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Quorum sensing during nest-site selection by honeybee swarms

Abstract This study addresses a question about the nest-site selection process of honeybee swarms: how do the scout bees know when to initiate the preparation for their swarm's move to their new home? We tested the quorum-sensing hypothesis: that the scouts do this by noting when one of the potential nest sites under consideration is being visited by a sufficiently large number of scouts. A falsifiable prediction of this hypothesis is that delaying the formation of a quorum of scout bees at a swarm's chosen nest cavity, while leaving the rest of the decision-making process undisturbed, should delay the start of worker piping (the prepare-for-takeoff signal) and thus the take-off of the swarm. In paired trials, we presented each of four swarms once with five nest boxes close to each other at a site and once with a single nest box. The multiple nest boxes caused the scouts visiting the site to be dispersed among five identical nest cavities rather than concentrated at one. We observed long delays in the start of piping and the start of takeoff in the five-nest-box trials relative to the one-nest-box trials. These results provide strong support for the quorum-sensing hypothesis.

Keywords Group decision making · Honeybees · Nest-site selection · Quorum sensing · Swarming

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Introduction

In the swarm-founding species of social insects—those in which colonies are initiated by swarms comprising one or more queens and numerous workers—the choice of a nest site demands an exceptional degree of coordination among a colony's members. First, they must work together to choose a suitable nest site for the swarm. This decision-making process typically involves finding several potential sites, making a multifaceted evaluation of each site, and, as a group, deciding on which is the best site discovered. Second, the colony's members must work together to get the entire swarm safely to the chosen site. The migration to a new dwelling place is a major endeavor, with hundreds or thousands of individuals sometimes traveling hundreds or thousands of meters. Recent studies of *Apis* (honey) bees and *Leptothorax* ants have shown that these social insects achieve these feats of coordination without centralized control (Seeley and Buhrman 1999; Visscher and Camazine 1999; Mallon et al. 2001; Pratt et al. 2002). Instead, the choosing of the home site and the guiding of the swarm's movement are distributed across a multitude of workers. The challenge in analyzing the nest-site selection process in these species is, therefore, to identify the behavioral rules that individual insects use to produce the adaptive behavior of the swarm as a whole. In this paper we address this challenge in the context of one particular mystery of honeybee swarms: how do the scout bees in a swarm know when to initiate the preparations for the swarm's move to the new nest site?

In honeybees, the colony-founding process starts when a strong colony divides by swarming. The mother queen and approximately half the worker bees leave the parental nest to establish a new colony, while a daughter queen and the balance of the workers remain behind to perpetuate the old colony. After leaving the parental nest, the swarm bees coalesce into a beard-like cluster that hangs from a tree branch for several hours or several days, during which time about five percent of its bees, the scouts, busy themselves with choosing a suitable nesting

cavity (reviewed by Lindauer 1971, Seeley and Visscher 2004). During this bivouac period, the vast majority of the 10,000 or so bees in a swarm remain quiescent to conserve the swarm's energy reserve: the 30–40 mg of rich sugar solution carried inside each bee (Combs 1972). As was shown by Heinrich (1981), the bees in the core of a cluster maintain a 30–40°C microclimate, by trapping the metabolic heat produced by the resting bees and by adjusting the cluster's porosity to control its heat loss. Meanwhile, the outermost bees in the cluster maintain themselves above a relatively low set-point of 15°C (Heinrich 1981), thus minimizing their energy expenditure for heat production but at the same time keeping their flight muscles warm enough to generate heat by shivering (Esch et al. 1991). Once the scout bees in a swarm have chosen its future nest site, the swarm decamps in a dazzling display of coordinated group behavior to fly to this site. All the bees in the swarm cluster launch into flight in about 60 s, form a cloud of swirling bees, and begin moving off together, with the scouts guiding the others to their new abode (Seeley et al. 1979; reviewed by Dyer 2000). Worker bees need a flight muscle temperature of at least 33–35°C for rapid flight (Esch 1976; Heinrich 1979); during the 10–30 min before takeoff the temperature gradient in a swarm cluster becomes abolished such that the bees in the cluster's mantle become as warm as those at its core (Heinrich 1981; Seeley et al. 2003). The warming of the mantle bees is a result of these bees generating heat by shivering (Esch et al. 1991), and it is stimulated by a vibrational signal (the wings-together form of worker piping) that the scout bees produce as they run over and through the mantle bees during the final hour or so before takeoff (Seeley and Tautz 2001).

