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## Worker piping in honey bee swarms and its role in preparing for liftoff

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**Abstract** Worker piping, previously reported only in hives, was observed in swarms as they prepared to liftoff to fly to a new home. Pipers are excited bees which scramble through the swarm cluster, pausing every second or so to emit a pipe. Each pipe consists of a sound pulse which lasts  $0.82 \pm 0.43$  s and rises in fundamental frequency from 100–200 Hz to 200–250 Hz. Many, if not all, of the pipers are nest-site scouts. The scouts pipe when it is time to stimulate the non-scouts to warm themselves to a flight-ready temperature (35°C) in preparation for liftoff. The time-course of worker piping matches that of swarm warming; both start at a low level, about an hour before liftoff, and both build to a climax at liftoff. When we excluded pipers from bees hanging in the cool, outermost layer of a swarm cluster, we found that these bees did not warm up. The form of worker piping that we have studied in swarms differs from the form of worker piping that others have studied in hives. We call the two forms “wings-together piping” (in swarms) and “wings-apart piping” (in hives).

**Keywords** Communication · Honey Bee · Sound · Swarming · Worker piping

### Introduction

After leaving the parental nest to start a new colony, a swarm of honey bees hangs from a tree branch in a beard-like cluster for several hours or several days while

its scouts choose a suitable nesting cavity (reviewed by Lindauer 1971; Seeley 1982). During this time, a swarm performs thermoregulation, maintaining its cluster-core temperature at 34–36°C and its cluster-mantle temperature above 15°C (Heinrich 1981). A swarm maintains these elevated temperatures mostly by reducing its heat loss rather than raising its heat production, thereby conserving its energy supply. However, as soon as the scout bees have chosen a new home, the swarm raises the mantle temperature to the core temperature, about 35°C (Heinrich 1981), which is the temperature required for rapid flight (Heinrich 1979). Once the mantle bees reach this high temperature, the thousands of bees in the swarm launch into flight, form a cloud of swirling bees, and begin moving together to their new domicile (described by Seeley et al. 1979).

How do the bees in a swarm achieve such a beautifully coordinated liftoff? One of the underlying mechanisms is the signal called buzz running (*Schwirrlaufen*). During the final 10 or more minutes before liftoff, excited bees force their way through the quiet bees in the cluster, running about in a zig-zag pattern, butting into the other bees, and buzzing their wings every second or so (Lindauer 1955; Esch 1967). Many, perhaps most, of these buzz runners are scout bees and their actions appear to loosen up the cluster (Seeley et al. 1979). Martin (1963) demonstrated, with a split-hive experiment, that only bees directly contacted by buzz runners will join the mass exodus when a swarm initially leaves the parental nest. Hence, it seems clear that buzz running plays a critical role in liftoff, probably triggering the final break up of the cluster. Buzz running is evidently not the whole story, however, because buzz runners appear only in the last few minutes before liftoff, whereas the rise in a swarm's temperature starts an hour or so before liftoff (Heinrich 1981). A second signal that might inform the relatively cool and quiescent bees in a swarm that it is time to warm themselves for liftoff is the shaking signal (sometimes called the vibration signal). To produce this signal, one bee grasps another and shakes this bee's body for 1–2 s at 16–18 Hz (see Fig. 1 in Seeley et al. 1998). There is strong evidence

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that the shaking signal acts as a modulatory signal that produces a general activation of worker bees in swarms (Visscher et al. 1999; Lewis and Schneider 2000) and in hives (Schneider et al. 1986; Nieh 1998; Seeley et al. 1998). However, because the warm-up period does not occur solely or even principally in the last hour before liftoff, it seems that the shaking signal is not the warm-up signal.

A third signal that possibly helps a swarm execute a well-coordinated liftoff, by stimulating the inactive bees to warm themselves for flight, is the high-pitched piping sound that the workers produce during the last hour or so before departure (Lindauer 1955; Seeley et al. 1979; Camazine et al. 1999). During this final hour, the piping by workers crescendos. Initially, the swarm cluster emits a weak and intermittent sound produced by just a few bees, but gradually the sound's intensity increases until at liftoff there is a loud and continuous sound produced by many bees. Because worker piping occurs solely during the warm-up period, and because it climaxes at liftoff, we hypothesized that it stimulates the inactive bees in a swarm cluster to warm themselves in preparation for liftoff. We tested this hypothesis by determining (1) the time-course of worker piping in relation to swarm warming, (2) the identity of the pipers, and (3) the temperature effects of excluding this signal from a subset of the mantle bees in a swarm shortly before liftoff. The properties of this acoustic signal are also described.

## Materials and methods

### Study site and bees

All observations were made at the Liddell Field Station of Cornell University, in Ithaca, New York (42° 26' N, 76° 30' W). This site is surrounded by woods containing many old trees with cavities, so the swarms studied had no difficulty finding suitable nest sites. All three swarms studied were artificial swarms prepared from colonies headed by "Buckfast" queens (a hybrid of *Apis mellifera mellifera* and *A. m. ligustica*; Adam 1987). To make each swarm, we first located a colony's queen and put her in a small wooden cage (3.2 cm × 10 cm × 1.6 cm) with wire screen on one side (a standard wooden queen cage). Then, using a large funnel, we shook 1.0 kg of worker bees (ca. 7,500 bees; Mitchell 1970) from the frames of the same colony into a swarm cage (15 cm × 25 cm × 35 cm) made of wood with wire-screen sides. We also placed the caged queen inside the swarm cage. For the next 48–72 h (until copious wax scales appeared beneath the swarm cage), we fed the caged bees ad libitum with a 50% (vol/vol) sucrose solution. Finally, the swarm cage was opened, the queen (still in her own small cage) was fastened to the swarm mount (see below), and the workers were shaken onto the base of the mount. Within an hour, the workers were clustered over the queen cage and behaving like a natural swarm. After several hours or a few days the swarm would finish choosing its nest site, lift off, and attempt to fly away. However, because the queen remained caged at the swarm mount the swarm always returned and resettled there. Several hours later, or the next day, the swarm would again lift off and fly away, only to return and resettle once more around the caged queen. In this way we were able to monitor repeatedly (two to six times) the preparations for liftoff with each of our three swarms.

