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ORIGINAL PAPER

An oligarchy of nest-site scouts triggers a honeybee swarm's departure from the hive

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Abstract Animals that travel in groups must synchronize the timing of their departures to assure cohesion of the group. While most activities in large colonies of social insects have decentralized control, certain activities (e.g., colony migration) can have centralized control, with only a special subset of well-informed individuals making a decision that affects the entire colony. We recently discovered that a small minority of individuals in a honeybee colony—an oligarchy—decides when to trigger the departure of a swarm from its hive. The departure process begins with some bees producing the worker-piping signal (the primer for departure) and is followed by these bees producing the buzz-run signal (the releaser for departure). In this study, we determined the identity of these signalers. We found that a swarm's nest-site scouts search for potential nest cavities prior to the departure of the swarm from its hive. Furthermore, we found that the predeparture nest-site scouts are the sole producers of the worker-piping signal and that they are the first producers of the buzz-run signal. The control of the departure of a honeybee swarm from its hive shows how a small minority of well-informed individuals in a large social insect colony can make important decisions about when a colony should take action.

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Introduction

Animals that move about in groups need to synchronize their departures to assure group cohesion (Conradt and Roper 2005; Conradt and List 2009). The decision of when to move may be despotic, whereby one individual decides when the group should depart. This is the case in white-faced capuchin monkeys (*Cebus capucinus*) where an individual located at the edge of a stationary troop initiates movement by producing specific trill vocalizations (Boinski and Campbell 1995). At the opposite extreme, the decision is reached through a democratic process whereby a majority of the group's members decide when to move (Conradt and Roper 2003). For example, in herds of the African buffalo (*Syncerus caffer*), a unified gaze in a specific direction by the majority of adult females triggers the group's movement in that direction (Prins 1996). Although most studies regarding group travel have shown that the timing of movement is decided by either a despotic leader or a democratic majority (Conradt and Roper 2003, 2005, 2007), a few reports have shown that the timing of movement is controlled by an oligarchy of well-informed individuals who trigger their group's movement when the conditions are right (Conradt and Roper 2003; Sumpter 2006). For example, in shoals of the golden shiner minnow (*Notemigonus crysoleucas*), a small group of individuals determines when to move to find suitable foraging sites (Reebs 2000). Because much of the research on collective movement has focused on vertebrate species (reviewed in Couzin 2006; Boinski and Garber 2000; Conradt and Roper 2003, 2005;

Conradt and List 2009), large gaps remain in our knowledge of the coordination mechanisms underlying group travel in invertebrate species (but see Franks et al. 2002; Pratt 2005; Buhl et al. 2006; Simpson et al. 2006), and regarding group travel by invertebrates, one intriguing mystery is the importance of oligarchic control of the timing of group movements in the large societies of insects, where democratic (decentralized) control of group behavior is the rule (Camazine et al. 2001).

Social insects are attractive for the study of group movements because their large colonies need a high degree of group integration in order to move as a cohesive unit (reviewed by Dyer 2000). Inside a large colony of social insects, there is usually little, if any, centralized control over daily activities. Instead, individuals respond to local information to make their own decisions (reviewed in Anderson and McShea 2001; Camazine et al. 2001; Jeanne 2003), but while the mechanisms of group integration in daily colony tasks have been widely studied, more research is needed on how social insects initiate and coordinate their group movements (Forsyth 1981; Dyer 2000; Schultz et al. 2008; Latty et al. 2009). In this study, we investigated an example of tightly synchronized movement by a social insect colony: the mass exodus of a honeybee swarm from its hive.

Honeybee (*Apis mellifera*) colonies reproduce by fissioning, whereby a swarm, composed of the old mother queen and roughly two thirds of the worker population, leaves its hive en masse while the remaining workers and a new daughter queen stay behind (Winston 1987; Martin 1963). The swarm clusters temporarily on a tree branch where it undertakes a complex house-hunting process. In a recent study of the signals that initiate a swarm's exodus from its hive, Rangel and Seeley (2008) discovered that starting about 1 h before departure, a few dozen bees start producing the worker-piping signal, which involves a bee pressing her thorax against other bees while producing a high-frequency (200–250 Hz) vibration of her flight muscles (Seeley and Tautz 2001; Seeley and Visscher 2004). The worker-piping signal primes the swarm bees for flight. Then, starting about 5 to 10 min before the swarm's departure, a few bees start producing the buzz-run signal, which involves a bee butting into other bees while buzzing her wings (Martin 1963; Rittschof and Seeley 2008). The buzz-run signal triggers the bees to fly out of the hive. Having determined what signals the bees use to initiate a swarm's exodus, we wanted to determine which bees produce these signals and thus control the timing of swarm departure.