To understand how a swarm controls its preparations for takeoff, we need to know how the scout bees know when to start producing their piping signals. In a previous study (Seeley and Visscher 2003), 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 sites, and their scouts started producing piping signals. We found that a consensus among the dancers is 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 potential nest cavities is consistently associated with the start of worker piping, which indicates that the quorum-sensing hypothesis may be true. Pratt et al. (2002) have already shown that *Leptothorax* ants use quorum sensing in their process of nest-site selection. In the present study, we further test the quorum-sensing hypothesis in honeybees by performing an experiment that tests the following prediction of the quorum-sensing hypothesis: delaying the formation of a quorum of scout bees at a swarm's chosen nest cavity, while leaving the rest of the decision-making process undisturbed, should delay the start of piping and thus the takeoff of the swarm.

Methods

Basic design of experiment

To delay quorum formation at the site chosen by a swarm, we limited the good nest sites available to swarms to one, and provided five close-together nest boxes at this site. This caused the scouts visiting the site to be dispersed among five identical nest cavities rather than concentrated at one nest cavity, which would be the normal situation. We then monitored the buildup of scouts at each of these nest boxes and the dancing and piping behavior at the swarm. For each swarm, we performed another control trial in which we provided just one nest box. The two trials for each swarm were performed using two different sites, so each trial began in the same way, with a scout bee discovering an attractive nest cavity at a new site. Also, which site had which treatment (five-nest-box or one-nest-box) and the order of the treatments in the two trials for each swarm was varied in a complete block design between swarms to control for possible treatment-order or site effects. Running each swarm with both treatments facilitated a paired data analysis and controlled for possible confounding factors such as different swarm age distributions and proportions of scout bees.

Study site

The experiment 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 few buildings; hence it has few natural nest cavities for honeybees. 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 four colonies that we moved to the island. Each colony was headed by a "New World Carniolan" queen that we had purchased from Strachan Apiaries in Yuba City, Calif. 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 combs 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 placed indoors 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 little cage containing the queen to a swarm mount (see Apparatus), and shook the workers onto the base of the mount. Within an hour, the workers had clustered around the queen and had begun to behave like a natural swarm. Eventually, the bees would choose a nest site, launch into flight, and start to move together to their new home. However, because we always kept the queen caged at the swarm mount, the workers were never able to complete their move; they instead returned to the swarm mount and resettled around their queen.

Apparatus

Swarms were placed on a swarm mount previously described by Seeley and Buhrman (1999). This mount consists of a vertical board, on which the swarm clusters, and a wire screen 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

Table 1 Number and location of the nest boxes used in each of the eight trials of the experiment. Note that each of the eight possible treatment/order/site combinations (e.g., five-nest-box treatment, used first, at Guano Bench) was used only once

Swarm	Trial, date	Treatment	Nest-box site
1	1, 28–29 June	Five-nest-box	Guano Bench
	2, 29–30 June	One-nest-box	Broad Cove
2	1, 4 July	One-nest-box	Guano Bench
	2, 5 July	Five-nest-box	Broad Cove
3	1, 8–9 July	Five-nest-box	Broad Cove
	2, 9–10 July	One-nest-box	Guano Bench
4	1, 23 July	One-nest-box	Broad Cove
	2, 24–25 July	Five-nest-box	Guano Bench

video recording the scout bees' dances, which we did to determine the amount of dancing for the nest-box site in each trial of the experiment. Our video equipment consisted of a digital video camcorder (Sony DCR-TRV50) and a video editing deck with variable-speed playback (Sony DSR-30).

To record worker piping within the swarm cluster, we mounted two small, 5-mm-diameter, custom-made microphones (flat frequency response from 20 to 6,000 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. We recorded the output of each microphone on one of the stereo channels of a digital minidisc recorder (Sony MZ-R37SP).

