm, liftoff occurred without there being unanimity among the dancers.

Swarm 3, day 1

This swarm was placed on the swarm mount at 1900 hours on 5 July 2002. On 6 July, at 1040 hours, a scout bee discovered the Devil's Glen nest box. A few minutes later, at 1106 hours, a scout bee discovered the Broad

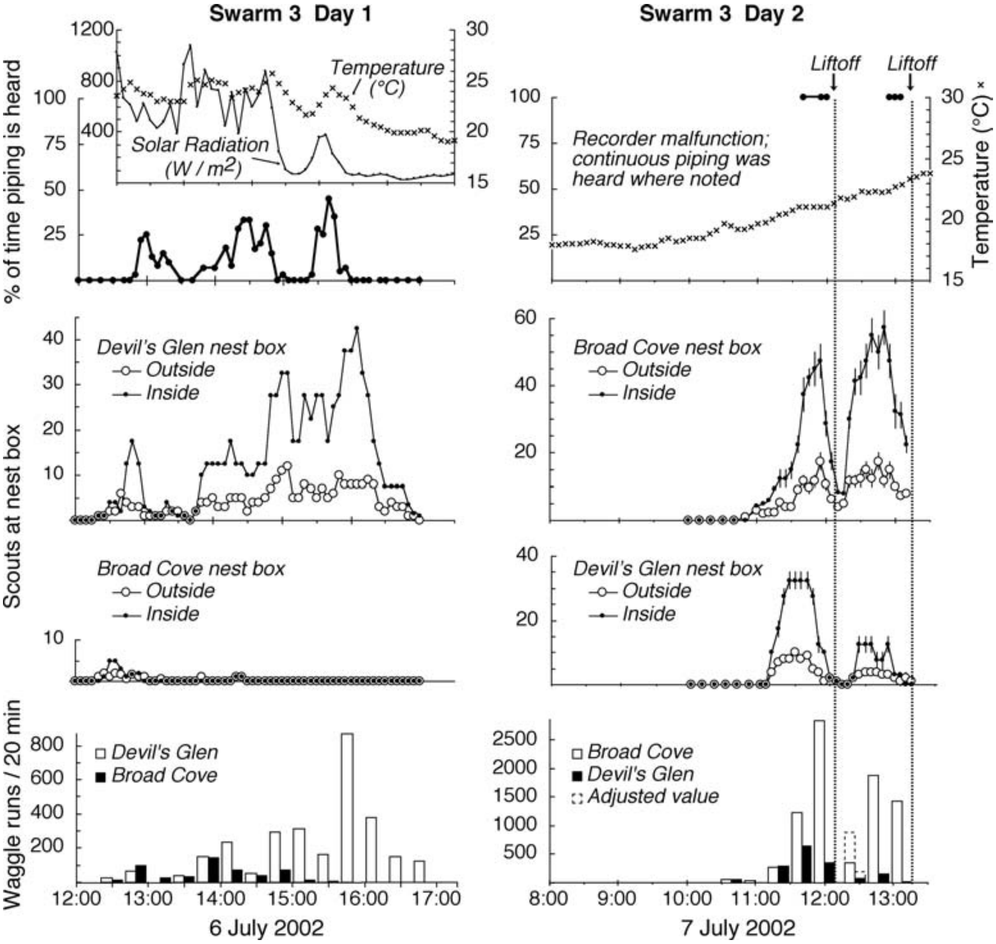

Fig. 2 Results from monitoring one swarm over 2 days as its scout bees chose between two potential nest sites and then began preparing for liftoff. Figure format follows that of Fig. 1, except on day 1 when we also include records of solar radiation (*inset*) because on this day changes in the weather greatly influenced the results

Cove nest box. The first dances for the Devil's Glen and the Broad Cove sites were recorded at 1223 and 1238 hours, respectively.