Once the bees in a swarm have left their hive and have settled into a temporary cluster hanging from a tree branch, they show two markedly different patterns of behavior. The large majority of the swarm bees are relatively inactive and serve as food reservoirs that keep the swarm supplied with energy (Combs 1972). However, a small minority (only about 5%, Seeley et al. 1979; Gilley 1998) are active and serve as nest-site scouts that discover and inspect potential nest cavities. If a scout finds a high-quality cavity, she will return to the swarm cluster and perform a waggle dance to recruit other bees to that location (Lindauer 1955; Seeley et al. 2006). The collective decision of where to move is reached through a process of competition among scouts visiting different sites, with scouts from the highest quality site producing the strongest waggle dances and thus attracting the strongest support for their site (reviewed in Seeley and Visscher 2004; Seeley et al. 2006; Visscher 2007). When a quorum of nest-site scouts has built up at one of the sites, and thus a new home has been chosen, this oligarchy of nest-site scouts starts producing the worker-piping signal to prime the inactive bees in the swarm for flight (Seeley and Tautz 2001; Seeley et al. 2003; Visscher and Seeley 2007). When all the swarm bees have warmed their flight muscles to a flight-ready temperature (35°C), the nest-site scouts begin producing the buzz-run signal to release the liftoff of the swarm (Visscher and Seeley 2007; Rittschof and Seeley 2008).

Given that the *same signals* are used to initiate a swarm's exodus from its hive and its takeoff from its clustering site, we wanted to see if it is the *same bees*—nest-site scouts—who control the timing of swarm departure in both scenarios. To do so, we sought to answer three questions about the process of swarm departure from the hive. First, do the nest-site scouts begin searching for homesites before the swarm leaves its hive? Second, if the nest-site scouts start their searching before the swarm leaves its hive, do they also begin recruiting other bees to potential homesites before leaving the hive? And third and most important, do the nest-site scouts produce the signals that trigger a swarm's exodus from its hive? The only prior information regarding these questions comes from Lindauer (1955), who observed in two colonies that nest-site scouts started to search for potential homesites 2–3 days before their colonies swarmed, and who also observed in one of these colonies that the nest-site scouts performed waggle dances before the swarm departed the hive.

To further investigate who triggers a swarm's departure from its hive, we took three honeybee colonies that were preparing to swarm to a location devoid of natural nest sites. We installed the colonies in observation hives and then provided them with an attractive nest box to see whether nest-site scouts would begin searching for a future homesite prior to their swarm's departure from the hive. When we found that they would do so, we labeled the nest-site scouts at the nest box and observed them back at their hive prior to the departure of the swarm, to see if they would produce the signals that would trigger the swarm's exodus from their hive.

Materials and methods

Study site

All work was done at the Shoals Marine Laboratory on Appledore Island, Maine (42°58′N, 70°37′W). This 39-ha island lacks large trees with cavities, hence it has few natural nest sites for honeybees. We were thus optimistic that nest-site scouts from our observation hives would discover and show interest in the nest box we provided.

Set up of observation hives

We brought to the island three medium-sized honeybee colonies, all headed by naturally mated New World Carniolan queens (*A. mellifera carnica*; Strachan Apiaries, Yuba City, CA, USA) and all preparing to swarm. On 1 July 2008, each colony was installed in a three-frame observation hive (described by Seeley 1995). The three frames chosen for each colony were covered with adult bees (approximately 6,000 workers plus the queen) and were roughly half full of brood and half full of pollen and honey. At least one frame had one or more queen cells, which the bees had started to produce in preparation for swarming back in June, the time of year when most swarms occur in Ithaca (Fell et al. 1977). Each hive was set up inside a barn and connected to the outside through an exit tube.

Before the glass sides were installed on the observation hives, we placed one electret condenser microphone (Radio Shack Model 33-3013, 70–16,000 Hz frequency response) at the center of the bottom frame inside the hive and another such microphone near the entrance outside the hive (see Video and audio recording) so that we would be able to hear the worker-piping signals made by bees in preparation for swarming both inside and outside of the observation hive. We monitored the colonies daily from 08:00 to 16:00, listening for piping signals every 15 min. When we heard piping at a rate higher than three signals in 30 s, we started to observe the colony closely and continued until its swarm departed.