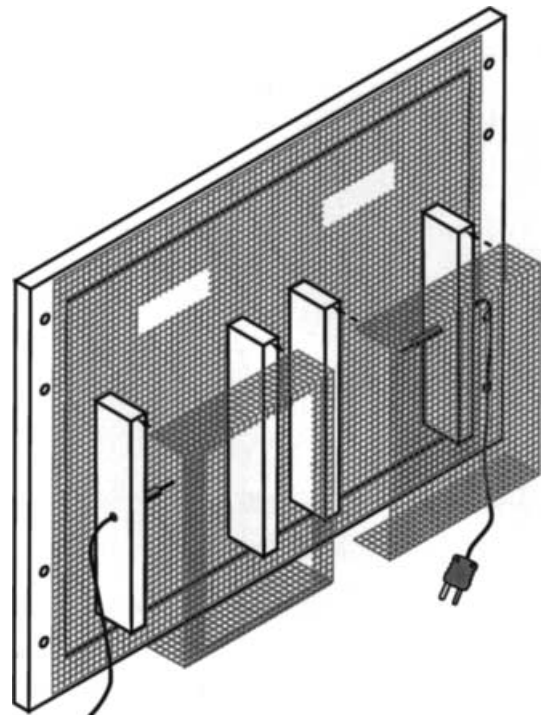
### Apparatus

Swarms were placed on the swarm mount which was described previously (see Fig. 1; Seeley and Buhrman 1999). This mount

consists of a flat vertical board, on which the swarm clusters, and a wire screen (of 8-mesh hardware cloth with several passageways for the bees cut into it) mounted vertically over the swarm's surface so that the outermost layer of the swarm is on the outside of the screen. This apparatus facilitates video recording the behavior of workers on the surface of the swarm cluster. Video recordings were made with a digital video camera (Panasonic NV-DS35EG). Recordings were converted to S-VHS format and analyzed using a videocassette player with variable-speed playback (JVC BR-S525U). To record the sounds produced by a worker while she was being videorecorded, we manually followed the bee with a small, 5-mm-diameter, custom-made microphone (flat frequency response from 20 Hz to 6,000 Hz, and sensitive only to pressure fluctuations) held approximately 1 cm from the bee, in a dorsal position, and slightly to the side so that it did not interfere with the video recording. This microphone's output was recorded on one of the video camera's audio channels. We recorded the behavior of bees that were producing piping sounds or waggle dances, or both. To obtain detailed records of the behavior of single piping workers, we removed the screen portion of the swarm mount immediately after several of the liftoffs and zoomed the video camera in on the one or two bees that were intensely piping on the screen of the queen cage.

To record the level of worker piping within the cluster, we mounted two of the small microphones, one on each side of the swarm, on the threaded rods supporting the screen of the swarm mount. This positioned each microphone deep inside the swarm cluster. The two microphones were connected to an amplifier whose stereo output was recorded with a digital minidisc recorder (Sony MZ-R37SP).

To record temperatures in the swarm, we used copper-constantan thermocouple probes and a digital thermometer (Bailey Bat-12). The swarm's core temperature was measured with a probe mounted in the middle of the cluster, directly in front of the queen cage. The swarm's mantle temperature was measured with a probe mounted in the center of the screen of the swarm mount. The



**Fig. 1** The swarm mount screen that was used to test whether mantle bees would warm themselves in preparation for liftoff when prevented from receiving signals from piping workers. The screen bears two cages, each equipped with a thermocouple probe. Both cages have covers of 8-mesh hardware cloth, but one cover has a large opening

distance of the screen from the board of the swarm mount was adjusted so that the layer of bees covering this probe was just one or two bees thick. The ambient temperature was measured with a probe mounted on the swarm mount, 2 cm below the board on which the swarm was clustered.

To see if mantle bees would warm themselves in preparation for liftoff when we prevented piping workers from contacting them, we performed an experiment in which we replaced the normal screen of our swarm mount with a screen bearing two symmetrically positioned cages (6 cm × 10 cm × 2 cm), each of which was equipped with a thermocouple probe (see Fig. 1). When a swarm was placed on the swarm mount, both cages became filled with mantle bees. One cage was closed by installing a cover of “8-mesh” hardware cloth (openings 3 mm × 3 mm) while the other cage was kept open by installing a cover identical to the first except that it had a large (6 cm × 9 cm) opening. The covers were installed only after we determined, by means of the stereo microphones, that the piping inside the swarm had become continuous.

#### Data analysis

The video recordings were analyzed in slow motion to determine (1) the spatiotemporal patterns of the movement and signaling behavior of piping workers, (2) the posture of workers while producing the piping signal, and (3) the pattern of behavioral transitions made by waggle-dancing bees as a swarm approached the moment of liftoff. To determine the latter pattern, we would choose at random a waggle dancer, follow her for 10 s, and note which of the following activities she was engaged in at the end of the 10-s period: waggle dancing, walking/running, piping, buzz running, shaking, or flying (these are all the possibilities). This procedure was repeated with 50 bees every half-hour, for several hours before the two observed liftoffs of swarm 3.

The audio recordings made by following individual bees were analyzed by transferring the digital data from the audio track of the video camera into a computer. We then used Avisoft SASLabPro to obtain sonagrams and spectrograms of the piping signal. To determine a distribution of the durations of piping sounds, we measured the durations of 50 randomly chosen pipes from swarm 2, recorded on 3 September.

The audio recordings made with the stereo microphones mounted inside the swarm cluster were analyzed to measure the overall level of worker piping within a swarm at different times before liftoff. The digital data from the minidisc recorder were transferred to a computer and analyzed using Avisoft SASLabPro. We measured the level of worker piping as the percent time that piping was audible in our stereo recording, and our procedure for making this measurement was as follows. First, for each swarm we chose a set of sampling periods; these sampling periods were short (3–5 min long) for the hour or so preceding liftoff and were relatively long (10–30 min long) for times more in advance of liftoff. Second, within each sampling period, we chose at random three 20-s intervals. Third, for each of these three 20-s intervals, we counted the number of 1-s subintervals ( $N$ ) in which worker piping was audible in our recording. Fourth, we estimated from these counts the percent time that piping was audible during each 20-s interval ( $N/20 \times 100$ ). Finally, using the three measurements for each sampling period, we calculated the mean and standard deviation of the percentage time that piping was audible for each sampling period.

