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The signals initiating the mass exodus of a honeybee swarm from its nest

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Animals that travel in groups must synchronize the timing of impending departures to ensure group cohesion. The mechanisms used by a honeybee, *Apis mellifera*, colony to organize the departure of a swarm from its nest remain a mystery. We examined the signals that trigger a swarm's explosive exodus from the parental nest, and we documented the concurrent changes in bee density and mobility. Using video recordings of swarms exiting observation hives, we analysed how bees in three swarming colonies prepared for and then performed their sudden departures. Over the 60 min before swarm exodus, the production of piping signals gradually increased and ultimately peaked at the start of the swarm departure. Also, during swarm exodus, bee density (number of bees in 100 cm^2) dropped markedly, whereas the average bee velocity (mm/s), and the production of buzz-run signals, spiked dramatically. Neither waggle runs nor shaking signals showed increases before or during swarm exodus. The explosive departure of a honeybee swarm from its parental nest shows how animals can use the same communication signals in different contexts; we now know that honeybees use piping and buzz-run signals to initiate both a swarm's departure from its nest and a swarm's take-off from its bivouac site. This study also shows how a small minority of individuals in a social insect colony can operate as an oligarchy to make an important decision, i.e. when a swarm should leave its nest to found a new colony.

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When animals that travel about in a group move from one location to the next, they must synchronize their departures so that the group does not disintegrate. The timing of a group's departure may be decided by means that are democratic, oligarchic, or despotic (Conradt & Roper 2003, 2005). In a democracy, the decision-making process involves a group of individuals signalling their preferences about when to leave, initiating the move only when a majority of the members are in agreement. For example, in red deer, *Cervus elaphus*, a herd that has settled for the night moves the next day only when more than 60% of the adults stand up in concert (Conradt & Roper 2003). In an oligarchy, only a small number of individuals have access to the information about the conditions that must be met for their group's move, and this minority makes the decision of when to depart. This oligarchic decision-making process is exemplified by colonies of rock ants, *Temnothorax albipennis*. During colony emigration, only a small percentage of a colony's members know when to initiate the move to the new nest site, and this minority stimulates the majority to do so using sophisticated mechanical signals (Mallon et al. 2001; Pratt et al. 2002). Finally, in a despotic situation, one individual controls when the group moves and this leader signals to the others when it is time to leave. Such is the case in the mountain baboon, *Papio ursinus*, among which a male or female leader initiates and specifies the direction of travel with exaggerated gestures of standing up (Byrne et al. 1990). Most of the studies of the mechanisms used by group-living species to initiate travel have focused on birds, cetaceans and primates (Boinski & Garber 2000), leaving large gaps in our knowledge of group travel in invertebrates (but see Simpson et al. 2006; Buhl et al. 2006). Given their large colonies, sophisticated communication systems and ease of study, social insects are attractive for exploring how animals initiate a group's move from one location to the next.

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Many studies of social insects have revealed how group decisions are made regarding nest building, brood rearing, food collecting and other aspects of colony life (Camazine et al. 2001), but still little is known about how a group of social insects decides when to move to a new location (Forsyth 1981; Dyer 2000). Most of our knowledge regarding these mechanisms comes from the study of honeybee, *Apis mellifera*, swarms. When a colony swarms, it splits into two colonies, with the mother queen and several thousand workers suddenly leaving the parental nest to found a new colony. The departing bees settle on a tree branch in a beard-like bivouac cluster, from which scout bees go searching for potential nest sites. Scout bees that find prospective home sites return to the swarm cluster and perform waggle dances to recruit other bees to their finds (Lindauer 1955). Once a sufficient number of bees has built up at one of the sites, the scout bees at this site return to the swarm and begin to produce the signals that initiate the swarm's take-off and flight to its new home (reviewed in Seeley et al. 2006; Visscher 2007).

The first signal is the high-pitched piping signal, which starts an hour or so before take-off and primes all the bees for take-off. While piping, scouts burrow among the quiet bees in the swarm cluster, pressing their thoraces against these bees and producing flight-muscle vibrations that stimulate the quiescent bees to warm their flight muscles to at least 35 °C, the temperature needed to take flight (Seeley & Tautz 2001; Seeley & Visscher 2004). Then, about 10 min prior to take-off, the same bees that were producing piping signals gradually begin to produce buzz-run signals, excitedly running about, pushing against other bees, and buzzing their wings in bursts that release the swarm's lift-off (Lindauer 1955; Rittschof & Seeley 2008). Additionally, the shaking signal (also known as the 'dorsoventral abdomen vibration signal', or simply, the 'vibration signal'), in which one bee grabs another bee and shakes her body for a second or so, seems to work as a nonspecific modulatory signal (Nieh 1998) that, in the context of swarming, aids in the general activation of swarm bees before the flight to the new home (Schneider et al. 1998; Lewis & Schneider 2000; Donahoe et al. 2003; reviewed in Schneider & Lewis 2004). Thus, whereas much is known about how honeybee swarms organize the take-off process after they have left the parental nest, almost nothing is known about how the explosive departure of a swarm is initiated inside the parental nest (Seeley 1985; Winston 1987).