Figure 2 depicts the results obtained from swarm 3 over the next 2 days. Worker piping was first heard at 1255–1300 hours, shortly after the number of bees at one of the nest boxes (Devil's Glen) had risen to a moderately high level, 15–20 bees, and the number at the other nest box was still at a low level, only 0–5 bees. Then, for some unknown reason, the number of bees dropped to almost zero at both nest boxes. This lasted from 1300 to 1340 hours at the Devil's Glen nest box and from 1300 hours to the end of the day at the Broad Cove nest box. Simultaneously, the worker piping dwindled. It started up again in the period 1350 to 1400 hours, which is when the number of bees at the Devil's Glen nest box had returned to a moderately high level, 15–20 bees. Although the number of scout bees at the Devil's Glen nest box remained high over the next 2 h of the afternoon, peaking at 40–50 bees around 1600 hours, the worker piping ceased suddenly when the sky darkened with thunderstorm clouds at 1445 hours (shown in the inset graph). No more piping was heard until 1520 hours, at which time the sky brightened and the piping rose rapidly to its highest level of the day. By 1540 hours, however, the sky had again filled with dark storm clouds and shortly thereafter the piping again ceased, even though bees remained in abundance at the Devil's Glen nest box and strong, unanimous dancing persisted for this nest box.

In summary, on this day this swarm showed three times when the worker piping started and three times when it stopped. All three times when the piping started were times when the number of scout bees at the Devil's Glen nest box had risen to at least 15–20 bees. Importantly, the first and second starts of piping occurred at times when the dancing was nearly evenly divided between the two nest boxes. Only the third start of piping occurred when the dancing was unanimous for the Devil's Glen nest box. The first stop of piping occurred when the number of bees at both nest boxes had dropped nearly to zero. The second and third stops occurred when the number of bees at the Devil's Glen nest box remained high but the weather had turned poor.

Swarm 3, day 2

This swarm resumed its decision making the next day, which started out cloudy and cool but by 1000 hours had become sunny and warm. As is shown in Fig. 2, the number of scout bees rose rapidly at both nest boxes starting around 1100 hours, and stayed high at both until shortly before liftoff at 1204 hours. Because of a malfunction in our recorder, we do not know when exactly the piping started, but we do know that there was no piping at 1100 hours and that by 1140 hours it had reached a high level. Hence the piping must have started sometime in the interval 1100–1140 hours, during which the number of bees at each nest box was at least 10–20 bees. There was also strong dancing for both nest boxes throughout this interval, and this division among the dancers persisted until the liftoff, though in the last 20-min period preceding liftoff the dancing was much stronger for the Broad Cove nest box than for the Devil's Glen one (2,824 vs. 360 waggle runs).

By 1148 hours it was clear from the intense piping that liftoff was imminent. Because this swarm still had numerous scouts at both of the nest boxes, and so had its "attention" split between the two sites, we wondered if it would be able to move successfully to one of them. To find out, we released the queen from her cage, whereupon she began to walk rapidly over the surface of the swarm cluster. At 1204 hours the swarm lifted off and the queen was seen to be among the earlier bees to take flight. Once in flight, the bees formed an unusually large cloud of bees split by Bartel's Hall, with some bees on the south side of the building (the direction to Devil's Glen) and some on its north side (the direction to Broad Cove). The majority of the bees seemed to be on the north side, and at 1209 hours these bees began moving slowly northwest, in the direction of the Broad Cove nest box. Their movement stopped, however, at 1211 hours, when the cloud they formed had traveled only about 40 m from the swarm mount. Simultaneously, a cluster of bees, apparently composed initially of bees that had been on the south side of Bartel's Hall, started to form back at the swarm mount. By 1215 hours, about half of the swarm bees had resettled on the swarm mount and the queen was seen, having alighted nearby. No bees arrived at the Devil's Glen nest box and only about 10 reached the Broad Cove nest box.