## Results

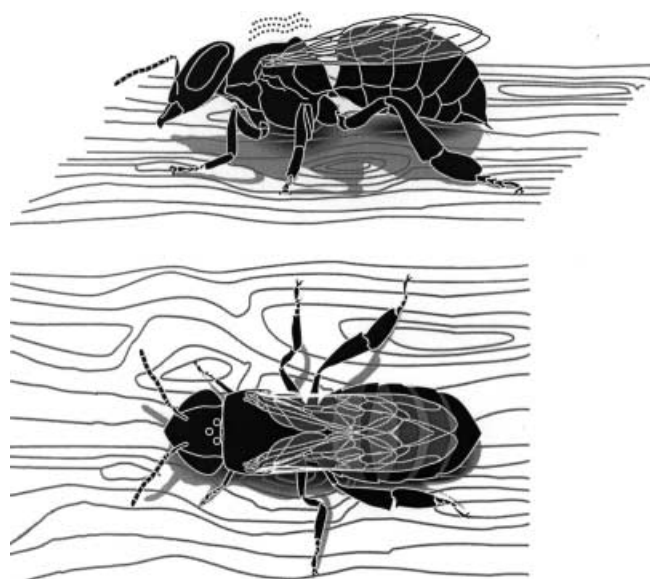
### Sights and sounds of piping workers

#### *Behavioral description*

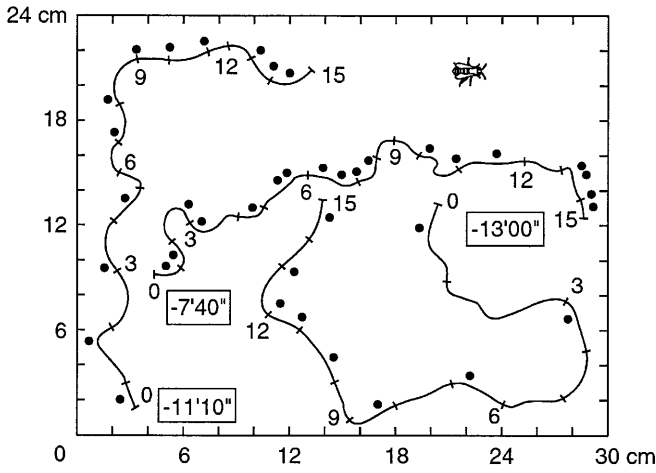
Piping was heard easily in swarms shortly before liftoff, but at first it was not easy to detect which bees

were producing these sounds, which are reminiscent of the revving of a Formula One racing car’s engine. Careful searching of the swarm surface in the region of a piping bee revealed a worker performing a striking behavior coincident with each piping sound: she paused briefly from running over other bees, pressed her thorax to the bee beneath her, and pulled her wings together over her abdomen, which arched noticeably downward during sound production (Fig. 2). In the vast majority of cases, the bee pressed her thorax to another bee while piping, but occasionally she pressed it against one of the wooden or wire screen surfaces of the swarm mount. The pressing down of the piper’s thorax during sound production suggests that she generates the sound with her wing muscles in the thorax and loads it into the substrate, which is almost always another bee. (The airborne vibrations that we heard and recorded may have included radiation of sound from substrate to air, as well as direct sound emission from the bee.) The bees contacted by pipers were ones hanging motionless in the cluster. They showed no behavioral response to the sound.

Pipers are strikingly excited bees which run over and burrow into the swarm cluster, pausing frequently to pipe (Fig. 3). Using our video recordings from swarm 2, we tracked 20 pipers for 10–24 s each as they ran over the swarm surface and measured the rate at which they piped:  $0.70 \pm 0.18$  pipes  $s^{-1}$  (mean  $\pm$  SD). We could not record longer trackings because pipers tend to burrow into the cluster or switch to waggle dancing.



**Fig. 2** A worker bee producing the piping signal that was studied (“wings-together piping”). Having briefly paused from running over bees in the swarm cluster, the bee presses her thorax to the substrate, pulls her wings together tightly over her abdomen, arches her abdomen, and activates her wing muscles to produce a vibration in the substrate. Although the substrate shown here is a wooden surface, almost always the substrate is another bee

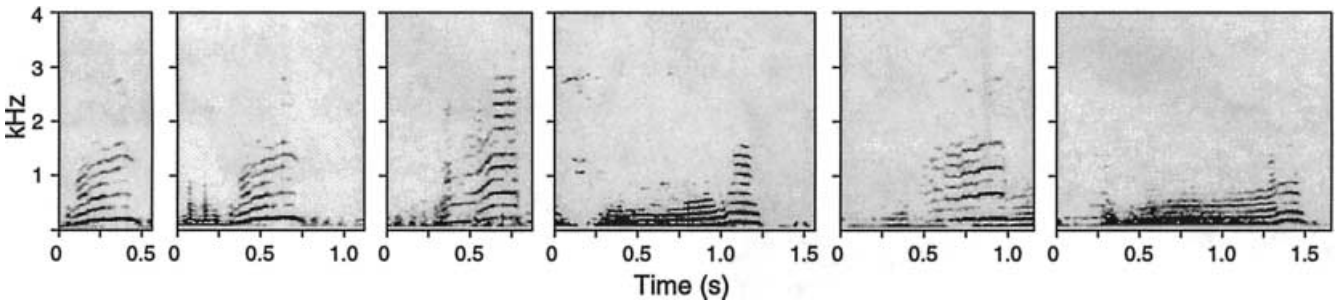


**Fig. 3** Travel patterns, from video recordings, of three piping workers as they ran over the surface of their swarm cluster. Each bee's record depicts a 15-s segment of her bout of piping; filled circles beside a bee's track denote when she piped. The time (min-s) inside the box at the start of each bee's record denotes the time until liftoff