What are the signals that initiate the explosive exodus of a honeybee swarm from the parental nest? To date, only Martin (1963) has studied what happens inside a nest prior to the exodus of a swarm. Working with colonies in observation hives, Martin reported that 15 min before the exodus, worker bees appeared quiet and calm. Then a sudden agitation started, with a few workers running back and forth, sometimes buzzing their wings, performing what he called the *Schwirrlauf*, or buzz-run. He reported that the buzz-runners were silent while signalling to other bees and that direct contact with other bees was necessary to activate them. He also reported that the mass exodus of the swarm began just a few minutes after the majority of bees in the colony had been contacted by the buzz-runners. Given that honeybees use the buzz-run to release a swarm's take-off from the bivouac site (Rittschof & Seeley 2008), it is likely that they also use the buzz-run to trigger a swarm's departure from the parental nest. Another signal that may play a role is the piping signal. Based on the studies of swarm take-off from the bivouac site, we know that bees start warming their flight muscles more than an hour before the buzz-runners appear on the swarm cluster. This increase in temperature is stimulated by individuals that perform the piping signal (Seeley & Tautz 2001). Although the ambient temperature experienced by bees living inside a nest is higher than that experienced by bees hanging from a tree branch, preswarm bees might also need to be stimulated to warm their flight muscles before buzz-runners can release their mass exodus from the nest.

Two other signals that might play a role in eliciting the swarm exodus are the shaking signal and the waggle dance. One study found that, during the reproductive season, the queen is increasingly shaken by workers several days before swarming, presumably to activate her for flight (Allen 1959a, b). The shaking signal on workers activates quiescent swarm bees, even before they warm their flight muscles for take-off (Visscher et al. 1999). As mentioned above, scouts perform waggle dances to indicate the locations of potential home sites (Lindauer 1955; Seeley et al. 2006). If the search for a new home starts even before the swarm leaves the parental nest, perhaps bees perform the waggle dance in increasing frequency in preparation for swarm departure.

In this study, we examined three swarms originating from honeybee colonies living in observation hives, to determine how bees initiate the mass exodus of a reproductive swarm from its parental nest. We report which signals are, and which are not, used for this purpose.

METHODS

Study Site and Bees

We conducted our study at the Liddell Field Station of Cornell University in Ithaca, New York, U.S.A. (42°26′N, 76°30′W). We created five medium-sized honeybee colonies from five larger colonies that lived in nearby bee yards, all headed by New World Carniolan queens (*Apis mellifera carnica*; Strachan Apiaries, Yuba City, California, U.S.A.). On 14 May 2007, we installed each of the five colonies with its original queen in a three-frame observation hive (described by Seeley 1995). Bees at the entrance had access to both sides of the hive. The three frames chosen to start each colony were covered with adult bees (roughly 6000 workers total) and were filled with sealed brood, honey and pollen, to create the conditions present in a natural colony preparing to swarm (Winston 1987). We standardized the amount of brood, food and workers across colonies by choosing frames that were approximately half-full of sealed brood, half-full of honey and pollen and entirely covered by workers. Two weeks after establishment, the colonies were actively foraging and growing and were more or less synchronized to start swarming in early June, which is when most natural swarms occur in the Ithaca area (Fell et al. 1977).

Video and Audio Recording

Before the observation colonies were sealed with glass covers, we placed an electret condenser microphone (Radio Shack Model 33-3013, 70−16 000 Hz frequency response) at the centre of the bottom frame on one side, so we could hear the sounds made by the bees during the swarming process. To detect these sounds, we connected the microphone to a voice-activated sound recorder (Sony ICD-P520), which gave us easy access to the sounds produced by each colony at any time. The observation hives were set up in a light-proof room to simulate the dark conditions inside natural honeybee nests, leaving the daylight coming in the hive entrance as a guide for the bees to find the exit. All video recordings were made in complete darkness using the night-vision function of a digital video camera (Sony DCR-TRV50), which had a field of view always positioned on the same side of each hive and consisting of an area of comb 100 × 133 mm located on the bottom frame, with the microphone placed at the centre.

We monitored the observation hives daily to determine which signals were produced to initiate the exodus of a swarm. Knowing that bivouacked swarms are primed for departure by nest-site scouts that perform piping signals during the last hour or two before take-off, we listened in on each colony in our observation hives every 15 min from 0800 to 1500 hours, checking for piping signals. When we heard piping at a rate of at least three signals in 30 s, we turned on the video camera, transferred the microphone output to the camera, and started recording until after the swarm had left the hive and the remaining bees returned to the quiescent preswarm state. The start of swarm departure was defined as the moment at which began a rapid outflow of bees from the hive (confirmed by observing the exodus from outside the hive). The end of swarm departure was defined as the time at which the swarm had settled on a tree branch and bees stopped flying out to join the swarm.

Video Analysis

The video recordings were sampled at intervals of 2.5 min (unless otherwise noted) and analysed at slow speed or frame-by-frame using a video-editing deck (Sony DSR-30). The following measurements were taken at every time interval: (1) Density, the number of bees present in a 10 × 10 cm area; (2) Mobility, the number of bees crossing a vertical 3-cm line in 30 s (the line was located in the centre of the camera's field of view); (3) Mobility index = bee mobility/bee density, as an index of bee mobility with a correction for the changes in bee density over time; and (4) Average velocity, the average number of millimetres travelled in 3 s by 10 randomly chosen bees. To choose 10 bees at random, we placed an acetate sheet over the video screen with 10 sampling dots dispersed across the screen and tracked the 10 bees closest to the dots. A plot of the movements made by each of the 10 randomly chosen bees was generated for one of the swarms, to illustrate the sudden spike in average bee velocity during the swarm exodus and to see whether there was consistent directionality in the movement of the bees. Using the input from the microphone connected to the video camera, we measured (5) Piping rate, the number of seconds the piping signal was heard during a 30-s period. Additionally, we scanned the entire screen of the video monitor from top-left to bottom-right to measure three more signals: (6) Buzz-run rate, the number of buzz-runners observed in 30 s, identified as individuals performing the behavioural sequence described by Rittschof & Seeley (2008); (7) Waggle-run rate, the number of waggle runs observed in 30 s; and (8) Shaking-signal rate, the number of worker−worker shaking signals observed in 30 s. Finally, we measured the total number of bees observed on the video screen and recorded what proportion of those bees were performing the buzz-run before and during swarm departure. We followed buzz-running bees at slow speed from 1 s before to 1 s after each time interval to make an accurate count of all signalling bees. We did so to check whether only a small minority of individuals in the colony initiated a swarm's exodus.

