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# The modulation of worker behavior by the vibration signal during house hunting in swarms of the honeybee, *Apis mellifera*

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**Abstract** During house hunting, honeybee, *Apis mellifera*, workers perform the vibration signal, which may function in a modulatory manner to influence several aspects of nestsite selection and colony movement. We examined the role of the vibration signal in the house-hunting process of seven honeybee swarms. The signal was performed by a small proportion of the older bees, and 20% of the vibrating bees also performed waggle dances for nestsites. Compared to non-vibrating controls, vibrating bees exhibited increased rates of locomotion, were more likely to move into the interiors of the swarms, and were more likely to fly from the clusters and perform waggle dances. Recipients responded to the signal with increased locomotion and were more likely than non-vibrated controls to fly from the swarms. Because vibration signals were intermixed with waggle dances by some vibrators, and because they stimulated flight in recipients, the signals may have enhanced nestsite scouting and recruitment early in the house-hunting process. All swarms exhibited increased vibration activity within 0.5–1 h of departure. During these final periods, numerous vibrating bees wove repeatedly in and out of the clusters while signaling and motion on the swarms increased until it culminated in mass flight. The peaks of vibration activity observed at the end of the house-hunting process may therefore have activated the entire swarm for liftoff once a new nestsite had been selected. Thus, the vibration signal may help to integrate the behavior of numerous groups of workers during nestsite selection and colony relocation.

**Key words** Honeybee · Vibration signal · Modulatory communication · Swarming · Waggle dance

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## Introduction

In highly social insects, cooperative activities such as food gathering and storage, brood rearing, and colony reproduction are regulated by collective decisions that arise from the interactions of subpopulations of workers, each performing different, but interdependent sets of tasks (Seeley 1995; Gordon 1996). For these cooperative efforts to be successful, behavior must be integrated both within and among the different worker groups. This integration is achieved in part by communication signals, which can be divided into two main categories. The first contains signals, such as the odor trails of ants and the waggle dance of honeybees, that are performed by a specific group of workers within a particular context, elicit a specific response, and help regulate one or a few behaviors by recruiting recipients to certain tasks (Hölldobler and Wilson 1990; Seeley 1995). In contrast, signals in the second category can be performed by different worker groups in a variety of contexts and elicit no clear-cut response. Rather, these “modulatory” signals function in a non-specific manner to shift the probability that recipients will engage in suites of behavior, with the specific response dependent upon contextual cues (Markl 1985; Hölldobler and Wilson 1990). Modulatory signals can therefore influence many different activities and worker groups simultaneously. Thus, an understanding of collective decision making requires detailed knowledge of the different communication signals that orchestrate worker activity and how these signals interact. However, while specific signals like the waggle dance have been extensively studied, the role of modulatory communication in insect societies has only recently begun to receive detailed attention (Schneider 1987; Hölldobler 1995; Nieh 1998).

An example of modulatory communication is the vibration signal of the honeybee, *Apis mellifera*, which consists of a worker rapidly vibrating her body dorso-ventrally for 1–2 s, usually while contacting another bee (Milum 1955). A vibrating bee often produces a series of signals lasting from several minutes to over an hour, dur-

ing which she may contact hundreds of different recipients scattered throughout the nest (Schneider 1986; Seeley et al. 1998). As a result, the vibration signal is one of the most common communication signals in honeybee colonies.

Two aspects of the signal suggest that it functions in a modulatory manner. First, it is triggered by a variety of stimuli and performed in several different contexts. Vibration signals are most frequently performed on other workers and are associated with successful foraging (Schneider 1986, 1989; Schneider et al. 1986a, 1986b; Painter-Kurt and Schneider 1998a; Seeley et al. 1998). The signal can also be triggered by queen activity and is performed on laying queens prior to swarming, developing queen cells in which virgin queens are reared, and newly emerged virgin queens prior to the onset of egg laying (Allen 1959; Fletcher 1975, 1978a, 1978b; Painter-Kurt and Schneider 1998b). Second, the vibration signal causes a non-specific increase in activity that is often expressed as increased locomotion (Schneider et al. 1986a; Schneider 1991; Nieh 1998). This heightened activity enhances the performance of a variety of tasks by workers, including foraging, brood care, and food processing (Schneider et al. 1986a; Schneider 1987; Schneider and McNally 1991; Nieh 1998), while in queens it may enhance swarming and mating flights and regulate aggressive interactions among virgin queens (Fletcher 1978a; Schneider 1991). Thus, the signal may help coordinate many different cooperative activities in honeybee colonies.

An opportunity to examine how the vibration signal may influence collective decision making is provided by the house-hunting process of honeybee swarms. When a colony undergoes reproductive swarming, about half the workers and the laying queen leave the natal nest and form a cluster in nearby vegetation. Scout bees search for potential new nest cavities and communicate the location of suitable sites by performing waggle dances on the swarm surface. Initially, a variety of different nest-sites are communicated, but eventually all waggle dance activity becomes focused on one location. When all waggle dancers are indicating the same cavity, the swarm becomes airborne and moves to the chosen site. The selection of a nestsite by achieving consensus among waggle dancers is one of the most spectacular and best-studied examples of collective decision making in animals (Lindauer 1955; Camazine et al. 1999; Seeley and Buhrman 1999; Visscher and Camazine 1999).

In addition to the waggle dance, house hunting may also be influenced by the vibration signal. The signal can be performed throughout swarming (Visscher et al. 1999); however, its role in house hunting is unknown. Vibration signals may interact with waggle dances to enhance recruitment for nest-sites, because in some swarms waggle dancers may also vibrate (Schneider et al. 1998). Alternatively (or additionally), the signal may help prepare a swarm for mass movement once a site has been chosen, because increased vibration activity can occur shortly before liftoff (Visscher et al. 1999). Determining

the function of the signal during house hunting will require detailed observations of the behavior of vibrators and recipients on swarms, the extent to which each group is associated with nestsite scouting and recruitment, and the relationship between the temporal patterns of vibration and waggle dance activity. Nevertheless, the available data suggest that the house-hunting process offers an excellent opportunity to distinguish among possible functions of the vibration signal and to explore how modulatory communication interacts with other signals during collective decision making.