The five nest boxes used in this study were the same as those used in a previous study (Seeley and Buhrman 2001). The cavity volume and entrance size of each of these nest boxes was adjustable, but in the present study we left these properties set at 40 l and 15 cm^2, so that each nest box provided a highly desirable nest cavity. Each nest box was housed in a separate, open-sided shelter (see Fig. 1 in Seeley and Buhrman 2001), so that the nest boxes had the same exposure to the wind, sun, and rain.

Experimental layout and data collection

The layout for each trial of the experiment consisted of a swarm mounted on the porch of Bartel's Hall and either one nest box or five nest boxes, depending on the trial, placed at one of two grassy sites on the eastern side of Appledore Island. One site was near Broad Cove while the other was 150 m away, in the vicinity of Guano Bench (these are the locations designated as sites 2 and 4 in Fig. 2 of Seeley and Buhrman 2001). These two sites were the same distance (250 m) from the swarm site, but in directions separated by an angle of 35°. Table 1 shows for each trial how many nest boxes were used (one or five), where they were located (Broad Cove or Guano Bench), and in which order they were presented to each swarm. In the five-nest-box trials, we positioned the boxes in a line so that their entrance openings all faced away from the swarm, were spaced 3.5 m apart, and were equidistant from the swarm. Given that the distance of the nest boxes from the swarm was 250 m, and given that the width of the five-nest-box array was 14 m=(4×3.5 m), the arc subtended by the five-nest-box array was only 3.2°. This angle is much smaller than the scatter of waggle dances for a single nest cavity at this distance (the mean divergence angle of consecutive waggle runs advertising one nest box at 250 m is approximately 9°, Weidenmüller and Seeley 1999); hence we can be confident that the dances representing any of the five nest boxes in the five-nest-box arrays used in this study would be indistinguishable, so that each whole array was a single recruitment target.

After setting out the number of nest boxes that was appropriate for a swarm's first trial, we installed the swarm on the swarm mount and we inserted a pheromone swarm lure (Brushy Mountain Bee Farm, Moravian Falls, N.C.) in each nest box. These pheromone lures release the assembly pheromone that scout bees release when they find a suitable home site, and they seemed to help the scout bees discover our nest boxes. Once the bees had settled

themselves on the swarm mount, an observer was stationed at the nest-box site to record when it was discovered by a scout bee and to be ready for the start of data collection. Immediately upon observing a scout bee at a nest box, we took several steps to begin data collection. First, the observer at the nest-box site pulled the pheromone lure from each nest box and stored it in a glass jar. We did this to prevent artificial pheromones, which were helpful in accelerating the discovery phase, from influencing the subsequent site-selection phase of the process. Second, the observer began making a set of counts, every 15 min, of the number of scout bees visible outside each nest box. The protocol for making these counts was as follows: (1) stand 2–3 m directly in front of each nest box for approximately 90 s; and (2) every 30 s, note the maximum number of bees seen simultaneously at this nest box over the preceding 30-s period. This procedure yielded three counts of the number of scouts outside a given nest box every 15 min. When the number of bees outside the nest box rose above 10, 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 turned on the video camera, so that the dances of the scouts would be recorded from their start. Fourth, this observer began making 60+s audio recordings at 15-min intervals using the microphones mounted inside the swarm cluster to determine the level of worker piping within the swarm.

Meteorological data—air temperature, solar radiation, and wind speed and direction—were recorded automatically by a weather station on Appledore Island that is operated by the National Oceanographic and Atmospheric Agency.

Data analysis

The three counts made at each nest box every 15 min were averaged to yield one mean value of the number of scouts visible at each nest box every 15 min. Thus, for each nest box (one or five, depending on the trial) we had a record of the number of scout bees outside the box from when the nest-box site was discovered to when the swarm lifted off to fly to this site. The video recordings were analyzed to estimate the number of waggle runs performed for the nest-box site over 10-min intervals before takeoff. By locating the nest boxes on the east side of the island, we placed them well away from the island's buildings and this made it easy to distinguish dances for our nest-box site from dances for any alternative site that the scouts might find, which is almost always a wall cavity in one of the older buildings on the island. We made our counts of the waggle runs by reviewing each video recording and focusing on the 2-min subinterval at the start of every 10-min interval (counted backwards from the time of swarm takeoff). Within this 2-min subinterval, whenever a bee began to dance for the nest-box site, we noted the time (indicated on the video record) and the location (specified using a system of quadrats on the video monitor) at which she began to dance, and then we counted the waggle runs contained in her dance during the 2-min period. By noting the starting time and starting location of each dance, we avoided double counting the waggle runs contained in any dance even if multiple dances were performed simultaneously. We estimated the total number of waggle runs performed for the nest-box site during each 10-min interval by multiplying by five our waggle-run count for the first 2-min portion of this 10-min interval.