Because the air temperature was high on the days of this study, the workers in two of the three hives formed a sizable cluster (a "beard") outside their hive's entrance opening to facilitate ventilation inside their hive (Lindauer 1955; Winston 1987). This was extremely fortunate, because these beards enabled us to check individual bees (with the outside microphone) for the production of piping signals, and doing so enabled us to determine whether scout bees from the nest box—bees labeled with paint marks, see below—were the pipers. Also, as will be shown below, these beards turned out to be where most of the nest-site scouts performed waggle dances and rested prior to swarm departure, where we first heard and saw bees piping, and where the buzz running started. Indeed, the whole process of initiating swarm departure appeared to begin in the beard.

Set up of nest box

A 40-L nest box with a 12.5-cm^2 entrance hole (described by Seeley and Morse 1978) was positioned approximately 225 m from the observation hives. The nest box, which had most of the characteristics favored by nest-site scouts during the house-hunting process, was placed inside a small hut for protection from the sun and wind. It was located in a direction in which there were no other potential nest cavities so that we could distinguish dances for this nesting site from dances for other sites that the scouts might find. On the front wall of the nest box, we placed a vial containing the blend of pheromones produced by the honeybee's Nasonov gland, which scout bees normally release at the entrance of a desirable homesite to help their fellow scouts find the site (Winston 1987). The lure was removed after the first scouts arrived at the nest box.

Scout labeling and data collection at nest box

Once the observation hives and the nest box were set up, one of us waited at the nest box for the arrival of the first scouts. After scouts began visiting the nest box, they were caught at its entrance in a small insect net (15-cm diameter, 20-cm depth) either by placing the net over the entrance opening to catch bees as they exited the box or by catching them in flight around the box's entrance. Every captured bee was labeled on the thorax with a dot of shellac-based paint (von Frisch 1967) and then was released from the net. We used a different paint color every day. Even though we tried to label every bee that visited the nest box, this goal was not achieved fully when scouts arrived in high numbers. After the bee labeling had begun, the person at the observation hives began inspecting them for labeled bees to know which colony to follow closely. This revealed that only one colony at a time had scouts returning from the nest box. The labeling continued until the colony of interest casts its swarm.

The following data were collected every 15 min at the nest box: (a) the number of bees labeled in the previous 15 min, (b) the number of bees seen outside the nest box, and (c) the proportion of the bees seen outside the nest box in a "snapshot moment" that were labeled. To measure the number of bees outside the nest box, we recorded the maximum number of bees visible in each of six consecutive 10-s blocks, and we took the mean of the six values. This censusing work revealed the visitation rate of scouts throughout the day. The proportion of labeled bees at the nest box gave us an estimate of the proportion of the nest-site scouts that were returning to the observation hive with labels.

Data collection at the observation hives

Once the labeling of scout bees at the nest box had begun, we started to monitor the activities of bees at the observation hives. We focused our attention on the colony whose scouts had begun scrutinizing the nest box. Throughout the day, we scanned the surface of the colony's beard every 15 min to make the following counts: (a) the number of bees performing waggle dances indicating the location of our nest box, (b) the number of bees producing the worker-piping signal (each one detected with a directional microphone; see below), (c) the number of bees running rapidly, and (d) the number of bees producing the buzz-run signal. For each of the above counts, we noted how many bees were labeled, how many were unlabeled, and for how many the possession of a label was unclear (because we could not always see the thorax clearly, such as when the focal bee was crawling under other bees).

Video and audio recording

Because the number of buzz-running bees increases dramatically during the final minutes prior to swarm departure (Rangel and Seeley 2008), we used video recordings to estimate the number of buzz runners at the peak of the swarming process. Having noticed that the buzz running started on the beard outside the hive, we positioned a digital video camera (Sony DCR-TRV50) directly in front of the beard. We connected to the camera an electret condenser microphone (Radio Shack Model 33-3013, 70–16,000 Hz frequency response) that we had mounted in a Tygon tube (40 mm long and 8 mm internal diameter) to make the microphone directional. When we detected with the microphone at least two piping bees in the beard, we turned on the video camera and recorded the bees in the beard until the swarm's mass exodus was underway. The start of the swarm's departure was defined as the moment at which the bees on the surface of the beard began to take off. This was soon followed by an outpouring of bees from the hive.