This study examined vibration signals during nestsite selection and movement in honeybee swarms. The specific objectives were to (1) compare the age and proportion of workers that perform vibration signals and waggle dances and visit potential nest-sites; (2) examine the behavior of vibrating bees to assess the extent to which their signaling is associated with house hunting; (3) compare the behavior of recipients and non-vibrated controls to assess their activity levels and their likelihood of becoming involved in nestsite scouting and recruitment; and (4) examine the temporal patterns of vibrating and waggle dancing, and in particular how the relationship between these patterns changes as a swarm approaches the time of departure.

## Methods

### Study sites and swarm setup

A total of seven different swarms (swarms A–G) were examined during May–July 1998 and March–May 1999 on the campus of the University of North Carolina at Charlotte. The swarms chose among nest cavities occurring in buildings and woods surrounding the study site. All swarms came from study colonies that were maintained in 45-l Langstroth hives or four-frame observation hives. Each study colony was established from a field colony by transferring the laying queen, 8,000–10,000 workers and frames of comb into a Langstroth hive or observation hive.

Vibration signal behavior was monitored in both naturally occurring and artificially created swarms. Natural swarms were obtained by allowing study colonies to rear queens and swarm naturally. Each swarm cluster was then captured and the queen was confined to a small cage. Artificial swarms were created following the methods of Lindauer (1955) and Morse and Boch (1971). The queen from an observation or a Langstroth hive was placed in a small cage which was then suspended inside a large, screen-mesh swarm cage (58×62×46 cm). The workers from the colony were shaken into the swarm cage and quickly clustered about the caged queen. The colony was then fed 50% sucrose solution ad libitum for 3–4 days, after which time workers were visibly engorged and some had begun to produce wax scales. These conditions simulate the preparations associated with natural swarming, and indeed artificial swarms behave identically to natural swarms and are frequently used to study the house-hunting process (Schneider 1995; Schneider et al. 1998; Camazine et al. 1999; Seeley and Buhrman 1999; Visscher and Camazine 1999). However, the two swarm types differ in the age structure of workers. A natural swarm contains workers of all ages, but there are more younger bees and fewer older bees than expected based on the age distribution of workers in the parental colony (Gilley 1998). An artificial swarm, however, has an age structure similar to that of the parental colony, because it is created by shaking bees at random from combs of the natal nest. Thus, while artificial swarms accurately portray the behaviors associated with house hunting, they may not reliably recreate the age structure typically associated with swarming.

**Table 1** The different swarms monitored, the nature of each, and the different aspects of the study for which a swarm was used (✓) (N natural swarm, A artificial swarm)

Swarm	Type	Age distribution	Percent of swarm that vibrated and waggle danced	Behavior of nestbox visitors	Behavior of vibrators and controls	Behavior of recipients and controls	Temporal patterns of activity
A	N	✓	✓				✓
B	N	✓	✓				✓
C	A				✓		
D	A			✓	✓		
E	N	✓	✓	✓		✓	✓
F	N	✓	✓	✓		✓	✓
G	N	✓	✓	✓	✓	✓	✓

Each natural and artificial swarm was set up for observation as follows. The caged queen was affixed to a swarm stand and the workers were shaken onto the ground at the base of the stand, whereupon they quickly flew or crawled to cluster about the queen. A swarm stand consisted of a 1.5-m pole embedded in a bucket of cement with two crossed wooden slats at the top to provide a surface for attaching the queen cage and facilitate cluster formation. Each stand was equipped with a feeder that dispensed 50% sucrose solution ad libitum. Although swarms typically exhibit only limited foraging activity, providing sugar syrup helps ensure that waggle dances will be performed for nestsites rather than food sources (Schneider 1995; Camazine et al. 1999; Seeley and Buhrman 1999).

We monitored a total of five natural and two artificial swarms. Once waggle dancing began, the process of nestsite selection frequently occurred quickly (within 4–6 h). We were therefore usually unable to examine for each swarm every aspect investigated in this study. Thus, we examined different components of vibration signal behavior in different swarms (Table 1). The proportion and age of workers that performed vibration signals and the temporal patterns of signaling behavior were investigated in only the natural swarms. The behavior of nestbox visitors and the behavior of individual vibrators and recipients were examined in both natural and artificial swarms (Table 1).

#### Establishing populations of bees of known age

To examine the ages of workers that performed vibration signals and waggle dances, we added to each study colony prior to swarming cohorts of 250–350 newly emerged workers of known age, each marked on the thorax or abdomen with a dot of Testors dope paint. All bees within a cohort received the same color and placement of mark, but each successive cohort was painted with a different color and mark location. In this manner, the age of each marked bee could be visually determined throughout the swarming process. Workers for marking were obtained from combs maintained in an incubator (34°C; 50% relative humidity) and all workers were marked within 24 h of emergence. Marked bees were added every other day during the 4- to 7-week period preceding swarming. Thus, by the time of swarming, each study colony had received 3,400–5,900 marked workers, ranging in age from 1–24 to 3–55 days during the house-hunting process.

Relatedness among workers may affect swarming behavior (Getz et al. 1982). We controlled for this potential influence by adding to each of our hives workers of known age that emerged from combs taken from the original field colony during the first 21 days after the study colony was established. Because the developmental time from egg to adult for honeybees is 21 days (Winston 1987), this ensured that all workers marked during this period had developed from eggs laid by the queen before she was transferred to the study colony. The workers added after this 21-day period were collected from combs taken from both the original field colony (these workers were progeny of the replacement queen), plus additional field colonies as needed to ensure an

adequate number of newly emerged workers. Thus, at the time of swarming, the study colonies contained primarily marked bees that were related to their unmarked nestmates, although some unrelated marked workers were also present.

#### Determining the age and proportion of workers that performed vibration signals and waggle dances and visited nestsites

All swarms were monitored continuously throughout each day from establishment on the swarm stands until departure. Observations began at 0700–0800 hours and terminated at 1800–1900 hours, by which time vibration and waggle dance activity had ceased for the day. Observations were conducted simultaneously by two to four different observers to ensure that all sides of the swarms were monitored. Each worker observed to vibrate or waggle dance was gently marked on the thorax or abdomen with a distinguishing color of paint. Workers that performed both communication behaviors received two separate color marks. Data sheets were used to keep running tallies of the number of vibrators and waggle dancers marked on each swarm cluster. We also recorded the age of each known-age bee observed to perform each communication behavior.