The audio recordings were analyzed to estimate the percentage of time that worker piping was heard at each sampling time (every 15 min). In each 60+ s audio recording we counted, for three non-overlapping 20-s intervals, the number of 1-s subintervals (n) in which worker piping was audible. We then converted these to percentages ($n/20 \times 100$) and averaged the three for each sampling time.

For each trial of each swarm, we measured the time to start of strong piping as the time that elapsed between when the scout bees began producing dances for the nest-box site and when their piping was heard at least 30% of the time. [We used 30% as our threshold because in previous work (Seeley and Tautz 2001; Seeley and Visscher 2003) it was found that, due to stochasticity in the pro-

duction of piping signals, the use of a lower threshold would result in many false starts, i.e., the piping would start and stop. The use of a 30% threshold, however, would almost always result in a true start, i.e., the piping would start and continue until takeoff.] Likewise, we measured the time to start of takeoff as the time that elapsed between when the scout bees began producing dances for the nest-box site and when the swarm began taking off to fly to this site. In making these time measurements, we counted only minutes when the scout bees were active, i.e., when at least one bee was performing a dance for the nest-box site. Thus our measurements of these two variables excluded time periods when bad weather or darkness prevented activity by the scout bees.

Results

Figure 1 shows the results of our experiment for the second of the four swarms that we studied. This swarm completed both trials of the experiment in just 2 days. As is shown in the weather records in Fig. 1, both days were warm (air temperature >22°C), sunny (solar radiation >300 W/m^2), and with light winds (<15 km/h), ideal for house hunting by honeybees. On the morning of 4 July 2003, we offered this swarm a single nest box at the Guano Bench site. A scout bee discovered this nest box at 1353 hours and at 1411 hours she returned to the swarm and began dancing strongly to advertise her find. At this point, the number of scout bees outside the nest box grew rapidly, to more than 15 bees by 1500 hours, and the number of waggle runs advertising the nest box increased steadily. By 1530 hours (79 min after the start of dancing), the piping had become strong (signals audible >30% of the time) and over the next hour the piping grew stronger until the swarm took off at 1629 hours (139 min after the start of dancing). The airborne swarm flew to-

ward the Guano Bench site, but because its queen remained caged at the swarm mount, the swarm returned to the mount and regrouped around the queen. At 1700 hours, while the swarm was resettling, the nest box at the Guano Bench site was moved to the Broad Cove site and the entrances of the other four nest boxes, already at the Broad Cove site, were opened, to offer the swarm a five-nest-box array. Shortly thereafter, at 1734 hours, we observed a scout bee inspecting one of the five nest boxes, but despite a close watch for dances at the swarm, we saw no dances advertising the nest-box site at Broad Cove this day, probably because it was discovered so late in the day.