Statistics

The descriptive statistics reported are the mean ± 1 standard error. For all statistical tests, the level of significance used was $\alpha = 0.05$. To increase the power of our tests, we used one-tailed tests when possible; we predicted a priori, based on previous studies, that (1) the density of bees would drop as bees left the hive (Martin 1963) and (2) the average velocity, piping rate and buzz-run rate would increase during the swarm departure process (Seeley & Tautz 2001; Rittschof & Seeley 2008). For each colony, we calculated the mean value for each mobility variable and each communication signal before, during, and after swarm departure. The number of measurements per mean varied depending on the length (in minutes) of each period in the departure process. We grouped the data from the three swarm departures and calculated one mean value for each mobility variable and communication signal using the means obtained for each swarming event. To test each measure for a difference between its mean value before and during swarm departure across the three swarms, we used paired *t* tests. The use of this test enabled us to keep the significance level at $\alpha = 0.05$, because for $n = 3$ (data pooled from three swarm departures), the nonparametric Wilcoxon signed-rank test would not have the power to discern differences at a significance level lower than $\alpha = 0.125$.

To test whether the direction of travel of the bees before and during swarm departure was consistent, we used the drawings of distances travelled by the 10 randomly chosen bees to measure average bee velocity (see above) to create a net travel vector from the start to the end point of each bee's travel. The angle was measured relative to straight up (=0°) and a circular histogram of vector angles was generated for each swarm. Mean vector bearing and mean vector length were calculated, and Rayleigh's Z test was used to test for nonrandom directionality of the bees' movements in each swarm (using Dr. Kirk Visscher's circular statistics software, Riverside, California, U.S.A.), with the null hypothesis that the circular distribution of the angles was drawn from a uniform circular distribution (as described by Gardner et al. 2008).

RESULTS

We obtained complete recordings of the departure of prime swarms from three of the five colonies. The swarm originating from colony 1 started the exodus at 1255 hours, the swarm from colony 2 originated at 1215 hours, and the swarm from colony 3 issued at 1020 hours. All three colonies showed similar patterns in the production of signals and the movement of bees before, during and after the swarm exodus, as exemplified by the signalling and mobility patterns observed in colony 1 (Fig. 1, Table 1). Over the hour or so before departure, there were no apparent changes in the behaviour of the bees, except for a gradual increase in the piping rate and a slight rise in the buzz-run rate when getting close to the departure. During the departure, the signals that showed strong increases were the piping and the buzz-run signals, with the production of buzz-runs surging most strongly. We did not observe any surges in the production rates of waggle runs or shaking signals. In fact, neither signal was observed at high rates for any of the three swarm phases. After the swarm left, all communication signals were barely produced.

As with the production of the piping and buzz-run signals, we observed conspicuous changes in density, mobility, mobility index and velocity during the swarm exodus (Fig. 1, Table 1). The density of bees sharply decreased, a not-surprising result as many bees were leaving the hive to join the swarm. Likewise, the mobility and the mobility index rapidly increased during the departure and then dropped to below preswarm levels after the swarm left. Similarly, the average velocity of 10 randomly chosen bees jumped during the exodus, and dropped dramatically after, indicating how the bees that remained in the colony went back to performing tasks that did not require much movement across the comb. For example, the distance and direction travelled by each of the 10 randomly chosen bees in colony 1 at time (t) = 20, 60, 100, 108, 120 and 160 min from the beginning of the video recording are shown in Fig. 2. Although most times the monitored bees were either motionless or barely moving, there was a sudden increase in distance travelled at $t = 108$ min, with some of the bees moving out of the field of view before the 3 s had passed. By $t = 120$ min, the bees in the hive were again nearly motionless. There was no 'goal-oriented' directionality in bees moving across the comb before or during swarm departure, indicating that the distribution of movement angles came from a uniform circular distribution (Rayleigh's Z test, Table 2).

To test for significant changes in the triggering signals and mobility variables during the exodus, we pooled the mean values for each measure from the three aforementioned swarming events and determined whether there was a difference between the overall mean values associated with before and during swarm departure. Figure 3 shows the values of the overall means for each variable. There was a significant increase in the piping signal rate ($P = 0.04$), as well as a significant increase in the buzz-run rate ($P = 0.02$) during the swarm departure. We found no significant change in either the waggle-run rate ($P = 0.84$) or the shaking signal rate ($P = 0.80$) comparing the periods before and during the exodus. For the aspects of mobility, there was a significant drop in the density ($P = 0.0078$) as bees left the nest. Moreover, there was a nearly significant increase in mobility ($P = 0.09$) and a significant increase in both mobility index ($P = 0.02$) and average velocity ($P = 0.0003$) during the swarm departure compared to before the departure.