For four of the swarms, we provided a 20-l experimental nestbox that contained a single 3.5-cm entrance hole and was equipped with one frame of empty wax comb and a lure filled with Nasonov pheromone. Wax and a pheromone lure enhance the quality of a potential nest cavity and are commonly used to attract and capture honeybee swarms (Schmidt et al. 1989; Schmidt and Thoenes 1990). Each nestbox was positioned in partial shade approximately 1.5 m aboveground and 7–10 m from the swarm. One observer monitored the entrance of the nestbox throughout the house-hunting process. Each bee visiting the nestbox was caught in a small nylon mesh net upon exiting the box entrance and marked on the thorax or abdomen with a distinguishing color of paint. Upon return to the swarm cluster, each was given separate paint marks if she vibrated or waggle danced. We also recorded the age of known-age nestbox visitors.

For each behavior monitored, a worker was marked only once when first observed to vibrate, waggle dance, or visit a nestbox. Repeated performances of these behaviors were not recorded and thus each bee was counted only once for each activity.

We estimated the total number of bees in each swarm by weighing the entire swarm and dividing by the mean weight of 30–50 individually weighed workers. Subsequently, we determined (1) the total number and proportion of bees that performed vibration signals, waggle dances, and both communication displays in each swarm, (2) the number and proportion of nestbox visitors that vibrated and waggle danced, and (3) the age distribution of workers engaging in the different activities monitored.

Contingency table  $\chi^2$  analysis was used to compare within each swarm the number of bees that vibrated and waggle danced, and to compare the number of nestbox visitors that performed these two displays. Wilcoxon two-sample tests (Sokal and Rohlf 1995) were used to compare the ages of workers that vibrated and

waggle danced in each swarm. We did not compare age distributions among swarms because each had a unique age structure depending on the duration of the preswarming period during which marked bees were added. The sequential Bonferroni adjustment (Rice 1989) was used to determine significance levels for the multiple comparisons made within each swarm.

#### Determining the behavior of workers that performed the vibration signal

Vibrating workers were selected randomly on three of the swarm clusters and observed for 10 min each. For every vibrator, we recorded (1) the number of vibration signals performed, (2) the number of workers walked across (as an estimate of locomotion rate), (3) the number of times she followed waggle dancers, and whether she (4) performed waggle dances, (5) flew from the swarm, or (6) went into the interior of the swarm cluster. This final aspect of behavior was monitored because the outer layer of swarm clusters contains primarily the older, foraging-age workers that include the nestsite scouts (Michener 1974; Gilley 1998). Thus, if the signal functions mainly to enhance recruitment to nestsites, then vibrators should remain on the swarm surface. Conversely, if the signal functions to generate activity necessary for mass flight, then vibrators should also move into the interior of the cluster. As far as was possible without disturbing the clusters, we monitored the behavior of vibrators that moved into the swarms to determine if vibration signals continued to be produced.

We monitored vibrators of known and unknown age. For each vibrator observed, we also monitored for 10 min a non-vibrating control that was as similar as possible to its vibrating counterpart with respect to initial location on the swarm and general level of locomotor activity. For known-age vibrators, we selected a control of the same age. For vibrators of unknown age, we selected a known-age control that was at least 18 days old, because the majority of vibrators were this age or older (see Results). All controls were monitored simultaneously with or immediately after the observation of the vibrating bees. Each vibrator and control was carefully marked with a distinguishing color of paint at the beginning of the 10-min observation period and no bee was observed more than once.

For both vibrators and controls, observations were terminated if they flew from the swarm or moved into the interior of the cluster to a depth that did not allow further monitoring. Observation times were measured with digital stopwatches. We restricted our observation periods to 10 min because (1) activity on the swarms frequently made it impossible to monitor reliably worker behavior for longer intervals and (2) this allowed us to maximize the number of workers examined during the relatively brief periods in which nestsite selection occurred.

We compared the locomotion rates of vibrators and controls within and among swarms using a two-way ANOVA for rank-ordered data (Sokal and Rohlf 1995). Each of the other behaviors was examined separately using 3×2×2 contingency tables [3 swarms×2 categories of workers (vibrators and controls)×2 responses (performing or not performing the behavior in question)] analyzed by log-linear models (Sokal and Rohlf 1995). In non-swarming colonies, vibrating workers exhibit greater locomotion and are more likely than controls to perform waggle dances and fly from the nest (Schneider 1986; Painter-Kurt and Schneider 1998a; Nieh 1998). We anticipated similar differences between vibrators and controls on swarms and thus we used one-tailed tests of significance for our comparisons. The sequential Bonferroni adjustment (Rice 1989) was used to determine significance levels for the different interaction terms among swarms, and for the multiple comparisons made within each swarm.

#### Determining the behavior of vibrated recipients

Recipients were selected for observation by following a vibrating bee until she clearly grasped and vibrated a worker on the surface

of the swarm. The recipient was then gently marked with a distinguishing color of paint and monitored for 10 min. For each recipient we recorded (1) the number of bees she walked across, (2) whether she flew from the swarm, and (3) whether she followed a waggle dancer. For each recipient, we also monitored a control that was not observed to receive a vibration signal, but was in the same general location on the swarm and exhibited the same general level of locomotor activity as the recipient. All controls were marked with a distinguishing color of paint at the beginning of the 10-min observation period and were followed immediately after or simultaneously with their recipient counterpart. If a control received a signal during the 10-min observation period, she was abandoned and another control chosen. During periods of intense vibration activity when controls were most likely to receive signals and be abandoned, several different observers would each follow a separate control simultaneously. As a result, we tended to monitor more controls than recipients in our swarms. Each recipient and control was monitored for only one 10-min period. The data were analyzed using the statistical procedures described above for vibrators and controls. Previous studies in non-swarming colonies have suggested that vibrated workers exhibit increased activity and are more likely to contact waggle dancers and leave the nest (Schneider et al. 1986a; Schneider 1987; Schneider and McNally 1991; Nieh 1998). Thus, we used one-tailed tests to compare the behavior of recipients and controls within our swarms. The sequential Bonferroni adjustment was used to determine significance levels within and among swarms.