Early the next morning, at 0644 hours, a scout bee again appeared at the array and again closely inspected one of the nest boxes. Dances for the five-nest-box site began to be performed at 0711 hours. For the next several hours, we recorded steady dancing and increasing numbers of scout bees outside the nest boxes at this site. It is important to note that the scouts visiting the five-nest-box site spread themselves out remarkably evenly among the five nest boxes. As is shown in Fig. 1, between 0700 hours and 1145 hours (shortly before the swarm took off) we made 20 rounds of counting the number of bees outside each of the five nest boxes. The mean numbers of bees counted per nest box in these rounds were as follows: box 1, 3.52 bees; box 2, 3.86 bees; box 3, 3.00 bees; box 4, 3.33 bees; box 5, 4.56 bees (see swarm 2 in Fig. 2). A one-way ANOVA ($F_{4, 95}=1.38$, $P>0.25$) shows that these means did not differ significantly among boxes. Because the scouts dispersed themselves among the five nest boxes, the number of scouts outside any particular nest box never rose above 10 bees, even though there was strong dancing for the five-nest-box site and the
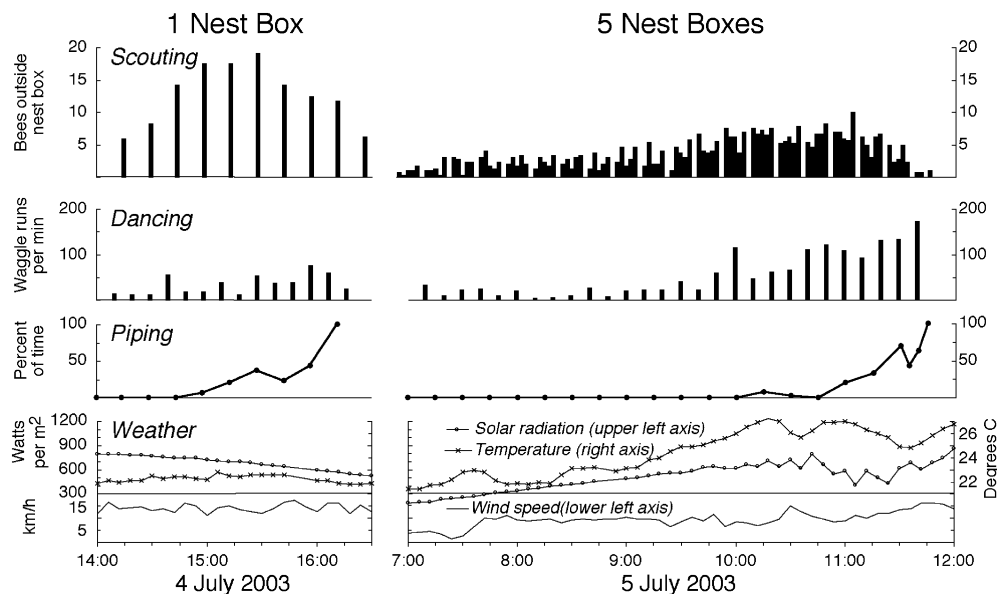

Fig. 1 Results of experiment for swarm 2. This swarm completed both trials of the experiment on 2 consecutive days, 4 and 5 July 2003. Weather records (*bottom*) indicate fair weather both days. In the one-nest-box trial, the number of scouts at the nest box rose rapidly and the piping became strong after only 79 min of dancing. In the five-nest-box trial, the number of scouts at any particular nest box did not rise above 10 bees, because the bees spread themselves among the five nest boxes, and the piping became strong only after 244 min of dancing
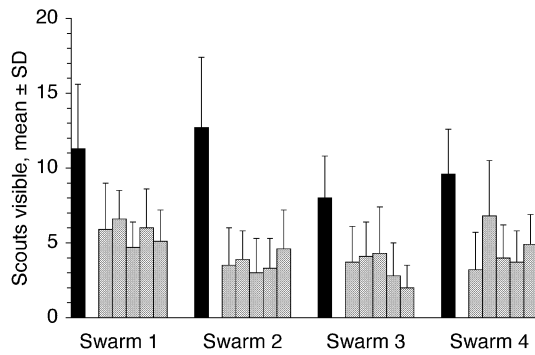
Fig. 2 Mean number of scouts visible on the outside of each nest box during one-nest-box trials (*black bars*) and five-nest-box trials (*grey bars*) of each swarm. In all swarms, the one-nest-box mean differs significantly from the five five-nest-box means

total number of scouts outside the five nest boxes there rose above 35 bees. It was not until 1115 hours (244 min after the start of dancing) that the piping rose above 30% and not until 1148 hours (277 min after the start of dancing) that the swarm took off. The airborne swarm then moved off in the direction of Broad Cove, but eventually returned to its queen and resettled on the swarm mount. At this point, we transferred the swarm to a hive to start the preparations for testing another swarm.