We measured the proportion of the bees that initiate a swarm's departure. The total number of bees on the video screen was about 200 before departure, but less than 1% of those bees had begun to buzz-run at the beginning of the exodus (Fig. 4). The proportion of buzz-runners increased to about 20% of the total number of bees appearing on the video screen in the middle of the swarm's departure, but this number is high owing to the low density of bees remaining in the colony, as most bees had exited at that time.

DISCUSSION

Although it has been known for centuries that the departure of a honeybee swarm from its nest involves a sudden and massive exodus of bees, to our knowledge, this is the first report that quantitatively documents this striking phenomenon and provides evidence regarding the signals that trigger this explosive event. In all three swarming colonies, we found that worker piping started 60+ min prior to swarm departure, gradually increased and then peaked during swarm departure. The buzz-running signal, however, was produced strongly only during the exodus process; it increased from nearly zero before departure to over 100 buzz-runs observed in 30 s during departure. Both signals disappeared after the swarm had left. Also, in all three colonies, the density of bees sharply decreased at the time of the exodus as a result of most bees evacuating the hive. In addition, the movement of the bees in the hive skyrocketed over the course of 5 min, with average mobility jumping as much as four-fold and the average velocity shooting up as much as six-fold, compared to before departure (Table 1). Within 12−18 min of the start of swarm departure, the high activity had ended and the density of bees had fallen markedly, from about 40 bees per 100 cm^2 to only 10−20 bees per 100 cm^2.

The patterns of signal production that we observed for initiating the departure of a swarm from its nest are nearly identical to those previously reported for priming and triggering the take-off of a swarm from its bivouac site, when it begins its flight to a new nest site (Seeley & Tautz 2001; Rittschof & Seeley 2008). During both processes, the

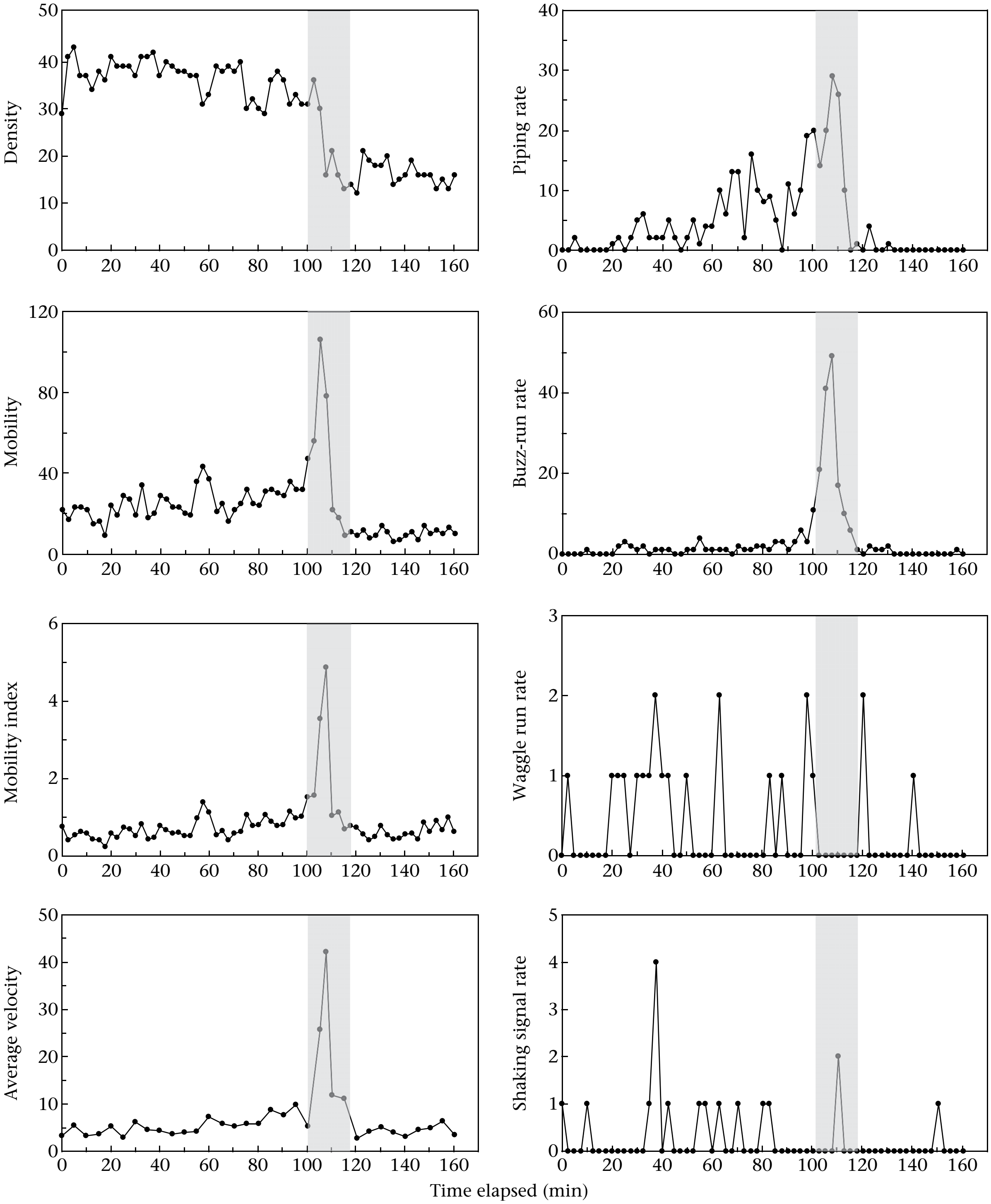


Figure 1. Changes in bee density, mobility and signal production inside the nest before, during (grey box) and after the swarm departure from colony 1. The time elapsed (min) was set at $t = 0$ when the video recording started; measurements were made every 2.5 min (except for measurements of average velocity, made every 5 min) for a total of 160.5 min. See Methods for the units of the variables plotted here.