#### Determining temporal patterns of vibration signal and waggle dance activity

Throughout the house-hunting process, we conducted at 30-min intervals two 1-min counts of (1) the number of vibration signals observed over the entire swarm surface and (2) the maximum number of workers that were simultaneously performing waggle dances for nestsites. A mean for vibration signal and waggle dance activity was then calculated for each interval. We focused our investigation on the final day of house hunting (day of swarm departure) in each swarm, because we wanted to assess how vibration signals and waggle dances were associated with liftoff. However, because it was not possible to predict precisely when departure would occur, each swarm had to be monitored throughout each day it was on the swarm stand to ensure that we obtained a complete record for the final day.

We examined the relationship between the temporal patterns of vibrating and waggle dancing by determining the degree to which "major" peaks of the two activities coincided (occurred during the same observation period) during the final day. A major peak was defined as an increase in vibration signaling or waggle dancing that was at least 1 SD greater than the mean value observed for that behavior on the day of departure. Contingency table  $\chi^2$  analysis was used to compare the number of major vibration and waggle dance peaks that coincided with one another.

All mean values are reported as  $\pm 1$  SE.

## Results

### Age and proportion of workers performing vibration signals and waggle dances

When viewed over the five natural swarms examined, vibrators accounted for 4.6±1.1% of the workers in the swarms (Table 2). Waggle dancers accounted for 3.6±0.8% of the total workers present (Table 2). In swarm A, similar numbers of vibrators and waggle dancers were observed ( $\chi^2=0.14$ ,  $df=1$ ,  $P>0.05$ ). In the other four natural swarms, there were significant differences between

**Table 2** Population size and the number and proportion of workers observed to perform vibration signals, waggle dances, and both communication signals over all days of observation in the five natural swarms examined

Swarm	Population size	Vibrators (% of swarm)	Waggle dancers (% of swarm)	Bees performing both signals (% of swarm)
A	8,565	348 (4.1%)	341 (4.0%)	79 (0.9%)
B	13,803	132 (1.0%)	333 (2.4%)	39 (0.3%)
E	11,735	551 (4.7%)	725 (6.2%)	76 (0.6%)
F	11,057	601 (5.4%)	414 (3.7%)	112 (1.0%)
G	20,894	1,637 (7.8%)	396 (1.9%)	117 (0.6%)

**Table 3** Proportion of the total vibrators marked on the swarm surface that also performed waggle dances and the proportion of marked waggle dancers that performed vibration signals over all days of observation

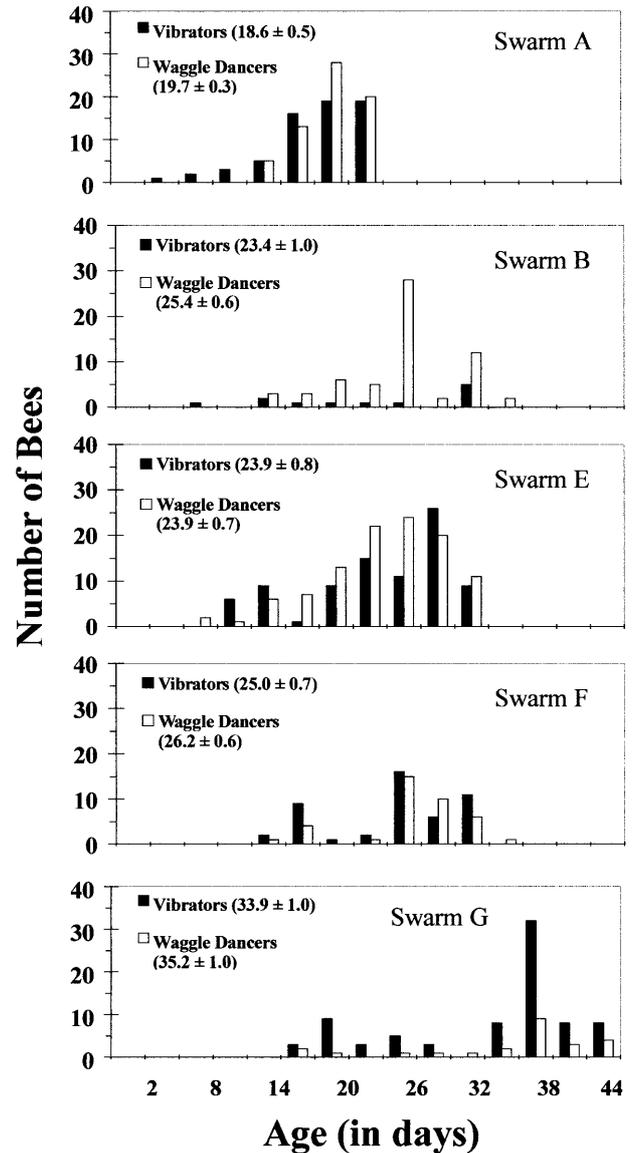
Swarm	Percentage of vibrators that waggle danced	Percentage of waggle dancers that vibrated
A	22.6	23.3
B	29.5	11.7
E	13.8	10.5
F	18.6	27.1
G	7.1	29.5

the number of workers that performed these two communication displays (for each swarm,  $\chi^2 > 23.0$ ,  $df=1$ ,  $P < 0.05$  at the adjusted alpha level; Table 2). However, there was no consistent pattern among swarms in the proportions of workers that vibrated versus waggle danced. In swarms F and G, a greater proportion of workers performed vibration signals than waggle dances, while in swarms B and E the opposite trend was observed (Table 2).

Workers that performed both vibration signals and waggle dances accounted for only  $0.7 \pm 0.1\%$  of the total bees in the swarms (Table 2). However, these workers comprised  $18.3 \pm 3.8\%$  of the marked vibrators and  $20.4 \pm 3.9\%$  of the observed waggle dancers (Table 3). Thus, on average, about one-fifth of the vibrators marked on the swarms engaged in nestsite recruitment. The remaining 70–90% of the marked vibrators, however, were never observed to waggle dance, even though the swarms were monitored by several observers simultaneously throughout the house-hunting process.