Video and data analysis

The video analysis focused on the final minutes before the beard took off. We sampled each video recording for 2 s at 1.0-min intervals (unless otherwise noted) and analyzed each 2-s interval at slow speed or frame-by-frame using a video editing deck (Sony DSR-30). We scanned the screen of the video monitor from top-left to bottom-right to count (a) the number of buzz runners and whether these bees were labeled or unlabeled; and (b) the total number of bees on the video screen, for calculating what proportion of these bees were producing the buzz-run signal before and during the swarm's exodus. We did so to see whether the bees that produced the buzz-run signal had previously been labeled at the nest box, hence were nest-site scouts, and to see whether only a small minority of individuals in the colony triggered the departure of its swarm.

Results

Scouting activity at the nest box before swarm departure

Scouts from colony 1 began to visit the nest box on 1 July, the evening of the day that the observation hives were set up. A total of 41 bees were labeled on 1 July, 155 bees were labeled on 2 July, and 266 bees were labeled on 3 July, the day of swarm departure. Thus, nest-site scouts from this colony searched for potential nest cavities prior to swarm exodus, and the scouts that found the nest box recruited other bees to this site before the swarm left the observation hive. Over the course of the day that the swarm departed, 3 July, the number of bees labeled at the nest box and the average number of bees seen around the nest box increased strongly (Fig. 1a, b). However, as the number of visitors increased, the task of labeling all of them became harder, and by 10:30, some of the bees counted at the snapshot moments were unlabeled. The number of unlabeled bees seen at the nest box increased over time until the swarm departure began (Fig. 1c). After the swarm bees had settled in a sumac bush outside the observation hive and then had been installed in a small hive, we opened the nest box to check for scout bees that had stayed inside the nest box while the swarm was issuing from the observation hive. To our surprise, we found approximately 200 labeled bees inside the nest box. They flew off in the direction of the observation hives after they were shaken from the nest box.

Scouts from colony 2 begun to appear at the nest box on July 5. From this colony, we labeled two bees on 5 July, five bees on 6 July, and 79 bees on 7 July, the day that colony 2 swarmed. Although the number of visitors to the nest box was smaller for colony 2 than for colony 1 in the days prior to swarm departure, nest-site scouts did recruit bees to the nest box in high numbers on the day of swarm departure.

Scouts from colony 3 discovered the nest box on 8 July. We labeled 351 bees on that day and 221 bees on 9 July, the day of swarm departure. In this colony, we did not observe a crescendo of visitors to the nest box like what we saw on the day of swarm departure in colony 1 (Fig. 2a–c). However, most of the bees that were counted at the snapshot moments