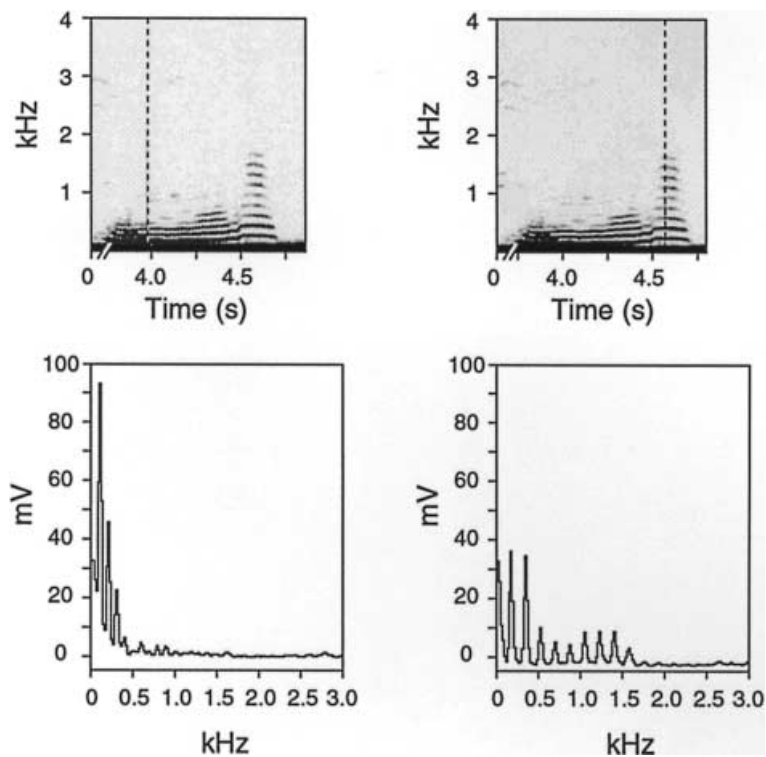
*Sound analysis*

Figure 4 shows sonograms for six pipes recorded from six different pipers in swarms 1 and 2. We see that a pipe consists of a single pulse with a conspicuous upward frequency sweep. Spectrograms for the early and late phases of one of these pipes (Fig. 5) show that at the beginning of a pipe the fundamental frequency is 100–200 Hz ( $177 \pm 22$  Hz,  $n = 10$  pipes) while at the end it is 200–250 Hz ( $236 \pm 20$  Hz,  $n = 10$  pipes). The harmonic nature of the later portion of each pipe, at least when recorded as an airborne sound, is also evident from Figs. 4 and 5. Analysis of the durations of 50 randomly chosen pipes from swarms 1 and 2 revealed a mean  $\pm$  SD of  $0.82 \pm 0.43$  s, a range from 0.09 s to 1.76 s, and a possibly bimodal distribution with modes at 0.3–0.5 s and 1.1–1.3 s (Fig. 6).

**Fig. 4** Sonograms of six piping signals recorded from workers in a swarm shortly before liftoff



**Fig. 5** Spectrograms for the early and late phases of a typical piping signal produced in a swarm shortly before liftoff. Notice the rise in the fundamental frequency and, simultaneously, the striking appearance of numerous high-frequency harmonics, toward the end of this pulse of sound. It is these harmonics that give this signal its characteristic high-pitched sound



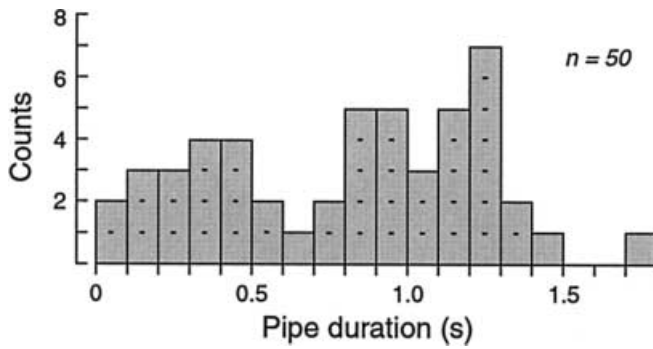


Fig. 6 Distribution of the duration of worker piping signals

## Worker piping and swarm warming

### Colony-level analysis

Figure 7 shows records of worker piping and swarm temperature for the 3-h period preceding liftoff in swarms 1 and 2. We see that in both swarms the percentage time that piping was audible rose from 0% to 100%, with most of the increase occurring during the last hour. Also, in both cases, the rise in the level of piping was not steady, though the main trend during the final hour was definitely upward. In swarm 1, the period of continuous piping lasted for about 10 min before liftoff while in swarm 2 it lasted for nearly 30 min. We also see in both swarms that the core temperature ( $T_c$ ) and the mantle temperature ( $T_m$ ) were kept well above the ambient temperature ( $T_a$ ), and that  $T_c$  was kept consistently above  $T_m$ . Notice that at liftoff  $T_c$  and  $T_m$  had risen to their highest levels, 35.5–36.5°C. In Table 1 we summarize the temperatures recorded at liftoff for all 12 liftoffs that we studied. Except for the 2 liftoffs observed on 6 September with swarm 2, liftoff occurred only after  $T_m$  had risen above 35.0°C.

Figure 7 also shows that there was a marked association between the rise in piping and the rise in temperatures in both swarms.  $T_c$  rose noticeably throughout the lengthy period when piping was audible. Moreover,  $T_m$  rose dramatically during the final 10- to 30-min period when piping was loud and continuous. In both cases,  $T_m$  tended to drop briefly when  $T_c$  began to rise (and piping was starting). These drops in  $T_m$  seemed to occur because when each swarm began to raise its  $T_c$ , it contracted its cluster slightly (presumably to reduce convective heat loss) and this contraction caused some thinning of the layer of bees covering the  $T_m$  probe.