Vibration signals and waggle dances tended to be performed by the older workers in the swarms. While bees less than 10 days old were observed to perform both communication signals, the mean ages of first performance ranged from 18.6 to 33.9 days for vibrating and 19.7–35.2 days for waggle dancing (Fig. 1). The two age distributions did not differ in any of the five natural swarms examined (for each swarm,  $U_s < 1.2$ ,  $P > 0.24$ ).

In summary, during the house-hunting process, vibration signals and waggle dances were produced by groups of similarly aged bees that comprised small proportions of the entire swarms. About 20% of the marked vibrators performed waggle dances, which suggested that these bees were directly engaged in nestsite recruitment. The majority of vibrators were never observed to perform waggle dances, and thus may have represented workers that were largely separate from those that were immediately involved in advertising nestsites.



**Fig. 1** Ages at which workers performed vibration signals and waggle dances throughout the house-hunting process on each of the five natural swarms examined. Values on the x-axis represent the midpoints of 3-day age categories (1–3 days, 4–6 day, etc.). Mean ages are given  $\pm 1$  SE

#### The behavior of nestbox visitors

A pheromone- and wax-baited nestbox was provided for four of the swarms (Table 1). However, only workers from swarms E and F visited these boxes.

Neither swarm selected the nestbox as the new nest cavity.

In swarm E, a total of 609 different workers were marked while visiting the nestbox. Of these, 110 were known-age bees and their mean age was  $24.0 \pm 0.6$  days. Of the 609 nestbox visitors, 24 (3.9%) produced vibration signals after returning to the swarm cluster, while 164 (26.9%) performed waggle dances for the nestbox ( $\chi^2=102.8$ ,  $df=1$ ,  $P<0.0001$ ). Only 4 (0.01%) of the nestbox visitors produced both communication signals. In swarm F, 64 workers visited the nestbox, of which only 8 were known-age bees (mean age  $23.6 \pm 2.5$  days). Of these 64 workers, 7 (10.9%) were vibrators, 7 (10.9%) performed waggle dances for the nestbox, and 3 (4.7%) performed both signals.

Thus, very small proportions of workers in the swarms visited the experimental nestboxes, and these bees were among the older workers present. Approximately 4–11% of the nestbox visitors produced vibration signals soon after returning to the swarm clusters, which suggests that investigating a suitable cavity may trigger signal performance in some scouts. However, the majority of nestbox visitors were never observed to vibrate during the house-hunting process.

#### The behavior of vibrating workers

We monitored vibrators and controls in swarms C, D, and G (Table 1), and these comparisons revealed three main aspects of the behavior of workers performing the signal. First, vibrators exhibited greater rates of locomotion. Compared to controls, vibrators crossed 3.2–12.0 times as many bees per minute ( $F=118.87$ ,  $df=1,174$ ,  $P=0.0001$ ; Table 4) and this trend was consistent among swarms ( $F=3.61$ ,  $df=1,2$ ,  $P>0.05$ ). Vibrators produced a mean of  $7.5 \pm 0.6$  signals/min (range 1.0–25.0/min) while roaming over the entire swarm. For most of the house-hunting process, waggle dance activity occurred in restricted regions of the swarms, but vibrators did not confine their signaling activity to these areas.

Second, vibrators tended to move into the interiors of the swarms. Vibrators were 1.6–3.1 times more likely than controls to move into the clusters ( $\chi^2=21.01$ ,  $df=1$ ,

$P=0.0001$ ; Table 4) and this difference was similar among swarms ( $\chi^2=3.07$ ,  $df=2$ ,  $P=0.108$ ). Vibrators continued to perform signals as they moved into the clusters, and thus vibrating was not restricted to the swarm surface. Vibrators often produced series of signals while weaving repeatedly into and out of the swarms and this behavior was especially pronounced during the final hour before swarm departure.

Third, vibrators were more likely than controls to fly from the swarms and perform waggle dances. (Vibrators and controls rarely or never followed waggle dancers and this behavior was excluded from the comparisons.) Significantly more vibrators than controls engaged in flight ( $\chi^2=4.24$ ,  $df=1$ ,  $P=0.013$ ; Table 4), and this difference was exhibited to similar extents in the three swarms ( $\chi^2=0.96$ ,  $df=1$ ,  $P=0.328$ ). More vibrators than controls performed waggle dances in swarm C (Fisher exact test,  $P=0.0034$ ) and swarm D (Fisher exact test,  $P=0.0024$ ). In swarm G, however, none of the monitored bees waggle danced (Table 4). Taken together, these results suggest that vibrating bees were more directly involved in house hunting than non-vibrating controls, and that they produced the signal while roaming throughout the swarm clusters, especially as departure approached.

#### The behavior of vibrated recipients

Recipients and controls were monitored in swarms E, F, and G (Table 1). Vibrated recipients exhibited increased locomotion (Table 5). Compared to controls, recipients crossed 3.2–12.8 times as many bees per minute ( $F=37.23$ ,  $df=1,147$ ,  $P=0.0001$ ) and this difference was similar among swarms ( $F=0.55$ ,  $df=1,2$ ,  $P=0.578$ ).

Recipients also exhibited greater flight activity (Table 5). Compared to controls, recipients were 4.0–6.0 times more likely to fly from the swarms during the 10-min observation periods ( $\chi^2=7.73$ ,  $df=1$ ,  $P=0.0027$ ) and the swarms did not differ in the extent to which this difference was exhibited ( $\chi^2=0.14$ ,  $df=2$ ,  $P=0.712$ ). Recipients that flew accounted for 24.3% of the 74 total vibrated bees monitored. However, the signal did not significantly increase the tendency to follow waggle dancers (Table 5). While more recipients than controls followed waggle dancers, only 8 of the 74 to-

**Table 4** Behavior of the vibrators and controls monitored over all days of observation in each of three swarms. Mean values are reported  $\pm 1$  SE

	<i>n</i>	Bees crossed/min	Moved into swarm	Flew from swarm	Performed waggle dances
Swarm C					
Vibrator	39	17.7 $\pm$ 1.9	29	9	10
Control	39	5.6 $\pm$ 1.3	16	2	1
Swarm D					
Vibrator	32	15.6 $\pm$ 2.1	25	6	8
Control	32	1.3 $\pm$ 0.5	8	0	0
Swarm G					
Vibrator	19	8.4 $\pm$ 1.5	11	3	0
Control	19	1.4 $\pm$ 1.0	7	2	0