first signal produced by bees is the piping signal, which evidently stimulates bees to warm their flight muscles in preparation for rapid flight. It is likely that the piping signal also serves as a primer for swarm exodus, stimulating the bees to warm up in preparation for their explosive departure from the nest. The evidence that piping actually causes bees to warm up, and is not simply correlated with their warming up, comes from Seeley & Tautz (2001). When they prevented a small group of bees in a swarm from getting piped prior to swarm take-off, they found that these bees did not warm themselves and fell to the ground when the rest of the swarm bees launched into flight. It would be interesting to document with a thermovision camera whether bees inside the nest increase their

Table 1. Duration of video recordings, aspects of honeybee mobility and production rates of potential triggering signals in three honeybee colonies that swarmed in June 2007

	Colony 1, 2 June 2007			Colony 2, 7 June 2007			Colony 3, 14 June 2007		
Observation	Before	During	After	Before	During	After	Before	During	After
Video duration (min)	100.5	17.5	42.5	40.0	12.5	10.0	52.5	11.25	46.25
Piping rate	5.0±0.8	14.3±4.3	0.3±0.2	4.1±0.8	26.0±1.4	0.0±0.0	2.8±0.8	12.8±3.1	0.3±0.1
Buzz-run rate	0.9±0.3	45.1±18.4	0.3±0.1	0.2±0.1	82.7±14.6	0.0±0.0	1.5±1.1	58.0±9.5	2.1±0.8
Waggle-run rate	0.5±0.1	0.0±0.0	0.2±0.1	0.1±0.0	0.0±0.0	0.0±0.0	0.0±0.0	0.0±0.0	0.1±0.1
Shaking-signal rate	0.3±0.1	0.3±0.3	0.1±0.1	0.6±0.2	0.6±0.2	1.2±0.7	1.0±0.3	0.6±0.3	1.3±0.4
Density	36.5±0.6	20.9±3.3	16.3±0.6	40.5±0.7	17.9±3.8	9.2±0.6	44.6±0.8	28.7±2.2	26.2±1.2
Mobility	25.7±1.2	42.9±14.3	10.1±0.6	32.5±1.8	54.7±10.6	2.9±0.6	22.0±3.8	98.0±14.4	8.7±1.7
Mobility index	0.7±0.0	1.9±0.6	0.6±0.0	0.8±0.0	3.4±0.5	0.3±0.0	0.5±0.1	3.4±0.4	0.3±0.1
Velocity (mm/s)	5.4±0.4	22.8±7.3	4.3±0.4	6.1±0.4	22.3±2.8	3.8±0.4	3.4±0.3	20.7±2.7	2.8±0.3

Each recording was divided into three segments: before, during and after the departure of a swarm from the parental nest. Values are shown as $\overline{X} \pm$ SE. See Methods for the units of each variable.

thoracic temperature after being piped, as do bees outside the nest in a swarm cluster (Seeley & Tautz 2001), and whether workers might pipe the queen to prime her to leave with the swarm.

The second signal that is used in both swarm departure contexts is the buzz-run. Buzz-runners begin to appear about 10 min before a swarm's exodus from the nest, and they appear in high numbers 5–10 min before a swarm's take-off from the bivouac site. Evidently, the small minority of bees that perform the buzz-run function as the ‘releaser’ of departure in both contexts. Rittschof & Seeley (2008) report that bees standing motionless in a small group are stimulated to activity when a buzz-running bee pushes through them. Forsyth (1981) reports a remarkably similar process of triggering immobile individuals to become active by buzz-running wasps in colonies of *Polybia occidentalis*.

It is interesting to note that the exodus of swarm bees from inside the nest is slower than the take-off of swarm bees from the bivouac site: the former takes about 10 min, whereas the latter takes only about 1 min (Seeley et al. 2003). Probably, this difference exists because in the first scenario the bees must funnel out a small entrance opening, whereas in the second they can simply launch into flight in the open air, not because the bees are differently stimulated for departure in the two scenarios.

Our finding that the buzz-run is a critical signal during the swarm departure process is consistent with Martin's (1963) observation that buzz-runners appeared near the entrance of an observation hive approximately 15 min before the swarm left the nest. He found that the buzz-runners tried to contact as many bees as possible by pressing into clusters of bees and making zigzag motions while actively buzzing their wings. We too observed this pattern of cluster break-up by buzz-runners during the beginning stages of the departure process inside the hive. Curiously, Martin did not report piping prior to swarm departure, and he even mentioned that the buzz-runners were silent while signalling to other bees. Because he did not plant microphones inside his observation hives, and because it is almost impossible to hear piping signals through the glass walls of an observation hive, it seems that Martin missed an important part of the preswarm behavioural sequence, namely, the production of piping signals for an hour or so before the exodus of the swarm.

We also found that neither the worker–worker shaking nor the waggle-run signals increased before or during the swarm departure. This result indicates that they are not directly involved in stimulating swarm bees to depart. It is probably not surprising that the waggle dance is not used in this context, because it is mainly used as a mechanism to communicate the locations of important resources, i.e. rich food sources and suitable nest sites (Lindauer 1955; Seeley 1995). Nevertheless, it is valuable to report for the first time that this important signal is evidently not used by bees to initiate swarm exodus.