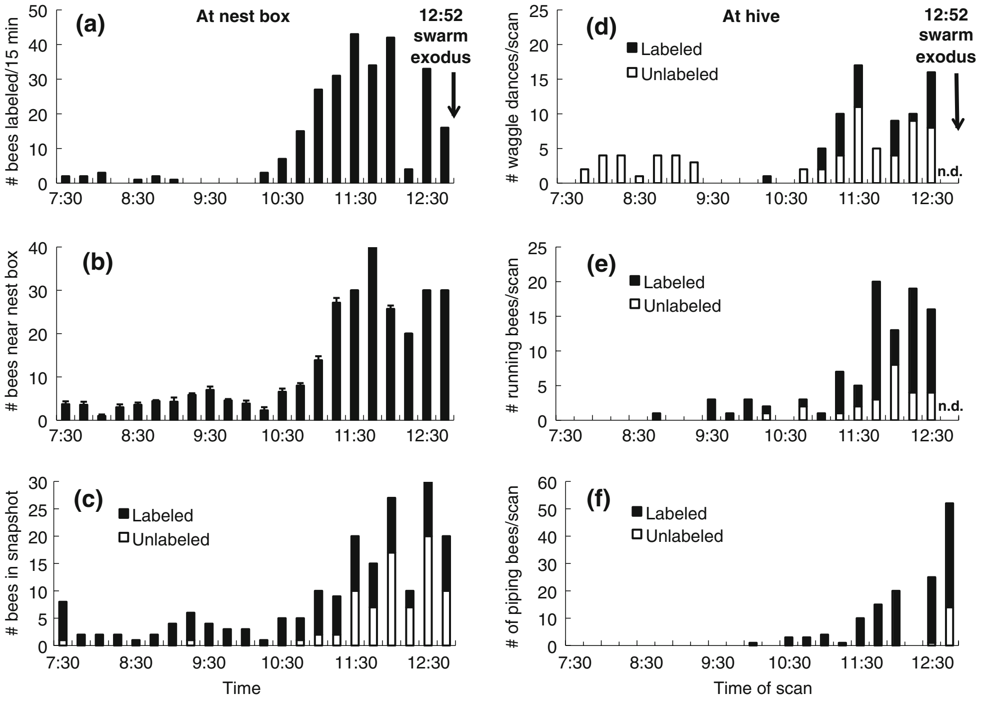

Fig. 1 Records of activity at the nest box and of the signals and aspects of mobility at the hive that changed in preparation for swarm departure in colony 1. Data were collected at the nest box (**a**–**c**) and at the beard of bees at the hive entrance (**d**–**f**) on day 3 of the trial, when the swarm departed. *Stacked bars* (**c**–**f**) represent the number of bees counted that were either labeled (*black*) or unlabeled (*white*). The number of bees seen around the nest box (**b**) is given as mean ± SE bars. The swarm departed from the hive on 3 July 2008 at 12:52. The abbreviation "n.d." indicates that no data are available for a given sampling interval

were labeled (Fig. 1c) because fewer scout bees from colony 3 visited the nest box compared to colony 1.

Signaling activity at the observation hive

The activity of bees on the surface of colony 1's beard increased throughout the day on 3 July, until the swarm initiated its departure at 12:52. Continuous observation inside and outside the hive revealed that the vast majority of the waggle dancing, and all the piping and buzz running, was done initially outside the hive on the surface of the beard. Only after the bees in the beard had taken flight did the pipers and buzz runners move inside the hive and take up activity there.

The number of bees producing waggle dances advertising the nest box rose over time. Many of these dancers were unlabeled, especially early in the day (Fig. 1d), and the proportion of labeled dancers was significantly less than would be expected from the proportion of labeled nest-site

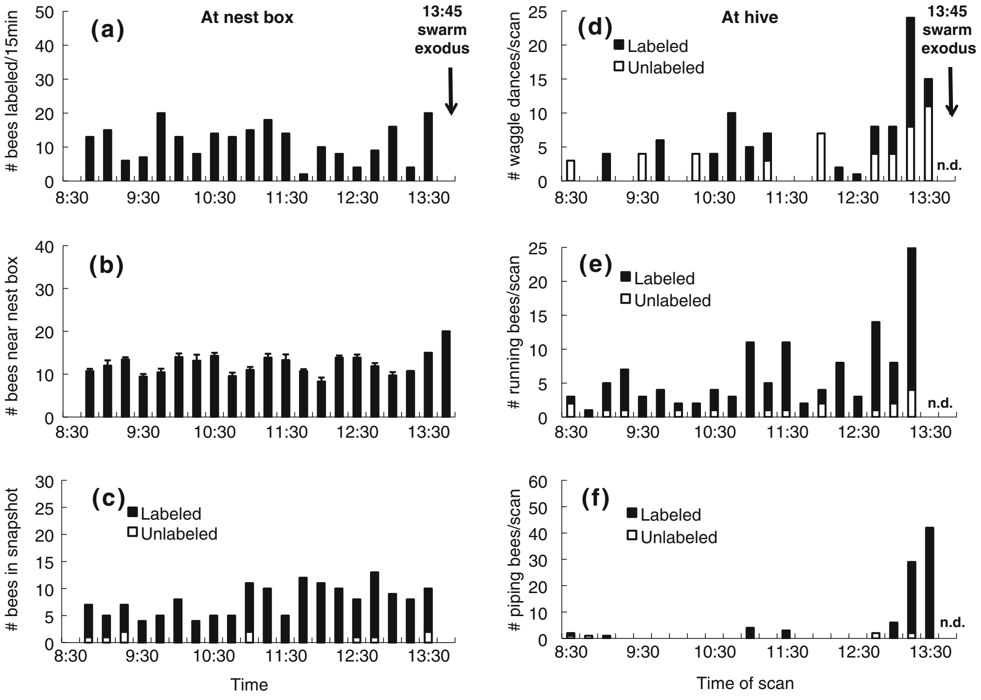

Fig. 2 Records of activity at the nest box and of the signals and aspects of mobility at the hive that changed in preparation for swarm departure in colony 3. Data were collected at the nest box (**a**–**c**) and at the beard of bees at the hive entrance (**d**–**f**) on day 2 of the trial, when the swarm departed. *Stacked bars* (**c**–**f**) represent the number of bees counted that were either labeled (*black*) or unlabeled (*white*). The number of bees seen around the nest box (**b**) is given as mean ± SE bars. The swarm departed from the hive on 9 July 2008 at 13:45. The abbreviation "n.d." indicates that no data are available for a given sampling interval