### Individual-level analysis

Who are the pipers? There are two indications that some, perhaps all, of the pipers are nest-site scouts. The first line of the evidence arose in the course of following individual pipers using our video recordings from swarms 1 and 2. Out of 20 pipers that were followed for at least

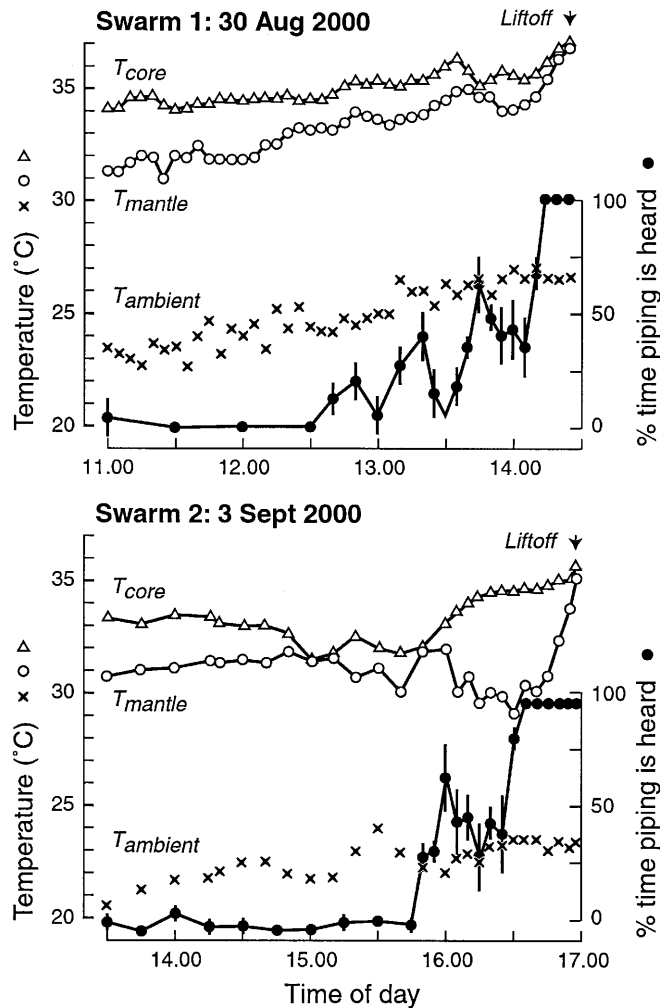


Fig. 7 Pattern of worker piping (filled circles), swarm temperature (open circles and triangles), and ambient temperature (crosses) during the 3-h period preceding liftoff for two swarms

10 s, we observed 8 switch from piping to waggle dancing. An example of this is shown in Fig. 8. Because the waggle dances that the pipers performed were always for the chosen nest site, and because only nest-site scouts perform dances for a nest site, we conclude that at least 40% of these pipers were nest-site scouts.

The second line of evidence came from following individual waggle dancers – hence bees that were nest-site scouts – in swarm 3. We followed each dancer for 10 s and noted what, if any, change in behavior she made during this time period. In this way we determined a set of behavioral transition probabilities for waggle dancers at various half-hour intervals leading up to liftoff. The results, shown in Table 2, were similar for both liftoffs of swarm 3. Initially, waggle dancers were persistent in their dancing; the probability of continuing to waggle dance was high (0.90 or higher) and the probabilities of transition to other behaviors were low. Gradually, however, the probability of continuing to waggle dance declined, ultimately falling below 0.40 in the period just before liftoff. And as the waggle dancers became less

**Table 1** Temperatures ( $T$ , °C) recorded at the start of 12 liftoffs observed with 3 swarms (*nd* no data)

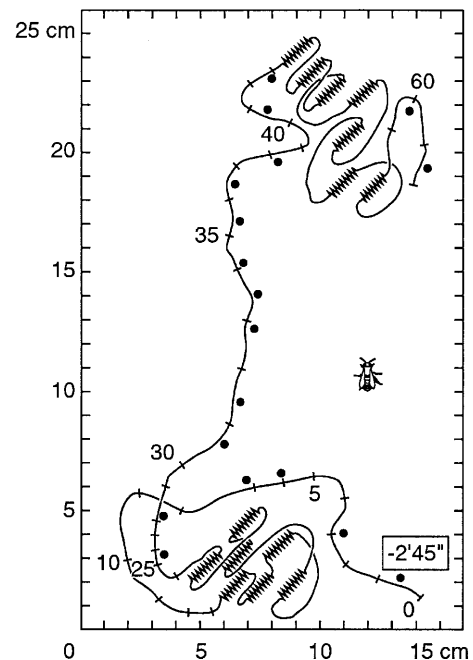
Swarm	Date	Time	$T_{\text{core}}$	$T_{\text{mantle}}$	$T_{\text{ambient}}$
1	28 Aug	18.03	nd	35.2	25.5
	29 Aug	09.24	nd	35.2	25.2
	29 Aug	11.45	nd	35.4	25.3
	29 Aug	14.02	nd	35.2	25.4
	29 Aug	16.32	35.7	35.0	25.4
	30 Aug	14.24	36.9	36.5	27.6
2	3 Sept	16.58	36.1	35.0	23.9
	5 Sept	13.40	36.1	35.1	15.8
	6 Sept	12.49	35.2	34.0	nd
	6 Sept	14.46	36.0	34.8	nd
3	Sept 19	15.19	36.0	35.2	22.6
	20 Sept	10.34	35.9	35.2	25.1

persistent in their dancing, they became more likely to switch to producing other signals: some shaking, some buzz running (though only in the final half hour before liftoff), and a good deal of piping. Note that in the second set of observations, the probability of a waggle dancer switching to piping rose from 0.00 (between 0830 hours and 0900 hours) to nearly 0.25 (between 1000 hours and 1034 hours) just before liftoff. Evidently, as liftoff approached the nest-site scouts became less and less motivated to stimulate their fellow scouts to visit the nest site and more and more motivated to stimulate their non-scout comrades to prepare for the liftoff.

#### Experimental test

We tested the hypothesis that the function of worker piping in swarms is to stimulate bees to warm up for liftoff by performing an experiment in which we prevented the pipers from making direct contact with a group of mantle bees and recorded the temperature inside this group of mantle bees. We prevented contact between pipers and mantle bees by closing, shortly before liftoff (as the piping became intense), the cover of a wire-screen cage which enclosed the mantle bees. Simultaneously, we treated a second and equal-sized group of mantle bees exactly the same as the first group, except that the cover to the second group's cage contained a large opening through which pipers could pass (see Fig. 1) We predicted, from our hypothesis, that the mantle bees in the closed cage would not warm themselves to a flight-ready temperature at the time of liftoff, whereas those in the open cage would do so.