Likewise, the worker–worker shaking signal does not seem to play a major role in triggering the mass exodus of a swarm. The level of worker–worker shaking was low before the swarms departed, did not increase during the departures and did not change after the swarms had left their nests. It is clear that worker–worker shaking functions as an activational signal that boosts the activity level of worker bees (Winston 1987; Nieh 1998) engaged in brood rearing, foraging, food processing, nest construction and nest maintenance (Allen 1959a, b; Schneider & Lewis 2004; Cao et al. 2007; Hyland et al. 2007). Likewise, in the context of swarming, worker–worker shaking acts as a nonspecific modulatory signal that causes a general activation of worker bees (Visscher et al. 1999; Lewis & Schneider 2000; Donahoe et al. 2003). A recent study reports an increase in shaking signal production before a swarm's departure from the parental nest that specifically targets the activation of the queen, with workers shaking her more and more often 2 to 3 days before swarm departure (Pierce et al. 2007). Presumably, this increased shaking of the queen serves to notify her of the imminent departure. Another recent study reports that during the queen-replacement process, virgin queens were shaken by workers 25 times more often in colonies that produced after-swarms than in colonies that did not, further indicating the role of the shaking signal in activating queens for departure (Schneider & DeGrandi-Hoffman, 2007). Thus, although the shaking signal evidently plays several important roles during swarming, it seems clear that at least

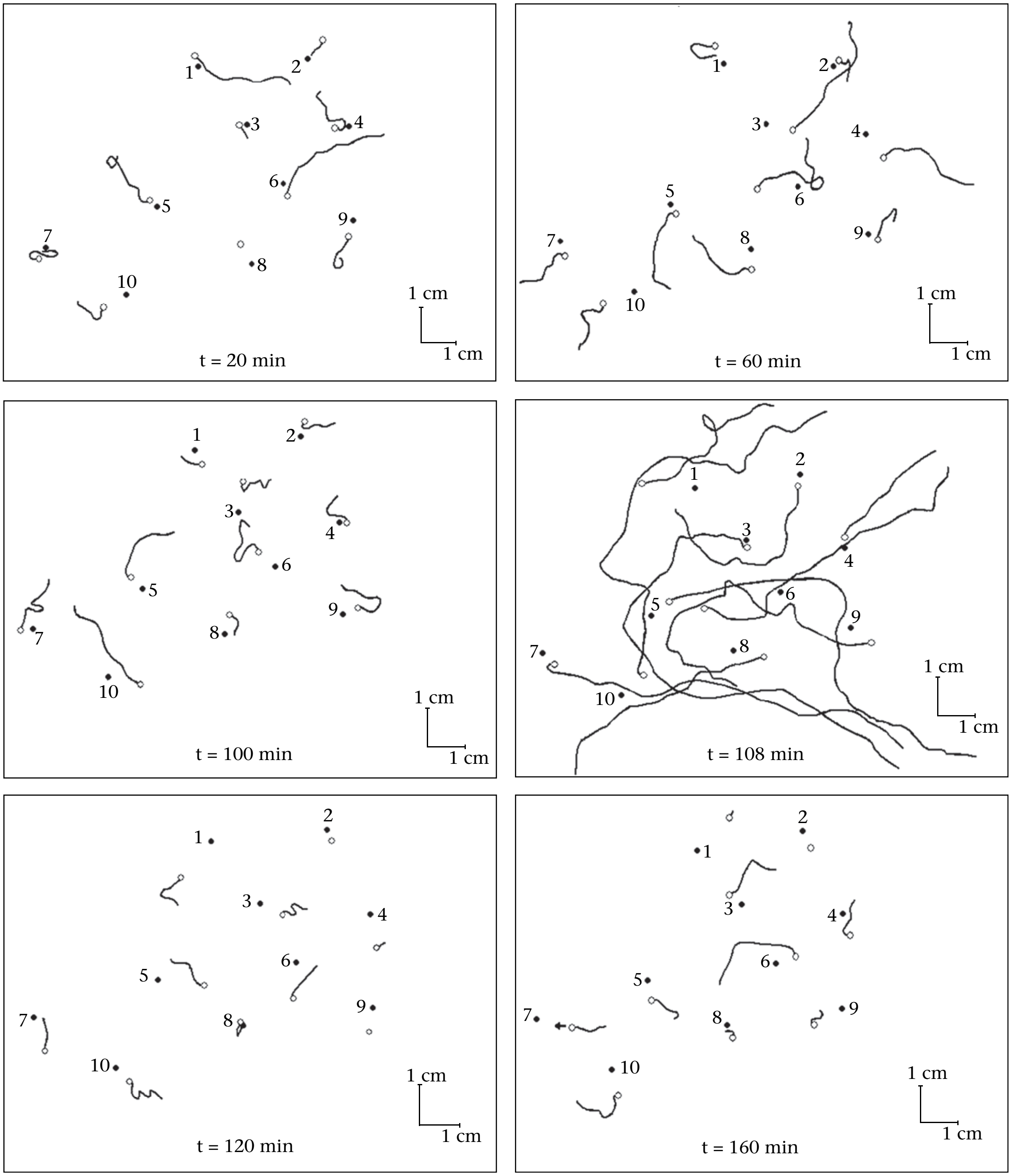
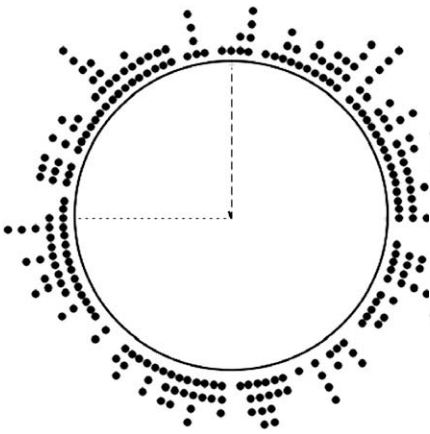
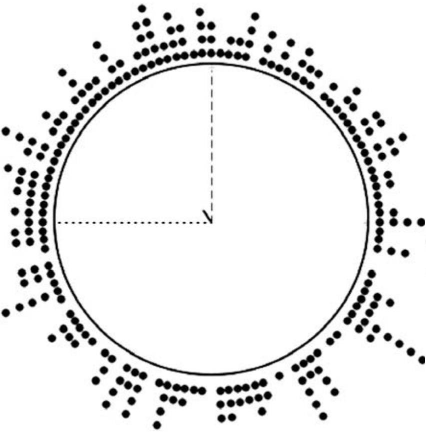
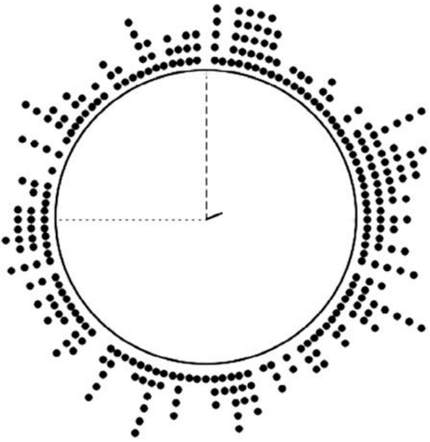