The pattern of results shown in Fig. 1 for swarm 2 (which we chose for our figure only because its two trials were completed the most rapidly and so its results could be shown most compactly) is typical of what we saw with all four swarms that we tested, as follows. First, in all four swarms the scout bees built up strongly at the box in the one-nest-box trials, whereas they evenly distributed themselves among all boxes in the five-nest-box trials, thereby building up at each box relatively weakly. Figure 2 shows for all swarms that the means of the number of scouts per nest box were decidedly different *between* the one-nest-box treatment and the five-nest-box treatment (lower in the latter), while at the same time the means were strikingly similar *within* the five-nest-box treatment (one-sided *t*-test, t_4 =6.47, 13.33, 4.38, and 3.23, $P<0.005$, <0.001, <0.01, and <0.02 for swarms 1–4, respectively). Second, in all four swarms there was strong dancing by the scout bees for the nest-box site, in both the one-nest-box trials and the five-nest-box trials. Table 2

shows that the average rate of waggle-run production (waggle runs/min) was the same for both treatments (paired *t*-test: $t_3=0.71$, $P>0.50$). Third, in all four swarms there was a dramatic delay to piping and takeoff in the 5-nest-box treatment relative to the one-nest-box treatment. The mean number of minutes with dancing that passed before the start of strong piping was 416 for the five-nest-box trials versus 162 min for the one-nest-box trials (paired *t*-test: $t_3=7.23$, $P<0.005$), and before the start of takeoff was 442 min versus 196 min (paired *t*-test: $t_3=5.28$, $P<0.008$). Because many more minutes of dancing transpired before the start of takeoff in the five-nest-box trials than in the one-nest-box trials, it is not surprising that the total amount of dancing (number of waggle runs produced) was far higher in the five-nest-box trials (20,208 waggle runs) than the one-nest-box ones (7,992 waggle runs; paired *t*-test: $t_3=2.54$, $P<0.05$).

Discussion

Evaluating the experiment

How do the scout bees in a honeybee swarm know when to initiate the preparations for their swarm's move to their new home? This study tested the quorum-sensing hypothesis by identifying a testable prediction of this hypothesis: that inducing a delay in the formation of a quorum at a swarm's chosen nest site should delay preparations for takeoff. The challenge in testing this prediction was to devise an experimental treatment that delays the buildup of scouts but does not disturb the rest of the swarm's decision-making process, especially the events that occur at the swarm cluster. We feel that our five-nest-box treatment did a good job of meeting this challenge.

Activity at the nest boxes

There is no doubt that the five-nest-box treatment slowed the buildup of scouts at each nest cavity relative to the one-nest-box treatment (Figs. 1, 2). We can also be certain that the five-nest-box treatment did not reduce the traffic of scout bees at the nest-box site or at the swarm

Table 2 Comparisons between one-nest-box and five-nest-box trials with respect to time to start of strong piping, time to start of takeoff, and level of dancing for the nest-box site

	Time variables				Dance variables			
	Minutes until piping is strong		Minutes until takeoff starts		Waggle runs per min.		Waggle runs total	
Swarm	One box	Five boxes	One box	Five boxes	One box	Five boxes	One box	Five boxes
1	267	525	287	538	44.4	35.3	12,730	19,010
2	79	244	138	277	34.2	55.1	4,715	15,255
3	161	417	211	439	46.0	36.0	9,700	15,815
4	140	477	150	515	32.2	59.7	4,825	30,750
Mean	162	416	196	442	39.2	46.5	7,992	20,208
SD	79	123	68	118	7.0	12.7	3,992	7,354
Significance	$P<0.005$	–	$P<0.008$	–	$P>0.50$	–	$P<0.05$	–

cluster relative to the one-nest-box treatment. On the contrary, the total number of scout bees at the nest-box site, and thus the level of traffic of bees between nest-box site and swarm cluster, was higher in the five-nest-box trials than in the one-nest-box trials (Fig. 2).

Dancing on the swarm

There is also good evidence that the five-nest-box treatment did not disturb the events at the swarm cluster. In devising this experiment, we were particularly concerned that providing five nest boxes at one site might reduce the level of waggle dancing at the swarm cluster. We were worried that a bee that encountered multiple nest cavities at one site or that experienced a slow buildup of scouts at her nest cavity might be less likely to dance. However, the mean rate of waggle-run production (waggle runs/min) did not differ for the two types of trial ($P>0.5$, paired t-test; Table 2). There was a pattern of the rate of dancing increasing in the second trial for each swarm ($P<0.04$, paired t-test), but the experimental design unlinked this from the number-of-nest-boxes treatment. In both types of trial the bees were always unanimous in their dancing. We enforced this unanimity through strict censorship; we removed from each swarm cluster any dancers that began advertising sites other than the nest box(es). In short, the bees at the swarm experienced similar rates of dancing under both treatments and it was always for a single location.