We performed four trials of this experiment, two each with swarms 2 and 3. To control for any differences between left and right cages, we swapped the locations of the open and closed cages between the two trials with each swarm. Results are shown in Fig. 9. In all four trials,  $T_m$  for the open-cage bees showed the typical pattern of a dramatic rise to approximately 35°C in the final minutes before liftoff, but  $T_m$  for the closed-cage bees did not show this pattern. Furthermore, at the end of each trial, once all the uncaged and open-cage bees had taken



**Fig. 8** Example of a bee switching between worker piping and waggle dancing as she scrambled over the surface of her swarm. Tick marks along her track denote 1-s intervals. Black dots mark times when she piped. This record began 2 min 45 s before liftoff and lasted for 62 s

off, we removed the cover of the closed cage and found that the bees inside were basically immobile. When prodded, they dropped to the ground instead of flying off, demonstrating that they hadn't warmed for flight.

## Discussion

### Form and function of worker piping in swarms

Nearly 50 years ago, Lindauer (1955) reported that a high-pitched sound is emitted from a swarm shortly before it breaks up to fly to its new home. Now we know that many, perhaps most, of the bees producing this acoustic signal are nest-site scouts and that these bees generate this sound with their wing muscles and transmit

**Table 2** Probabilities of transition from waggle dancing to some other behavior (including more waggle dancing) over a 10-s observation period, for various half-hour intervals prior to liftoff. Note that the list of transition behaviors is complete, that is, it includes all the behaviors adopted within 10-s by a waggle dancing bee on a swarm

Transition to:	Time interval (hours)					
	1230–1300	1300–1330	1330–1400	1400–1430	1430–1500	1500–1519
Swarm 3, 19 September; liftoff at 1519 hours						
Waggle dancing	0.94	0.80	0.54	0.64	0.58	0.38
Walking/running	0.04	0.20	0.30	0.28	0.26	0.38
Piping	0.00	0.00	0.10	0.02	0.06	0.12
Buzz running	0.00	0.00	0.00	0.00	0.00	0.08
Shaking	0.00	0.00	0.00	0.00	0.06	0.00
Flying	0.02	0.00	0.06	0.06	0.04	0.02
Transition to:	Time interval (hours)					
	0730–0800	0800–0830	0830–0900	0900–0930	0930–1000	1000–1034
Swarm 3, 20 September; liftoff at 1034 hours						
Waggle dancing	0.90	0.92	0.90	0.76	0.62	0.32
Walking/running	0.08	0.08	0.06	0.18	0.18	0.34
Piping	0.00	0.00	0.00	0.02	0.10	0.24
Buzz running	0.00	0.00	0.00	0.00	0.00	0.06
Shaking	0.00	0.00	0.00	0.04	0.02	0.00
Flying	0.02	0.00	0.04	0.00	0.08	0.04

it to others by pressing the thorax onto other bees. Moreover, we have found that the form of this acoustic signal is rather unusual for insects in that there is a marked modulation of the fundamental frequency in the midst of each sound pulse. Another example of this phenomenon also occurs in honey bees: the frequency sweep present at the beginning of each tooting signal of a queen bee (Michelsen et al. 1986a). In the case of the worker piping signal, the transition to the higher fundamental frequency is accompanied by the appearance of numerous harmonics in the range of 400–2000 Hz (Fig. 4). No doubt it is these harmonics that give the worker piping signal its characteristic high-pitched sound (to humans). Assuming this upward frequency sweep is functional – for example, it may help distinguish it from other forms of worker piping (see below) – we are faced with questions regarding the production and perception of this frequency modulation. Perhaps it is produced by changing the resonant properties of the thorax, which is the mechanism proposed by Nachtigall and Wilson (1967) to explain how flies control their wingbeat frequency. If so, then it is tempting to speculate that the reason that bees pull their wings together while producing this acoustic signal (see Fig. 2) is to stiffen the whole thoracic mechanism, thereby raising its resonant frequency.

What is the function of worker piping in swarms shortly before liftoff? Camazine et al. (1999) suggested that this signal plays a role in *triggering* liftoff. Our results are most consistent with a slightly different hypothesis for this signal's function: worker piping in swarms plays a role in *preparing for* liftoff. These preparations include getting each bee warmed to a flight-ready temperature (Heinrich 1981), and may also include getting each bee properly groomed, fueled, and

sensitized to the buzz-run signal, which we suspect is the signal that actually triggers liftoff.

Three lines of evidence support the hypothesis that the function of worker piping in swarms is to stimulate bees to prepare for liftoff. The first is that the time-course of worker piping is strikingly coincident with that of swarm warming. We have seen (Fig. 7) that the two phenomena start together at a low level, typically an hour or so before liftoff, and that they both build to a climax at liftoff. Second, we have seen (Fig. 8, Table 2, and related text) that many, if not most, of the bees that produce the piping signal are nest-site scouts. These are the bees that choose the swarm's future home, so presumably they are the bees that can sense most easily when a choice has been made, hence when it is time to begin preparing for liftoff. In other words, the senders of the piping signal are especially well suited to initiate liftoff preparations. Third, the results of our experiment are consistent with the hypothesis that worker piping stimulates swarm bees to warm up in preparation for liftoff. We have seen (Fig. 9) that when pipers are excluded from the mantle bees of a swarm, the mantle bees do not warm up. We recognize that our experiment excluded all signals that require direct contact between sender and receiver, not just the worker piping signal, so we cannot conclude that worker piping is the only signal that stimulates warm up. In particular, the shaking signal was also excluded so it is possible that this signal also helps stimulate swarm bees to get ready for liftoff, as has been suggested by Visscher et al. (1999) and Lewis and Schneider (2000). However, because the shaking signal, unlike the piping signal, does not occur solely or even primarily during the last hour before liftoff – the warm-up period – it appears that the activational effects of the shaking signal are less specific to liftoff preparations than are those of the piping signal.

The decisive test of our hypothesis for the function of worker piping will be playback experiments in which mantle bees of a swarm receive only piping signals. If these signals induce the mantle bees to warm themselves and perhaps make other preparations for liftoff (grooming, etc.), then it will be certain that working piping does stimulate swarm bees to prepare for liftoff.