Figure 2. Distances travelled by 10 randomly chosen bees before, during and after the swarm departure of colony 1. Each bee followed was the bee closest to one of the points numbered from 1 to 10 at each time interval. The open circles indicate the positions of the bees' thoraces at the start of a 3-s period, and the lines indicate the paths taken by the bees during that interval. We observed different bees in each sampling period. Departing bees left the hive through the entrance at lower right corner. Video was taken for a total of 160.5 min, and the distances travelled were measured every 5 min. Here we show travel patterns before ($t = 20$, 60 and 100 min), during ($t = 108$ min) and after ($t = 120$ and 160 min) the swarm left the hive.

worker–worker shaking is not a main signal for triggering a swarm's exodus from its nest.

Although this study reports the conspicuous use of mechanical modes of communication for triggering swarm departure (i.e. the piping and buzz-running signals), honeybees may also use other signal modalities to initiate swarm departure, including chemical signals. Such signals are used by other social insect species for triggering group departures. For example, the carpenter ant, *Camponotus herculeanus*, relies on strong chemical signals to synchronize the departure of males and females when they swarm out on mating flights (Hölldobler

Table 2. Circular histograms and statistics for the movement directions of bees before and during swarm departure in three observation colonies. If bees had moved mainly toward the entrance, the mean vector bearing would have been 135°

	Colony 1	Colony 2	Colony 3
			
N (angles)	241	253	301
MVB (°)	346.1	327.0	68.5
MVL	0.05	0.09	0.12
Rayleigh's test (Z)	0.53	2.12	4.09
P value	>0.1	>0.1	>0.1

MVB: mean vector bearing; MVL: mean vector length. MLV is unitless and measures the scatter of the angles.

& Maschwitz 1965). Males begin the swarming process by 'sunbathing' for a few hours just outside the nest entrance. Once they have reached a threshold body temperature, they release a mandibular pheromone that attracts females to emerge from the nest entrance and crawl up the tree trunk to an elevation above the males. The swarm of reproductives takes off with both sexes combined in a cloud. Also, a recent study of honeybee

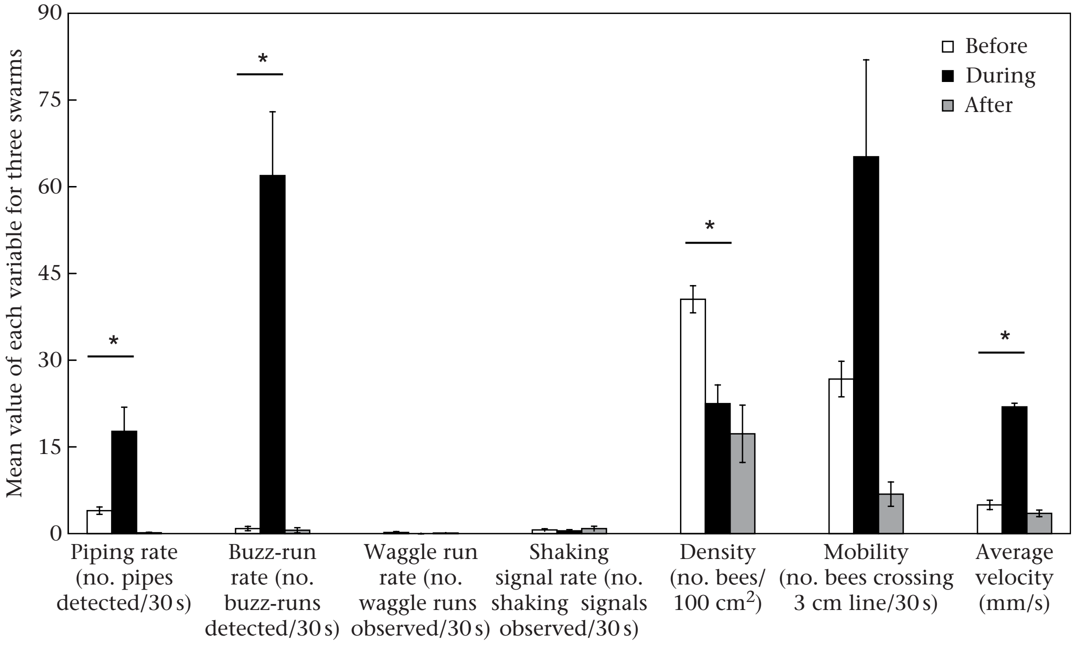


Figure 3. Mean ± SE values of honeybee density, mobility variables and triggering signals for before, during and after three departures of swarms from their nests. We conducted *t* tests on the difference between the three swarm means for before and during swarm departure. Horizontal lines and asterisks indicate in which pairs of means there were significant differences ($P < 0.05$).