Other stimuli

There remains the possibility that there is some other stimulus, besides those just discussed, that informs the scout bees when to start piping and that this was reduced by our five-nest-box treatment. One possibility for such a stimulus is the shaking signal (also called the vibration signal), a signal that stimulates a general activation of the bees in a swarm (reviewed by Schneider and Lewis 2004). We did not monitor the production of shaking signals in our swarms, so we do not know if their production was reduced in the five-nest-box trials. But given that the five-nest-box treatment did not depress either the traffic of scout bees at the swarm cluster or the production of the all-important waggle dances at the swarm cluster, it seems unlikely that this treatment depressed the level of other stimuli, such as shaking signals, at the swarm cluster.

The total number of scouts at all of the nest boxes in the five-nest-box trials was generally greater than we observed at the single box in the one-nest-box trials, but the average level of dancing at the swarm did not differ. This suggests either that individual scouts were more likely to dance in the one-nest-box trials or that some other process constrains the total number of dances performed on the swarm. These effects may occur, but are not as great as the data of Fig. 2 and Table 1 suggest, because the rate of waggle-run production reaches a crescendo in the 30–60 min before takeoff. In the relatively short one-nest-box trials, this portion of the process represents a larger proportion of the total, and thus increases the mean rate of waggle runs for one-nest-box trials relative to five-nest-box trials. Furthermore, we compared the ratio of waggle runs of dancing to number of scouts counted during each hour for each of the four swarms, and in none of them was the difference in these ratios between the one-nest-box and five-nest-box trials statistically significant ($P>0.25$, t-test).

In sum, we believe that the delays to start of piping and to start of takeoff that we observed with the five-nest-box trials relative to the one-nest-box trials occurred because of the slower buildup of scouts at each nest box, not because of a reduction in some stimulus at the swarm cluster or other change in scout behavior. Consequently, we conclude that the results of our experiment, which confirm the prediction of the quorum sensing hypothesis, provide strong support for this hypothesis, and that the buildup of a quorum of scouts at the nest site is the key stimulus for scouts to terminate their swarms decision-making process and initiate swarm takeoff.

What cues do bees use in sensing a quorum?

The conclusion that slowing the buildup of scouts delays takeoff raises the question of what exactly a scout bee senses about the buildup of scouts at a nest cavity to know when she should start piping. The name of our hypothesis, quorum sensing, implies that we suppose that a scout senses the number of other scouts present at the nest cavity. Consistent with this idea is the finding in our previous study (Seeley and Visscher 2003) that a buildup of 10–15 bees at a nest box was consistently associated with the start of worker piping. We saw basically the same phenomenon in this study: piping began when the number of bees outside one of the nest boxes reached 10–15 bees. (The number of scouts did not reach as high a level at any box in the five-nest-box trials as it did in the one-nest-box trials, an effect more pronounced in swarm 2, shown in Fig. 1, than in other swarms.) There are, however, various possible ways for a scout to sense the number of other bees at a potential nest cavity. One is by visual perception. For a human being, and perhaps for a honeybee, the mobile scout bees are easily seen outside the cavity and even inside it, at least near the entrance opening, where the light level is above the visual threshold of honeybees (see data and discussion in Seeley and Visscher 2003). Another possible means of sensing the number of scout bees at a potential nest cavity is by tactile perception. Curiously, once a site acquires several scouts, these bees begin to make frequent contacts with one another. Some even begin to perform buzzing runs (first described by Lindauer 1955; see also Martin 1963 and Esch 1967) on the inner and outer walls of the cavity, and so butt against the other bees. It seems plausible, therefore, that a scout bee could use the rate of contacts with scouts in general, or with buzz runners in particular,

as an indicator of the number of fellow scouts at a possible nest cavity, or even sense buzz running from substrate or air vibrations without contact. Olfactory cues from other bees are also a possibility, sensed either at a distance or in close contacts. In our observations, contacts between nest-site scouts are brief, but even these may suffice to recognize another bee, and possibly to discriminate whether it is a swarm mate or not (see below).