The swarm quickly reorganized itself for a second liftoff followed by a successful move to the Broad Cove nest box. By 1230 hours, the swarm cluster was rebuilt, scout bees had begun to reappear at both nest boxes, and dances were again being performed for both nest boxes (see Fig. 2). Unlike in the morning, however, the buildup of scouts at the two nest boxes was not balanced; the counts at the Broad Cove nest box greatly exceeded those at the Devil's Glen nest box. Likewise, the dancing was mainly for the Broad Cove nest box. Although we do not know when exactly the worker piping restarted, we can say that it was sometime between 1220 (when no piping was heard) and 1240 hours (when much piping was heard), hence it occurred when there were at least 10 bees at the Devil's Glen nest box and at least 40 bees at the Broad Cove nest box. Finally, at 1313 hours, the swarm lifted off again and moved to the Broad Cove nest box.

In summary, on this day this swarm performed two liftoffs. In both cases, the start of the liftoff preparations (worker piping) began when the number of scout bees at both nest boxes had risen to at least 10–20 bees. The first round of liftoff preparations began without a dance consensus while the second round began when nearly all the dances were for the chosen nest box. As for the actual liftoffs, only the second one occurred when there was clear unanimity among the dancers.

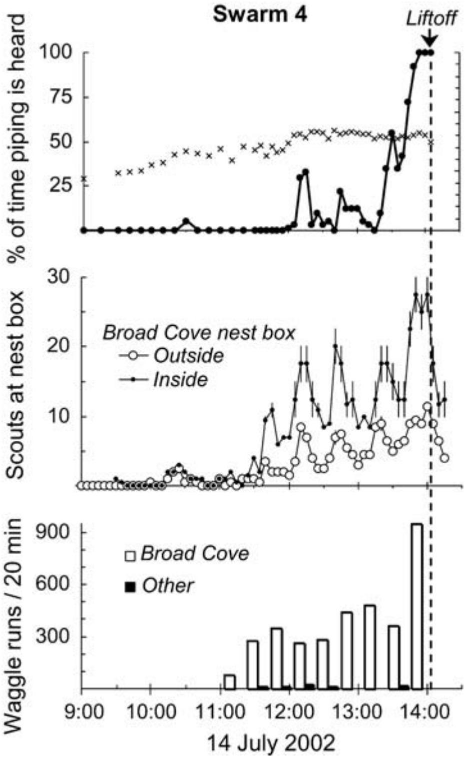

Fig. 3 Results from monitoring one swarm as its scout bees discovered one potential nest site and then began preparing for liftoff. Figure format follows that of Fig. 1

Swarm 4

This swarm was placed on the swarm mount at 1930 hours on 12 July 2002. On 14 July, at 0928 hours, one scout bee discovered the Broad Cove nest box and around 1030 hours two more bees evidently also discovered it, for up to 3 bees were seen simultaneously there. At 1117 hours the dancing for this nest box began.

Figure 3 shows the results for the remainder of the day. Shortly after the dancing began for the Broad Cove nest box, the number of bees there began to rise. When it reached a total of about 20 bees (15 inside and 5 outside), at 1210 hours, the piping started. But when the number of bees fell well below this level, at about 1220 hours, the piping stopped. By 1240 hours the number of bees had returned to a moderate level of about 25 bees (20 inside and 5 outside), and the piping had resumed. Then, once again, the number of bees at the Broad Cove nest box dropped off, falling to only about 10 bees total by 1300 hours, and the piping again stopped. By 1325 hours the count had risen again to about 20 bees (15 outside and

5 inside) and the piping again became audible. Yet once more, starting at about 1330 hours, the number of bees at the nest box began to decline and this was matched by a decline in the piping, but this time neither variable fell to a low level. Finally, starting at 1340 hours, the number of scouts at the nest box surged to its highest level, some 35 bees total, the piping became loud and continuous, and ultimately the swarm lifted off at 1403 hours. Throughout this time, no scout bees appeared at the Devil's Glen nest box, which had been open and available until 1205 hours when it was closed so we could concentrate on making observations at the Broad Cove nest box. Also throughout this time virtually all the dancing was for the Broad Cove nest box; only occasionally was a dance performed for some other, unidentified site.