scouts (Table 1). The number of bees running across the beard escalated dramatically across the morning, rising from fewer than four runners per scan before 10:00 to nearly 20 runners per scan in the hour prior to swarm departure. The vast majority of bees running on the surface of the beard were labeled (Fig. 1e). Piping bees first appeared at 10:00, more than 2 h before the swarm's exodus, and their numbers rose to 52 at 12:45, the last scan before the swarm departed at 12:52. For each scan, all the pipers were labeled except for the last scan in which 14 out of 52 of the pipers were unlabeled (Fig. 1f). The proportion of labeled pipers was greater than would be expected from the proportion of labeled nest-site scouts (Table 1).

Colony 2 swarmed on 7 July at 10:58. Because colony 2 was less populous than the other two colonies, it did not create a beard outside the observation hive, so we were unable to watch for waggle dancers, count runners, and listen for piping bees on the surface of a beard. Thus, we could not identify which individuals were producing the piping signal and whether the pipers were labeled.

Table 1 Comparisons of the proportions of scout bees at the nest box that were labeled and the proportions of waggle dancers, pipers, and buzz runners at the hive that were labeled

	Colony 1	Colony 3
Nest-site scouts		
Labeled	111	147
Unlabeled	78	10
% Labeled	59	94
Waggle dancers		
Labeled	30	68
Unlabeled	67	44
% Labeled	31	61
Chi-square value	31.0	20.1
P value	<0.001	<0.001
Pipers		
Labeled	123	86
Unlabeled	13	4
% Labeled	90	96
Chi-square value	56.1	0.60
P value	<0.001	>0.44
Buzz runners		
Labeled	33	24
Unlabeled	213	227
% Labeled	13	10
Chi-square value	211.1	2,952.0
P value	<0.001	<0.001

The nest box scouts' counts are the totals of censuses taken on the day of swarm departure. Note that the percentages of the labeled waggle dancers and the buzz runners were significantly less than the percentages of labeled scouts, whereas the percentages of the labeled piping bees were significantly more than or not different from the percentages of labeled scouts

In colony 3, as in colony 1, we found that most of the waggle dancing for the nest box, and all the piping and buzz running, was done initially outside the hive on the surface of the beard. Waggle dancers were observed on the surface of the beard as early as 08:30 on 9 July, the day of swarm departure, and their numbers increased over time until the swarm left the observation hive at 13:45 (Fig. 2d). As in colony 1, the proportion of labeled dancers was significantly less than would be expected from the proportion of labeled nest-site scouts (Table 1). The number of bees running across the beard stayed relatively low (no more than 11 per scan) throughout the day until a half hour before swarm departure, when it rose rapidly to 25 bees at 13:15. The vast majority of the bees running across the beard's surface were labeled (Fig. 2e). Finally, the piping signal was heard sparingly as early as 08:30. The number of pipers rose to 42 at 13:30, the last scan before the swarm departed at 13:45 (Fig. 2f). Almost every piper bee was labeled. The proportion of labeled pipers matched what would be expected from the proportion of labeled nest-site scouts (Table 1).

When we measured the proportion of the bees that triggered each swarm's departure, by performing buzz runs, we found that the total number of bees visible on the video screen before the exodus was about 300 bees in colony 1 and nearly 600 bees in colony 3. We also found that there were fewer than 15 buzz runners visible on the video screen in colony 1 and fewer than 20 in colony 3, when the swarm departure started. Therefore, in both colonies, less than 5% of the bees seen on the video screen had begun to buzz run at the start of the exodus (Fig. 3). In both colonies, the proportion of buzz runners increased to nearly 60% of the bees visible on the video screen in the middle of each swarm's departure. The first buzz runners appeared about 10 min prior to each swarm's departure, and many bees in this small minority were labeled individuals. As the departure progressed, a higher number of unlabeled individuals started to make buzz runs, so that by the peak of the exodus, the vast majority of the individuals performing the buzz run were unlabeled. In both colony 1 and colony 3, the proportion of labeled buzz runners was markedly less than would be expected from the proportion of labeled nest-site scouts (Table 1).