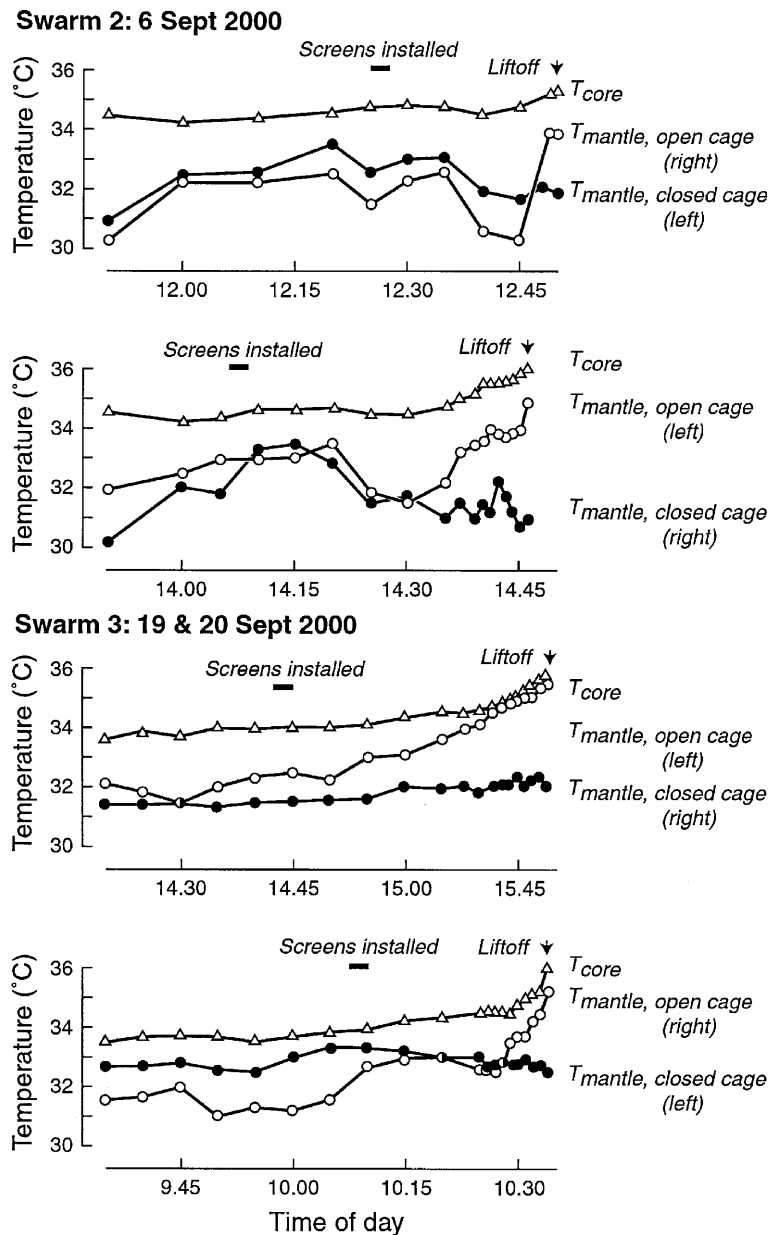
Comparison of different forms of worker piping

Several investigators have reported worker piping in contexts other than the one that we have studied, in a swarm shortly before liftoff. Armbruster (1922) first described worker piping, based on bees that he observed in a hive, and named this signal for its similarity to the

well-known piping of queen honey bees (reviewed by Kirchner 1993a). Subsequent descriptions by Örósi-Pál (1932), Ohtani and Kamada (1980), and Pratt et al. (1996) detailed the posture assumed by a worker piping in a hive: she presses her thorax to the comb, lifts her abdomen, raises her wings and spreads them slightly (making an angle of about 40°), and vibrates her wings to emit a loud sound. These authors also report that a piping worker repeats this behavior at a rate of 1–6 pipes min<sup>-1</sup>, with each pipe lasting 0.2–2.2 s, and that the sound she produces is a single pulse with little or no frequency modulation and a fundamental frequency of 300–400 Hz.

The form of worker piping that Armbruster (1922), Örósi-Pál (1932), Ohtani and Kamada (1980), and Pratt et al. (1996) have described appears to be different from

**Fig. 9** Results of four trials of the experiment that tested whether the mantle bees in a swarm cluster are stimulated to warm themselves to a flight-ready temperature (ca. 35°C) by receiving signals from piping workers. In all trials, the mantle bees in the closed cage (see Fig. 1) were prevented from being contacted by piping workers and did not raise their temperature to 34–35°C at liftoff, while the mantle bees in the open cage were contacted by piping workers and did raise their temperature to 34–35°C at liftoff



the one that we have studied. Although both forms of worker piping are evidently produced by rapid contractions of the thoracic muscles, are transmitted by the bee pressing her thorax onto her substrate, and consist of single pulses of sound lasting from 0.2 s to about 2.0 s, they differ in several ways. The most conspicuous are how they sound to a human observer and how the worker's wings are positioned during sound production. The form of worker piping that we have studied is a frequency-modulated sound that changes from a relatively pure, low-frequency (100–200 Hz) tone to a mixed, higher-frequency (200–2000 Hz, including harmonics) sound, and is reminiscent of the revving of a racing car's engine. While producing this form of piping, the worker pulls her wings together tightly (Fig. 2). In contrast, the form of worker piping that others have studied is primarily a low frequency (300–400 Hz) sound with little, if any, frequency modulation, and is reminiscent of the bleating of sheep. While producing this form of worker piping, the worker spreads her wings slightly. For clarity in discussing these two forms of worker piping, we will call the former “wings-together piping” and the latter “wings-apart piping”.

Besides their conspicuous differences in sound pitch and wing position, these two forms of worker piping differ with respect to the speed of worker movement while piping (*wings-together piping*, worker is usually running just before piping; *wings-apart piping*, worker is usually walking just before piping), and the rate of signal production (*wings-together piping*, 30–60 pipes/bee/min; *wings-apart piping*, 1–15 pipes/bee/min).

Given that the wings-together and wings-apart forms of worker piping differ markedly in their acoustical properties and production patterns, it is likely that they also differ in signal message (the information provided by the sender) and signal meaning (the response generated by the receiver) (Smith 1977 discusses signal message and meaning). As we have seen, wings-together pipes are produced by nest-site scouts in swarms as they prepare to liftoff, hence the message of wings-together pipes seems to be something like “get ready for flight.” Given that this signal evidently elicits a warm-up response, its meaning to the non-scouts in the swarm cluster seems to be something like “warm up in preparation for flight”. Wings-apart pipes are produced by various types of workers in diverse contexts, including egg-laying workers in queenless colonies (Ohtani and Kamada 1980) and pollen foragers, water collectors, and water receivers in queenright colonies (Pratt et al. 1996). It is unclear what the various contexts associated with wings-apart piping have in common, hence what conditions cause bees to produce wings-apart pipes. Moreover, it is unclear how workers respond to wings-apart pipes. Thus, the message and the meaning of wings-apart pipes remain mysterious.