In summary, this swarm seriously considered just one of our nest boxes and so had unanimous dancing for this site throughout its decision-making process. Also, this swarm showed three times when the worker piping started and two times when it stopped. All three times when the piping started were times when the number of scout bees at the Broad Cove nest box had risen to at least 20 bees, and both times when the piping stopped were ones when the number of bees at the nest box had fallen to only about 10 bees.

Discussion

Knowing when to start liftoff preparations

The main aim of this study was to learn how the scouts in a honey bee swarm know when a decision has been reached regarding the new home site, that is, when it is appropriate for them to begin producing the piping signals that will stimulate their swarm-mates to prepare for the flight to their new home. Our results, summarized in Table 1, enable us to draw two conclusions regarding this puzzle:

1. The consensus sensing hypothesis is false. We observed that a consensus among the dancers was neither necessary (as shown by the results of swarm 3 on both days 1 and 2) nor sufficient (as shown by the results of swarm 4) for the start of worker piping.
2. The quorum sensing hypothesis may be true. We observed that a buildup of 10–15 or more bees at one of the nest boxes was consistently associated with the start of working piping (as shown by the results of swarms 1, 2, and 3, and especially of swarm 4).

Our observations are consistent with what has been reported previously. Prior observations suggested that the consensus sensing hypothesis is false. Lindauer (1955) described how 2 of the 19 swarms that he studied took off without their dancers having formed a consensus. Apparently, the scouts in these two swarms, like those in our swarm 3, did not need to sense a consensus among the dancers to begin their preparations for liftoff. One could, however, interpret Lindauer's report of two swarms lifting off without consensus as anomalies. We feel that our finding that a swarm's liftoff preparations often precede the formation of a consensus provides thoroughly convincing evidence against the consensus sensing hypothesis.

Table 1 Summary of the conditions under which worker piping started during the decision-making processes of four swarms of bees. For each time that worker piping started on a swarm, we note whether or not there was a dance consensus at the swarm cluster and whether or not there was a buildup of scouts at the nest site. In swarms 1 and 2, the worker piping started just once, but in swarms 3 and 4 the worker piping started several times

	Conditions when worker piping started	
Swarm	Dance consensus?	Buildup of scouts?
1	Yes, but temporary	Yes, 10–15 bees
2	Yes, but temporary	Yes, 30–40 bees
3, day 1	No, no, yes	Yes, 15–20 bees each time
3, day 2	No, yes	Yes, 10–20 bees each time
4	Yes, yes, yes	Yes, 20+ bees each time

Prior observations also suggested that the quorum sensing hypothesis is true. Seeley and Buhrman (2001) reported that in all five of the swarms that they studied (see their Fig. 5), the liftoff was preceded by a population of at least 10 bees outside (and an unknown number inside) the chosen nest box during the last hour or two before liftoff. Thus the scouts in each of these five swarms could have sensed a buildup of 10–20 or more bees at the chosen site when they began to stimulate their swarm-mates to begin preparing for liftoff. The pattern of scout bee buildup outside the chosen site reported by Seeley and Buhrman (2001) matches the pattern described earlier for one swarm by Seeley et al. (1979, see their Fig. 1).

A rigorous test of the quorum sensing hypothesis remains to be done with honey bee swarms. Although our finding that the start of worker piping is tightly correlated with the buildup of scouts at one of the sites (see Fig. 2 and 3) is strongly supportive of the quorum sensing hypothesis, what needs to be done is an experiment in which the number of bees at a nest site is manipulated independently of other variables in the decision-making process, and it is noted whether or not the scout bees start their piping when and only when the number of bees at the nest site exceeds a quorum requirement. Such an experiment is planned. Already, however, the phenomenon of quorum sensing has been conclusively demonstrated in a study of group decision making during colony emigration in the ant *Leptothorax albipennis* (Pratt et al. 2002). In this species, when a colony's nest is damaged, the ants perform a two-stage decision process in choosing a new home. Initially, a minority of active ants in a colony search for potential new sites and those that discover such sites recruit others to their finds via the relatively slow process of tandem running, in which a single follower is lead all the way to the new site. The better the site, the shorter the latency between discovery and start of tandem running, hence the more rapid the buildup of ants at the site (Mallon et al. 2001). Eventually, the population of ants at one of the prospective sites (usually the best site, given the quality-dependent delays in initiation of recruitment) exceeds a quorum requirement and the active ants begin rapidly recruiting the passive majority of the colony to this site via transports, in which nestmates are simply carried. By performing experiments with just one nest site, and in which they manipulated the number of ants in this site, Pratt et al. (2002) were able to demonstrate that ants use a quorum of nestmates (approx. 9–17 individuals) as the cue indicating when they should begin bringing others to the site using the faster, transport method of recruitment. Future studies in other social insects may reveal that quorum sensing is an important and widespread feature of the functional organization of colonies.