Discussion

Nest-site scouts become active before swarm departure

Our results indicate that nest-site scouts in honeybee colonies that are preparing to swarm can start the house-hunting process before the swarms from these colonies leave their hives. Our observations also show that when

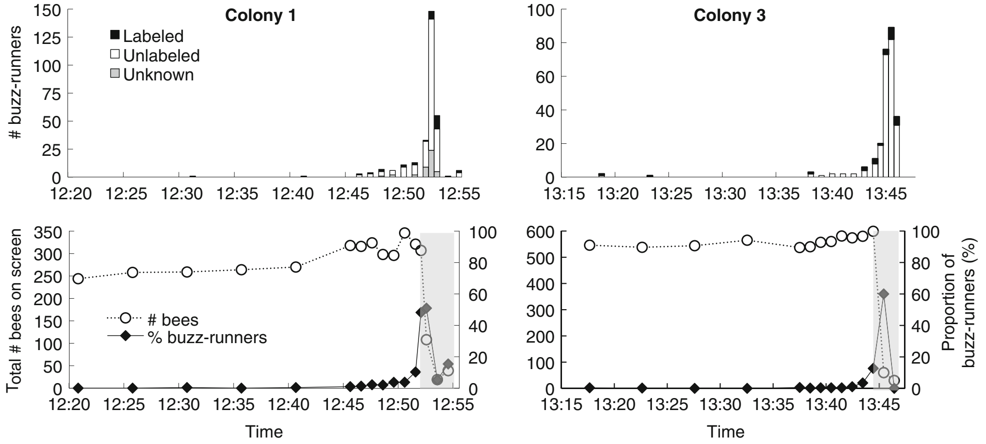

Fig. 3 The number of buzz runners before and during (*gray box*) the swarm's departure in colonies 1 and 3 (*top graphs*). *Stacked bars* represent the number of buzz runners observed on the surface of the beard that were labeled (*black*), unlabeled (*white*), or unknown (*gray*, if we were unable to determine the presence/absence of a label on the buzz runner). Also shown are the total number of bees seen on the video screen before and during the swarm's departure and the proportion of these bees that produced the buzz-run signal over time (*bottom graphs*)

predeparture nest-site scouts are interested in a potential homesite, they can return to their hive and recruit nestmates to that site by performing waggle dances.

Lindauer (1955) also reported observing nest-site scouts starting the house-hunting process a few days before their swarm departed its hive. One of the experiments that he conducted was performed on a North Friesian island with few nest sites besides artificial ones, much like the conditions of our experiment on Appledore Island. Lindauer took to the island a hive of bees that was ready to swarm and watched to see if nest-site scouts would start inspecting his nest boxes even before the swarm issued from the hive. Three days before the swarm emerged from the hive, Lindauer observed a few scouts exploring his nest boxes and other possible nest sites around the island such as holes leading to cavities between rocks. Lindauer concluded that scouts begin the search for nest sites prior to a swarm's departure, but that they do not choose their future homesite before the swarm leaves its hive.

Scout bees produce the signals that initiate swarm departure

A previous study (Rangel and Seeley 2008) showed that honeybees use the piping signal and the buzz-run signal to trigger a swarm's exodus from the hive. The present study shows that it is the nest-site scouts who produce these signals. These scouts are the primary, if not the sole, producers of the worker-piping signal that primes the swarm bees for departure, and these scouts are the first producers of the buzz-run signal that triggers the bees to swarm out of their hive.

Our findings resemble what is known about how a bivouacked swarm initiates the flight to its new home. Seeley and Visscher (2003) found that when at least ten to 15 scout bees are together outside a possible homesite, these bees sense that a quorum has been reached at that site. They then return to the swarm and start producing the piping signal to prime the swarm bees for liftoff and flight to the chosen site. The piping signal stimulates the quiescent bees on the swarm to warm their flight muscle to at least 35°C, the minimum temperature needed for rapid flight (Heinrich 1981; Seeley and Visscher 2003). In a follow-up study, Visscher and Seeley (2007) discovered that it is only the nest-site scouts from the chosen site that produce the piping signal. Our results are also consistent with those of Rittschof and Seeley (2008) who discovered that on clustered swarms that are preparing to take off to fly to their new home, the nest-site scouts also produce the buzz-run signals that trigger takeoff. Thus, it now seems clear that the nest-site scouts are important producers of the piping signal and the buzz-run signal in both contexts of swarm departure: from the parental hive and from the bivouac site.