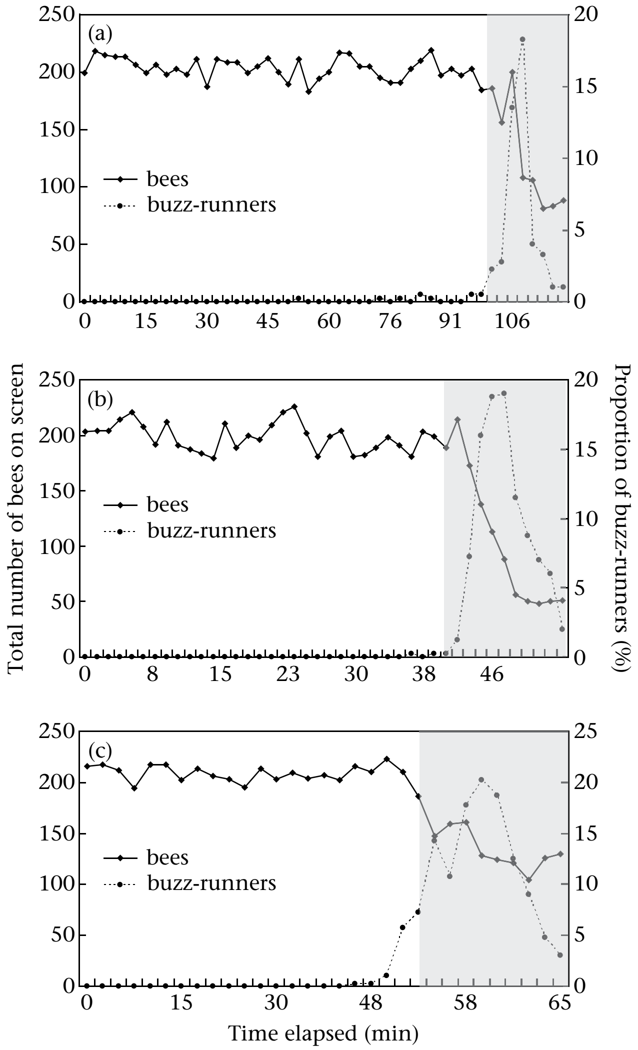


Figure 4. Total number of bees seen on video screen and the proportion of those bees that produced the buzz-run signal over time, for three swarms. Buzz-runners were observed at the beginning and throughout the swarm's exodus (grey box). Measurements were taken every (a) 2.5 min for colony 1, (b) 1.25 min for colony 2 and (c) 2.5 min for colony 3.

signalling by Thom et al. (2007) has shown that the famous waggle dance is not simply a mechanical/acoustical signal, but also has a chemical component. We wonder if one or both of the signals that we have found important in initiating swarm departure—worker piping and buzz-running—might likewise have a chemical component along with their conspicuous mechanical components.

Some tantalizing puzzles remain to be solved about swarm departure in honeybees. Which bees produce the piping and buzz-running signals? Are the pipers and buzz-runners the same individuals? Presumably the bees that signal to the rest of the group that it is time to leave home must be informed about the weather conditions outside, for swarms depart only when the weather is sunny and warm (Winston 1987). This observation makes us suspect that the pipers and buzz-runners are either foragers or nest-site scouts. Prior studies of the swarm's house-hunting process provide us with some appealing leads. Lindauer (1955) reports that some nest-site scouts are engaged in exploring for nest sites even before their colony swarms. Also, when Visscher & Seeley (2007) labelled nest-site scouts at nest boxes on an island in Maine, U.S.A., they found that the pipers on a swarm cluster are the scouts from the site chosen for the swarm's new home. Rittschof & Seeley (2008) reported that the buzz-runners on a swarm cluster are the same bees as the pipers; the bees that start the piping on a swarm cluster gradually add buzz-running to their signalling repertoire and ultimately perform mainly buzz-runs just before a swarm's take-off to fly to its new home. Does the same thing happen inside a nest when a swarm prepares for departure? To find out if it is one group of bees that produces both the piping and the buzz-run signals inside a nest prior to a swarm's exodus, and if so, to determine who these bees are, one could label foragers at feeders or scout bees at nest boxes shortly before swarm departure (both forager bees and scouts would know when the weather conditions are ideal for swarm bees to leave the protection of the parental nest). Video analysis of the swarm exodus process could reveal whether the same bees produce both the piping and the buzz-run signals and whether it is foragers or nest-site scouts that produce the two signals.

The departure of a honeybee swarm from its parental nest provides a prime example of how a small minority of individuals in a social insect colony can operate as an oligarchy to make an important decision, i.e. when to leave the nest. Only a small percentage of the bees in a colony appear to trigger the exodus on an entire swarm. Presumably, the individuals that initiate the mass departure of a swarm have special access to information about the conditions necessary for the group to leave the nest safely.

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