In the context of group decision making by honey bee swarms, we have learned that the consensus sensing hypothesis is false, and that the quorum sensing hypothesis may be true. If we tentatively assume that the quorum sensing hypothesis is true in honey bee swarms, we face intriguing questions of both behavioral mechanism and functional design. With respect to behavioral mechanism, there is the question of how a scout bee senses the number of other bees at a nest site. One possibility is by visual perception. For a human observer, and perhaps also for bees, the constantly moving scout bees are easily detected visually outside the cavity and even inside it, at least around the entrance opening, which admits considerable light. Measurements of the light level inside a model nest cavity found light levels of 1–2 lx near the entrance opening, which is where most of the traffic of scout bees occurs, though less than 0.5 lx elsewhere inside the cavity (see Fig. 15 in Seeley 1977). The threshold level of illumination for bee flight (hence good vision) is approximately 1.0 lx (Schricker 1965). Another possible means of sensing the number of scout bees at a site is by tactile perception. It is a curious fact that as soon as a site acquires multiple scouts, they begin to make frequent contacts with one another. Many of the scouts even start to perform buzzing runs (first described by Lindauer 1955; see also Martin 1963 and Esch 1967) on the inner and outer surfaces of the nesting site. That is, the scouts make excited, zig-zag runs that are punctuated by bouts of buzzing their wings and butting against other bees. So it seems entirely possible that a bee could use the rate of contacts with scouts in general, or encounters with buzz runners in particular, as an indicator of the number of fellow scouts at a site.

With respect to functional design, there is the question of why bees do not use consensus sensing and appear instead to use quorum sensing. This question is made prominent by the fact that a consensus among the dancers helps a swarm execute a successful move to a new home site. Indeed, a consensus, or at least a near consensus, among the dancers may be a requirement of a successful move. In three reported instances of a swarm lifting off when its dancers were strongly split between two sites (Lindauer's 1955 Balcony and Moosach swarms and our swarm 3), the airborne swarm divided, stalled in its move, and resettled. Two of these swarms went on to achieve a dance consensus and a successful move, but one (Lindauer's Balcony swarm) lost its queen when it split itself in midair and so experienced complete failure.

Why do the scouts not use consensus sensing and so avoid the risk of their swarm suffering a fatal fragmentation upon liftoff? One possibility is that it would be exceedingly difficult or costly, or both, for the scouts to sense a consensus among themselves as they perform dances on a swarm. To do so would require that each scout devotes much effort to polling her fellow scouts, presumably by traveling over the swarm cluster, reading some sample of the dances, and keeping a tally of the readings. Moreover, the larger the swarm, the more numerous the scouts, and perhaps the greater the difficulty (or cost) of consensus sensing. Quorum sensing, however, need not become more difficult with increasing swarm size, because the quorum size could be fixed, and so independent of swarm size. Another possibility is that consensus sensing would greatly slow the decision-making process. Franks et al. (2002) have pointed out that there is a fundamental trade-off in decision making between speed and accuracy. It seems likely that consensus sensing would provide maximum accuracy in a swarm's decision making, for a swarm would not proceed to liftoff preparations until the dancers were in agreement over the home site. This maximum accuracy in decision making would come, however, at the cost of taking extra time, for in principle even a single scout bee that mistakenly dances vigorously for an inferior site could prevent liftoff and so prolong the decision making. There can be no doubt that there is a cost associated with a honey bee swarm taking more time to decide. A swarm clinging to a tree branch is exposed to drenching rains and is consuming its energy reserves; the 30–40 mg of rich sugar solution carried inside each bee (Combs 1972).