**Table 5** Behavior of the recipients and controls monitored over all days of observation in each of three swarms. Mean values are reported  $\pm 1$  SE

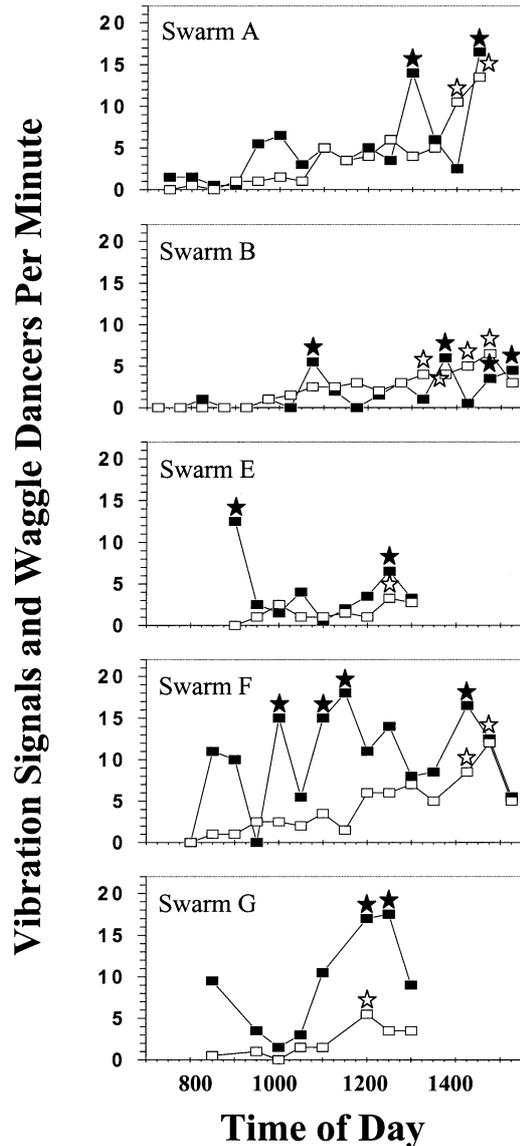
	<i>n</i>	Bees crossed/min	Flew from swarm	Followed waggle dancer
Swarm E				
Recipient	21	2.9 $\pm$ 0.8	6	1
Control	23	0.9 $\pm$ 0.5	1	1
Swarm F				
Recipient	16	7.7 $\pm$ 2.9	4	5
Control	16	0.6 $\pm$ 0.2	0	1
Swarm G				
Recipient	37	4.1 $\pm$ 0.8	8	2
Control	40	1.2 $\pm$ 0.2	2	0

tal recipients and 2 of the 79 controls did so during the observation periods. This difference was not statistically significant ( $\chi^2=2.25$ ,  $df=1$ ,  $P=0.0669$ ). Because of the small numbers of followers observed, our samples sizes were insufficient to draw definite conclusions about the influence of the signal on following behavior. Nevertheless, the available data suggest that the vibration signal elicits increased activity that may contribute to a greater tendency to fly from the swarms, although this increased flight does not necessarily result from increased contact with dancers for potential nestsites.

#### Temporal patterns of vibration signal and waggle dance activity

We examined the patterns of vibration signal and waggle dance activity during the day of swarm departure in each of the five natural swarms (Table 1). Vibration signals were performed continuously throughout the house-hunting process and vibration activity tended to increase throughout the final day (Fig. 2). However, there was considerable variability among consecutive observation periods within swarms, and large differences in the levels of vibration activity observed among the different swarms (Fig. 2).

We observed three main features for peaks of vibration activity on the days of swarm departure. First, major vibration peaks could occur at any time of the day, but in all five swarms at least one major peak occurred within 0.5–1 h of swarm liftoff (Fig. 2). In swarms A and B, we continued to observe heightened vibration activity on the swarm surface up until the moment of departure. In contrast, in swarms E, F, and G, vibration signaling on the swarm surface exhibited a major peak within 1 h of departure, but then declined as liftoff approached. However, these declines may not have accurately reflected the level of vibration behavior immediately before departure. During the final hour, we observed numerous vibrators weaving rapidly in and out of the swarm interiors. We may therefore have inadvertently conducted some of



**Fig. 2** Temporal patterns of the number of vibration signals (*filled squares*) and the number of waggle dancers (*open squares*) during the day of swarm departure in each of the five natural swarms examined. Major peaks in vibration activity are indicated by a *filled star*, those for waggle dance activity by an *open star*. Liftoff occurred in each swarm within 5–20 min of the final 30-min observation period

our 1-min counts when many vibrators had moved inside the swarms. In all five swarms, the final peaks in vibration activity coincided with increased movement of bees over the clusters, such that shortly before liftoff, the swarms had the appearance of “boiling.” In contrast, on days of observation preceding the final day, vibration activity tended to decline or cease in late afternoon and the swarms became calm. Thus, the final peaks observed on the days of departure may have been specifically associated with liftoff.

A second feature observed for the temporal patterns of vibration activity was that all five swarms exhibited increased signaling in the morning hours when little or

no waggle dancing was observed. This morning activity met our criteria for a major peak in swarms B, E, and F, but represented more minor levels of vibrating in swarms A and G (Fig. 2).

Finally, major peaks of vibration and waggle dance activity tended to occur independently of one another. We observed a total of 14 major peaks in vibration activity, 6 of which coincided with a major peak in waggle dancing and 8 of which did not (Fig. 2). Likewise, of the 10 major peaks of waggle dance activity observed, 6 coincided with a major peak in vibrating while 4 did not (Fig. 2). When viewed over the entire day, there was no consistent temporal relationship between the occurrence of major peaks in the two activities ( $\chi^2=0.18$ ,  $df=1$ ,  $P>0.50$ ). Both communication behaviors increased within 1–1.5 h of swarm departure. However, although five of the seven major vibration peaks observed during the final hour coincided with a peak in waggle dancing (Fig. 2), this was not statistically significant ( $\chi^2=0.05$ ,  $df=1$ ,  $P>0.50$ ). In fact, immediately before departure, vibrating and waggle dancing appeared to become increasingly uncoupled. During the final 3–5 min before liftoff, we continued to observe numerous vibrators, but waggle dancing declined or virtually ceased. However, because we collected our data at 30-min intervals, this phenomenon was often not reflected in the values we collected (Fig. 2).