In essence, scout bees use quorum sensing as a method of gathering information on the "opinions" (see Franks et al. 2002) of others regarding a potential nest site. It seems, therefore, that what a quorum-sensing bee needs to know is how many other bees have independently concluded that the site is a suitable home. One complication is that probably not all of the bees visiting a site have reached this conclusion. Many are apt to be bees that are newly recruited to the site and are still engaged in evaluating it, a process that requires some 20–40 min (Seeley 1977); such bees probably should not be counted by the quorum-sensing bees as they attempt to determine whether the number of swarm mates at a potential nest site exceeds the quorum threshold. One possible solution to this complication is for the quorum-sensing bees to count only encounters with bees producing the buzz-run signal, which may be a sign that the signaler has concluded that this is a suitable nest site.

Other implications

The use of quorum sensing suggests that group size may have a strong effect on the nest decision. If the required quorum size does not change in swarms of different size, a smaller proportion of the scouts will be needed in a more populous swarm, and the increased number of recruits available might result in faster buildup to a given level. On the other hand, as suggested above, it could be that the number of dances or dance followers places a rate-limiting constraint on recruitment so that swarm size has little effect. Further observations will be needed to resolve this question.

Another implication of quorum sensing is that it could be strongly affected if scouts from more than one swarm simultaneously scout the same site. If foreign-swarm scouts had the same effect as swarm mates, they might lead a swarm to begin takeoff preparations early. This could be advantageous in speeding up the decision making in a context where multiple swarms are competing for the same site, but could also lead to premature takeoff. Alternatively, if there is nestmate recognition among scouts (most likely from cuticular chemical cues), the effect could be an acceleration (because of the urgency of competing for the site) or a deceleration (if there is fighting, for example) of the decision making. Again, further experiments will be needed to test these possibilities.

Why quorum sensing?

Besides the mechanistic puzzle of how bees sense a quorum, there is the functional question of why bees use quorum sensing as opposed to, say, consensus sensing to time the takeoff preparations of swarms. The quorum itself may be significant, not only for indicating that many bees have reached the same conclusion about the nest site, but to insure that there is at least some minimum number of scouts that know the precise location of the nest site. This is probably crucial for the next step in the process: cross-country flight of the swarm, presumably guided by scouts that know where to go (Lindauer 1955). A swarm that only discovers one nest site could not rely on consensus sensing alone, since there is unanimity from the first dance, and yet it would be premature to take off before more scouting occurs, both because other, better, discoveries may be made and because of the need for a quorum of scouts familiar with the site.

The most thought-provoking role of quorum sensing, however, is that its use may reflect a trade-off between speed and accuracy in decision making. If an animal has to make a swift decision, it may be prone to make a poor decision, either because it cannot sample its options sufficiently broadly or because it cannot deliberate on its options sufficiently deeply (Franks et al. 2002). The speed–accuracy trade-off in decision making has been demonstrated empirically in studies of individuals (humans: Osman et al. 2000, bees: Chittka et al. 2003) and groups (ants: Franks et al. 2003), so there is no doubt that decision makers must solve the problem of finding a suitable compromise between swift decisions and accurate ones. Quorum sensing appears to be a way of solving this problem in group decision making by honeybees. With respect to speed, the requirement of a quorum (as opposed to a consensus) means that preparations for takeoff can begin as soon as enough bees have approved of one of the potential nest sites, even if some others are still scouting other sites. With respect to accuracy, the quorum requirement evidently promotes a high level of accuracy, for it appears that scouts will not begin producing piping signals for takeoff preparations until the number of bees present simultaneously outside a nest cavity reaches 10–15. Having a quorum this high ensures that a swarm's preparations for takeoff will not be initiated by scouts that have erred, i.e., that have judged a poor site to be a good one. If a scout makes a mistake and recruits strongly to a poor site, her followers will correct her mistake by judging the site less favorably, not recruiting others to the site, and so preventing the premature 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 *Leptothorax albipennis*. We suggest that the quorum size is a parameter of the bees' decision-making process that has been tuned by natural selection to provide an optimal balance between speed (favored by a small quorum) and accuracy (favored by a large quorum).

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