Quorum sensing may provide a good balance between accuracy and speed in decision making. With respect to accuracy, the quorum requirement promotes a high level of accuracy, for we observed that scout bees will not begin producing piping signals for liftoff preparations until the number of bees present at the site surpasses a threshold of some 10–20 or more bees. Having a quorum requirement this high helps ensure that liftoff preparations are not initiated by scouts that have erred, judging a poor site to be a good one. If a scout makes an error, and recruits strongly to a poor site, her followers will likely counter her mistake by judging the site less highly than she, advertising it with weaker dances (if any), and so putting off the start of piping. This idea has been developed rigorously by Pratt et al. (2002) in their study of group decision making during colony emigration in the ant *L. albipennis*. By modeling the decision-making process, they showed that a moderate quorum requirement helps a colony choose the best available site, by preventing the launch of the rapid transport process to a given site until numerous individuals have each been convinced of the worth of the site. Thus, even a rather moderate quorum requirement reduces the chances of emigration to an inferior site.

With respect to speed of decision making, the requirement of a quorum, but not a consensus, means that preparations for liftoff can begin as soon as enough scout bees have approved of one of the nest sites, even if some others are still scouting other sites. We suggest that the quorum size is a detail of the bees' decision-making process that has been tuned by natural selection to provide an optimal balance between accuracy (favored by a large quorum) and speed (favored by a small quorum). It is likely that quorum size has also been influenced by the need to have sufficient scout bees familiar with the chosen site's location to pilot the flying swarm to this site.

The use of a quorum requirement does seem to suffer from at least one major weakness, in that it can lead to liftoffs without a dance consensus. As discussed above, such liftoffs do occur occasionally and they can be costly mistakes. The swarm is apt to split after liftoff, thereby failing to move to either site while at the same time expending much energy. It may even lose its queen. Presumably the reason that most liftoffs occur when there is a consensus, even though a consensus is not required for the start of liftoff preparations, is because there is the strong positive feedback process of vigorous dancing for the chosen site, which attracts more and more dancing for this superior site (Seeley and Buhrman 2001). Moreover, there is the steady attritional process of individuals ceasing to dance, especially for the inferior, non-chosen sites (Camazine et al. 1999; Seeley 2003; Visscher 2003).

Knowing whether to continue liftoff preparations

Our results also enable us to draw several additional conclusions on the topic of what factors determine whether piping (and thus preparation for liftoff) continues once it has started. The continuation of piping may depend on previously piping scouts continuing to pipe, or on previously non-piping scouts starting to pipe, or both.

1. A consensus among the dancers is not necessary for the continuation of piping and eventual liftoff (as shown by the results of swarm 1, swarm 2, and swarm 3 on day 2).
2. A quorum of some 10–20 bees at one of the potential nest sites appears to be necessary for the continuation of piping (as shown by the results of swarm 3 on day 1 and swarm 4), except at the end of the period of liftoff preparations. The number of bees at the chosen site usually plummets shortly before liftoff and yet liftoff preparations will continue and liftoff will occur (as shown by the results of swarm 1, swarm 2, and swarm 3 on day 2).
3. Favorable weather is necessary for the continuation of piping and eventual liftoff (as shown by the results of swarm 3 on day 1).

Thus it seems clear that the scout bees, even after some have started to stimulate their swarm-mates to prepare for liftoff, remain sensitive to the weather conditions and the number of bees at the chosen site. If the weather deteriorates or the number of bees at the chosen site falls to a low level (at least, during the early stages of liftoff preparations), the piping will decrease. Such behavioral flexibility is highly adaptive for it seems clear that only if both the weather conditions remain favorable and the nest-site decision remains strongly supported should a swarm undertake the momentous act of launching into flight to start its journey to a new home.

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