## Discussion

The selection of a new nestsite by honeybee swarms involves four main components. First, workers must locate and evaluate potential nestsites. Second, other workers must be recruited to these specific locations. Third, the array of potential nestsites must be winnowed down to one choice. Fourth, once the new site has been selected, the swarm must lift off and move en masse to the chosen location. The regulation of these four events may occur primarily through two communication signals: the waggle dance and the vibration signal.

Waggle dances are at the heart of the selection process per se, because they are the means by which potential sites are advertised and the ultimate choice is formulated (Lindauer 1955; Camazine et al. 1999; Seeley and Buhrman 1999). Yet, despite the central role that waggle dances play in the selection process, very small proportions of workers perform these displays. We observed that only 2–6% of the total workers in our swarms waggle danced for nestsites, and similar values have also been reported by Gilley (1998) and Seeley and Buhrman (1999). Thus, the choice of a new home is dependent upon the communication behavior of only a small subset of the entire swarm. Likewise, we observed that only 1–8% of workers produced vibration signals, which suggests that the role of this signal in swarming is also dependent upon a tiny fraction of the total bees present. Yet our results suggested that the vibration signal is involved in at least three stages of the house-hunting process.

## Nestsite scouting

Two observations suggested that vibration signals may have been associated with scouting for potential nestsites. First, some of the workers visiting the experimental nestboxes produced vibration signals upon returning to the swarms. Investigating a suitable cavity may therefore have triggered signal production in at least a small number of bees. Second, recipients were more likely than non-vibrated controls to fly from the swarms. Because virtually all flight during house hunting is associated with searching for and visiting nestsites, the vibration signal may have increased the probability that some recipients would engage in scouting.

## Recruitment to nestsites

Our results were equivocal on the extent to which the vibration signal may have influenced recruitment to specific nestsites. Vibrators and waggle dancers were the same age, and about 20% of observed vibrators performed waggle dances, often intermixing the two communication behaviors. This intermixing could potentially have enhanced recruitment to nestsites, similar to the manner in which the intermixing of vibrating and waggle dancing by successful foragers may enhance recruitment to food sites (Schneider et al. 1986a; Nieh 1998; Seeley et al. 1998). Also, all of the natural swarms exhibited heightened vibration activity in the morning, which preceded the onset of waggle dancing. Because the signal elicited greater locomotion in recipients, morning vibrations may have helped activate workers for scouting and nestsite recruitment. Similarly, non-swarmer colonies often exhibit an early morning peak of vibration activity, which precedes foraging and may influence the level of food site recruitment that occurs later that same day (Schneider et al. 1986a, 1986b).

Thus, a portion of vibrators were immediately involved in nestsite recruitment and those that never waggle danced could have potentially helped to generate levels of activity that facilitated recruitment. However, we were not able to demonstrate that the vibration signal increased waggle dance following. While we observed that more recipients than controls followed waggle dancers, this difference did not reach statistical significance because of our small sample sizes. Similarly, Nieh (1998) observed in non-swarmer colonies that vibrated recipients had an increased (but statistically non-significant) tendency to contact waggle dancers for foraging sites. Thus, while vibration signal production may be linked with waggle dance performance, we do not know the extent to which the signal influences the chance that recipients will contact these dances and be recruited to specific nestsites. Resolving this issue will require monitoring a larger number of recipients, perhaps for more than 10 min each.

## Selection of the chosen site

Vibration signals are probably not directly involved in determining the ultimate selection of the new nestsite. Schneider et al. (1998) reported that  $31.3 \pm 9.2\%$  of all nestsite dancers in swarms vibrated, but the signals were not performed predominantly by dancers for the chosen site. Indeed, dancers for unchosen sites were as likely to perform vibration signals as were those for the site ultimately selected for the new nest (Schneider et al. 1998). Thus, the vibration signal does not appear to be an integral part of the process that focuses waggle dance activity on one particular location.

The signal may, however, influence the time required to winnow possible nest choices down to one specific selection. Schneider (unpublished data) found a significant, negative correlation between the proportion of nestsite dancers that vibrated and the duration of the house-hunting process ( $r = -0.771$ ,  $df = 5$ ,  $P < 0.05$ ). This suggests that even though the signal may not be directly involved in the selection of one particular site, it may somehow enhance the speed with which the choice is made. We did not assess the duration of house hunting in the present study because intermittent periods of inclement weather made it impossible to accurately determine for three of our swarms, the exact amount of time required for the selection process. We did, however, observe considerable variation among swarms in the degree to which workers intermixed vibration signals and waggle dances. While we do not know what caused this variation, it may have been associated with differences in the speed with which a new site was chosen. Experiments that compare swarms from which vibrators are and are not removed will be necessary to elucidate this possible role of the vibration signal.

## Swarm departure

Three lines of evidence suggest that a major function of the vibration signal during the latter portion of house hunting is to activate the entire swarm for liftoff and flight to the new nest cavity. First, peaks of vibration activity were observed within 0.5–1 h of swarm departure, and these peaks coincided with heightened locomotor activity over the entire swarm surface. Second, vibrating bees moved into the interiors of the clusters, and shortly before takeoff many wove repeatedly in and out of the swarms while producing series of signals. Third, vibrated workers exhibited increased locomotion and were more likely than non-vibrated controls to fly from the swarms. Thus, the peak of vibration activity shortly before departure may have helped to generate a level of movement throughout the entire cluster that facilitated the simultaneous flight of the swarm. An association between the vibration signal and flight has also been suggested in the contexts of foraging (Schneider et al. 1986a; Nieh 1998), orientation flights of younger workers (Painter-Kurt and Schneider 1998a), and swarm-

ing and mating flights of queens (Allen 1959; Schneider 1991).