There is a third piping sound which workers produce with their thoracic muscles and transmit through the substrate: the “begging signal” (Esch 1964; Michelsen et al. 1986b) or “stop signal” (Nieh 1993; Kirchner

1993b). We will use the latter name, because it more accurately describes this signal's function. This signal is acoustically distinct from both forms of worker piping discussed above. Although the stop signal has the same fundamental frequency as wings-apart pipes (300–400 Hz), its sounds are much shorter, averaging only 0.14 s and ranging only 0.05–0.2 s (Esch 1964; Michelsen et al. 1986a; Kirchner 1993b). Because the sounds of the stop signal are so brief, they have sometimes been described as “beeps” or “short squeaks” rather than “pipes” (Kirchner 1993a, 1993b). Furthermore, the information content of the stop signal is distinct from that of either of the other two forms of worker piping. The stop signal is produced primarily by tremble dancers when they encounter a nestmate performing a waggle dance for a nectar source (Nieh 1993). Its effect is to inhibit waggle dancing, thus recruitment, to nectar sources (Nieh 1993; Kirchner 1993b). Evidently, the message of the stop signal is “stop waggle dancing.”

Further studies of worker piping need to focus on identifying the conditions that cause bees to produce the wings-apart form of worker piping. It may be that what we are calling wings-apart piping is really a suite of distinct signals, which could explain why it has been difficult to identify a consistent context associated with this type of worker piping. Deciphering the message(s) and meaning(s) of the still mysterious, wings-apart form of worker piping will be a major contribution to a comprehensive understanding of acoustical communication in honey bees, the diversity of which has only begun to be adequately described and analyzed.

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## References

- Adam B (1987) Beekeeping at Buckfast Abbey. Northern Bee Books, Hebden Bridge
- Armbruster L (1922) Über Bienenötöne, Bienensprache und Bienengehör. Arch Bienenk 4:221–259
- Camazine S, Visscher PK, Finley J, Vetter RS (1999) House-hunting by honey bee swarms: collective decisions and individual behaviors. Insectes Soc 46:348–360
- Esch H (1964) Beiträge zum Problem der Entfernungswegung in den Schwänzeltänzen der Honigbiene. Z Vergl Physiol 48:534–546
- Esch H (1967) The sounds produced by swarming honey bees. Z Vergl Physiol 56:408–411
- Heinrich B (1979) Thermoregulation of African and European honeybees during foraging, attack, and hive exits and returns. J Exp Biol 80:217–229
- Heinrich B (1981) The mechanisms and energetics of honeybee swarm temperature regulation. J Exp Biol 91:25–55
- Kirchner WH (1993a) Acoustical communication in honeybees. Apidologie:24:297–307

- Kirchner WH (1993b) Vibrational signals in the tremble dance of the honeybee, *Apis mellifera*. *Behav Ecol Sociobiol* 33:169–172
- Lewis LA, Schneider SS (2000) The modulation of worker behavior by the vibration signal during house hunting in swarms of the honeybee, *Apis mellifera*. *Behav Ecol Sociobiol* 48:154–164
- Lindauer M (1955) Schwarmbiene auf Wohnungssuche. *Z Vergl Physiol* 37:263–324
- Lindauer M (1971) Communication among social bees. Harvard University Press, Cambridge
- Martin P (1963) Die Steuerung der Volksteilung beim Schwärmen der Bienen. Zugleich ein Beitrag zum Problem der Wanderschwärme. *Insectes Soc* 10:13–42
- Michelsen A, Kirchner WH, Andersen BB, Lindauer M (1986a) The tooting and quacking vibration signals of honeybee queens: a quantitative analysis. *J Comp Physiol A* 158:605–611.
- Michelsen A, Kirchner WH, Lindauer M (1986b) Sound and vibrational signals in the dance language of the honeybee, *Apis mellifera*. *Behav Ecol Sociobiol* 18:207–212
- Mitchell C (1970) Weights of workers and drones. *Am Bee J* 110:468–469
- Nachtigall W, Wilson D (1967) Neuro-muscular control of dipteran flight. *J Exp Biol* 47:77–97
- Nieh JC (1993) The stop signal of honey bees: reconsidering its message. *Behav Ecol Sociobiol* 33:51–56
- Nieh JC (1998) The honey bee shaking signal: function and design of a modulatory communication signal. *Behav Ecol Sociobiol* 42:23–36
- Ohtani T, Kamada T (1980) ‘Worker piping’: the piping sounds produced by laying and guarding worker honeybees. *J Apic Res* 19:154–163
- Örösi-Pál Z (1932) Wie tütet die Arbeitsbiene? *Zool Anz* 98:147–148
- Pratt SC, Kühnholz S, Seeley TD, Weidenmüller A (1996) Worker piping associated with foraging in undisturbed queenright colonies of honey bees. *Apidologie* 27:13–20
- Schneider SS, Stamps JA, Gary NE (1986) The vibration dance of the honey bee. I. Communication regulating foraging on two time scales. *Anim Behav* 34:377–385
- Seeley TD (1982) How honeybees find a home. *Sci Am* 247:158–168
- Seeley TD, Buhrman S (1999) Group decision making in swarms of honey bees. *Behav Ecol Sociobiol* 45:19–31
- Seeley TD, Morse RA, Visscher PK (1979) The natural history of the flight of honey bee swarms. *Psyche* 86:103–113
- Seeley TD, Weidenmüller A, Kühnholz S (1998) The shaking signal of the honey bee informs workers to prepare for greater activity. *Ethology* 104:10–26
- Smith WJ (1977) The behavior of communicating. An ethological approach. Harvard University Press, Cambridge
- Visscher PK, Shepardson J, McCart L, Camazine S (1999) Vibration signal modulates the behavior of house-hunting honey bees (*Apis mellifera*). *Ethology* 105:759–769