Swarm departure is controlled by an oligarchy

This study provides evidence that it is a tiny minority of well-informed individuals, the nest-site scouts, who initiate a honeybee swarm's departure from the parental hive. This oligarchic mechanism of decision making ensures that the important decision of when the swarm should leave the hive is made by bees who know when the conditions are right, both inside the hive (queen cells are ready) and outside the hive (weather is good).

Even though some of the piping bees observed on the beards of our two study colonies were not labeled, we think it is likely that all the piping bees were nest-site scouts because not all the nest-site scouts were labeled. Furthermore, in both colony 1 and colony 3, the proportion of the pipers who were labeled matched or exceeded the proportion of the nest-site scouts who were labeled. We doubt, however, that all the buzz runners were nest-site scouts because in both colonies 1 and 3, the proportion of the buzz runners that were labeled was much smaller than the proportion of the nest-site scouts that were labeled. The study by Rittschof and Seeley (2008), which looked at the buzz runners in swarms preparing to take off from bivouac sites, found that the piping bees turned into the buzz runners, so in this context, it looks like both signals are produced exclusively by the nest-site scouts. Our study suggests, however, that in the context of a swarm's departure from the parental hive, the buzz-run signal is produced by various bees, not just the nest-site scouts. It appears that the mass exodus of a swarm is started by nest-site scouts that produce both the piping signal and the buzz-run signal, but that the colony later implements "relay communication" to accelerate the departure process. In this type of communication, first suggested by Wilson (1971, p. 270), the receivers of a signal start producing the signal themselves thereby creating a chain reaction of signal production that grows exponentially. Thus, the threshold level of signaling needed to elicit action (in our case, the departure of a swarm from its hive) is reached quickly. Relay communication could certainly explain why at first many of the buzz runners in our study were labeled and thus were nest-site scouts, but why later on most of the buzz runners were unlabeled and thus probably were not nest-site scouts. It is also possible that some of the unlabeled buzz runners were unlabeled nest-site scouts, though this is unlikely in colony 3 in which nearly all the nest-site scouts were labeled.

Few studies have reported oligarchic control of the timing of group movement. One example comes from a study of domestic cattle (*Bos taurus*). Ramseyer et al. (2009) reported that a group's movement is preceded by a 30-min period of preparation in which the activity level (i.e., head movements, number of awake heifers, and alignment of bodies) of a small number of individuals increased. The initiation of a departure depended on the behavior of a few first movers and on how well they relayed this information to other group members. This led to a higher number of individuals behaving similarly, ultimately releasing the entire group's move.

A second example of oligarchic control of the timing of group movement comes from rock ants (*Temnothorax albipennis*). During nest-site selection, a small percentage of a colony's members function as the scouts who make the decision of when their colony should migrate to a new home, usually a rock crevice. When a scout discovers a high-quality site, she recruits other scouts to the site, and when the number of scout ants reaches a critical threshold (quorum) at this site or some other site, then the scouts from the winning site start carrying the rest of the colony to their site. Thus, nest-site selection is rather centralized in that a small minority of the colony's population (the scouts) assesses the discovered sites, chooses among them, and ultimately initiates the colony's migration to its new home (Mallon et al. 2001; Pratt et al. 2002).

The present study reports how, in the context of swarming in honeybees, an oligarchy of workers exerts control over a colony-wide action. It shows that a relatively small group of nest-site scouts searches for and recruits to potential nest sites prior to a swarm's exodus from the parental hive. It also shows that these nest-site scouts control the timing of the swarm's departure by producing the signals that initiate the mass exodus. In the future, it will be important to investigate whether it is common for nest-site scouting and recruitment to potential nest sites to occur before swarming, and whether any colonies that do not have bees' scouting prior to swarm departure use different mechanisms to trigger swarm exodus. Based on Lindauer's (1955) and our observations, we predict that colonies usually do have bees searching for and recruiting to potential nest sites prior to swarm exodus, and that nest-site scouts are the individuals who trigger swarm exodus by producing the piping and buzz-run signals. We also predict that the length of time that a swarm spends at its bivouac site reflects how popular one of the scouted sites has become before the swarm leaves its hive.

To better understand the importance of oligarchic control of group movements, we need more studies that examine the possibility that within an animal group, there can be a small number of individuals who decide when their group should make its moves.

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