Several other signals have also been suggested to play a role in triggering swarm takeoff. Departure may be initiated by the unanimous dancing for the chosen site. Shortly before departure, there are typically numerous waggle dancers scattered over much of the swarm surface, all indicating the same location (Lindauer 1955; Seeley and Buhrman 1999). Increased contact with these dancers could stimulate liftoff. However, there are usually never more than 20–30 workers performing waggle dances simultaneously prior to departure, and their activity is confined to the swarm surface. While many of the older bees in the surface layers may contact these dancers, the younger workers in the interior of the swarm (which make up the bulk of the cluster) are unlikely to do so shortly before departure. Furthermore, in several of the swarms examined in the present study, waggle dance activity declined or virtually ceased 3–5 min before departure, while vibration activity increased (see also Schneider et al. 1998). Thus, while unanimity among nestsite dancers may indicate that a decision has been reached, such consensus is probably not the main trigger for swarm liftoff (also see Lindauer 1955; Camazine et al. 1999).

Liftoff may also be triggered by the signal called the “buzz-run” (Schwirrlauf), which often increases on swarms around the time of departure (Lindauer 1955). Furthermore, several authors (Lindauer 1955; Seeley et al. 1979; Camazine et al. 1999) report that workers on swarms produce a high-pitched “piping” sound shortly before takeoff, which may also be involved in departure. However, the responses of workers who perceive buzz-running and piping are unknown. At present, only the vibration signal has been shown to generate the increased locomotion and flight activity that may be necessary for takeoff. Nevertheless, departure may involve a cascade of signals, and may itself provide an opportunity to further study how different communication systems interact to formulate and adjust a collective decision.

Thus, by operating in a non-specific modulatory manner, the vibration signal may influence several activities during house hunting. Early in the process, the signal may facilitate scouting and recruitment to nestsites in some bees, while later it may be associated primarily with preparing the entire swarm for departure (see also Schneider et al. 1998; Visscher et al. 1999). The modulatory influence of the signal may therefore help coordinate the activities of many groups of workers during swarming. But, why is such modulation necessary? While the vibration signal can help adjust foraging, swarming, queen rivalry, and house hunting, all of these processes can occur with little or no vibration activity (Schneider et al. 1986a, 1998; Painter-Kurt and Schneider 1998b). Why then is a non-specific signal sometimes used to influence cooperative activities for which other, specific signals and cues exist that alone can regulate these behaviors?

## Possible role of the vibration signal in honeybee behavior

The primary function of modulation may be to adjust responsiveness to stimuli and thus to fine-tune the degree of behavioral integration among workers (Schneider et al. 1998; Beshers et al. 1999). The vibration signal could potentially influence responsiveness in two ways. The heightened locomotion that the signal elicits could increase contact with stimuli, so that a recipient more quickly reaches the threshold for triggering a response. Alternatively (or additionally), the signal could lower thresholds so that less stimulation is required to release a response. At present, the manner in which the vibration signal influences worker behavior is unknown, but its effect could help to integrate activity both within and among worker groups.

During house hunting, the vibration signal may help coordinate activity within the group of older workers that scouts and recruits for potential nestsites. By altering responsiveness to stimuli that trigger flight and perhaps waggle dancing, the vibration signal could potentially influence the time required to select a new nest cavity. In a similar manner, the signal may help coordinate food gathering among older, foraging-age bees, because it increases contact with the waggle dances and other cues that regulate foraging (Schneider et al. 1986a; Seeley 1995; Nieh 1998). Thus, within the age groups that house hunt and forage, the vibration signal may interact with other signals and cues to facilitate scouting and recruitment (Schneider et al. 1986a; Seeley et al. 1998).

The vibration signal may also help integrate activity among different worker groups that perform interrelated tasks, but that attend to different stimuli. Swarm liftoff must occur simultaneously in all workers, yet it is primarily the older bees in the outer layers of the cluster that have a direct knowledge of nestsite selection. By generating increased activity throughout the cluster, the vibration signal may help to coordinate mass flight among all worker groups, despite their different levels of experience in the house-hunting process. Similarly, the signal may help to integrate tasks such as food processing, comb building, and brood care, all of which are related to foraging but are performed by younger bees that have no direct knowledge of the foraging environment. Rather, these tasks are directed by cues received from brood areas and food stores of the nest (reviewed in Seeley 1995). Responsiveness to these stimuli may become especially important during sustained periods of foraging success, when food processing, comb construction, and brood rearing may all need to be increased simultaneously and in a balanced manner. Vibration activity increases after 3–4 days of elevated foraging success (Schneider et al. 1986b) and vibrating foragers often produce prolonged series of signals while roaming throughout the nest and contacting hundreds of recipients of all ages (Gahl 1975; Schneider 1986; Painter-Kurt and Schneider 1998a). Younger bees respond to these signals with increased time spent tending brood, capping cells,

and processing food (Schneider 1987; Schneider and McNally 1991). By operating in a modulatory manner, so that specific responses are determined by contextual cues, the vibration signal may therefore help coordinate several worker age groups, each of which acts on different sets of information but each of which performs tasks that must be integrated into a colony-level response.

Thus, in addition to adjusting behavior within tasks, vibration signals, and modulatory signals in general, may represent a mechanism for adjusting behavior among tasks, by coordinating different worker groups that engage in related activities, but that attend and respond to different stimuli. Indeed, modulation may be necessary in any system in which individual units that act on only local information must interact within and among subgroups to produce collective responses. For example, modulatory synapses in animal nervous systems do not generate specific responses, but rather alter the sensitivity of neurons to other inputs, which modifies the strength and duration of their subsequent activity (Katz 1995, 1998). Neuromodulation allows for the fine-tuning of an on-going behavior, enhanced integration of different neural pathways, and even the reorganization of entire neuronal networks (Katz 1995, 1999). Modulatory signaling is extremely pervasive in nervous systems (Katz 1995), and may be similarly prevalent in highly social animals (Markl 1985; Schneider et al. 1986a; Beshers et al. 1999). The behavior of neural pathways cannot be fully understood without incorporating the effects of neuromodulation (Katz 1999). Similarly, we may not be able to fully understand how colony-level responses emerge from the interactions of workers in social insects unless we take into account the role of modulatory communication in group decision processes.

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