

K. Donahoe · L. A. Lewis · S. S. Schneider

The role of the vibration signal in the house-hunting process of honey bee (*Apis mellifera*) swarms

Received: 25 March 2003 / Revised: 13 May 2003 / Accepted: 11 June 2003 / Published online: 3 July 2003
© Springer-Verlag 2003

Abstract The function of the vibration signal of the honey bee (*Apis mellifera*) during house hunting was investigated by removing vibrating bees from swarms and examining the effects on waggle dancing for nest sites, liftoff preparations and swarm movement. We compared house hunting among three swarm types: (1) test swarms (from which vibrating bees were removed), (2) manipulated control (MC) swarms (from which randomly selected workers and some waggle dancers were removed), and (3) unmanipulated control (UC) swarms (from which no bees were removed). The removal of vibrating bees had pronounced effects on liftoff preparations and swarm movement. Compared to the MC and UC swarms, the test swarms had significantly greater liftoff-preparation periods, were more likely to abort liftoff attempts, and in some cases were unable to move to the chosen site after the swarm became airborne. However, the three swarm types did not differ in overall levels of waggle dance activity, the time required to achieve consensus for a nest site, the rate at which new waggle dancers were recruited for the chosen site, or the ability to maintain levels of worker piping necessary to prepare for flight. The removal of vibrating bees may therefore have altered liftoff behavior because of a direct effect on vibration signal activity. A primary function of the signal during house hunting may be to generate a level of activity in workers that enhances and coordinates responses to other signals that stimulate departure and movement to a new location.

Keywords House hunting · Modulatory communication · Swarm · Vibration signal

Introduction

Cooperative activities in social insect colonies often are regulated by collective decisions that arise through decentralized systems of control (Gordon 1996; Beshers et al. 1999; Camazine et al. 2001). These decision-making processes frequently involve complex systems of communication that synchronize and integrate the behavior of different worker groups. A central objective in the study of insect sociality, therefore, is to understand the different communication signals that organize colony labor and how they interact to formulate and adjust group-level decisions.

One of the best studied examples of collective decision making is the house-hunting process of honey bee (*Apis mellifera*) swarms, which is controlled by at least four different communication signals: waggle dances, worker piping, buzz running, and vibration signals. Waggle dances are performed by scout bees on the surface of swarm clusters and communicate the location of potential nest cavities. Initially a variety of sites are communicated, but typically all waggle dance activity becomes focused on one location, which represents the new site to which the swarm will relocate (Lindauer 1955; Seeley and Buhrman 1999; Visscher and Camazine 1999; Visscher 2003). Once large numbers of recruits are visiting one particular nest site, which usually coincides with the onset of consensus among waggle dancers, some scouts begin producing a sound called “wings-together worker piping” (henceforth referred to as piping) on the swarm cluster (Seeley and Visscher 2003). Piping consists of a series of pulsed vibrations, each of which has a frequency of 100–250 Hz and lasts for approximately 1 s (Seeley and Tautz 2001). Piping is performed at an increasing rate throughout the final hour or so in which the swarm is preparing for departure, and may cause recipients to warm their thoracic muscles to a flight-ready temperature (Seeley and Tautz 2001). Shortly before departure, some bees begin to perform buzz running, which consists of a worker running over the swarm in a zigzag pattern while buzzing its wings every second or so (Lindauer 1955;

Communicated by R. Page

K. Donahoe · L. A. Lewis · S. S. Schneider (✉)
Department of Biology,
University of North Carolina,
Charlotte, NC 28223, USA
e-mail: sschnedr@email.unc.edu
Tel.: +1-704-6874053
Fax: +1-704-6873128

Esch 1967). Buzz running has been suggested to trigger the final break up of the cluster for liftoff (Lindauer 1955; Martin 1963), although its role in swarming is unclear (Camazine et al. 1999).

House hunting also involves the vibration signal, which consists of a worker rapidly vibrating her body dorso-ventrally for 1–2 s, usually while grasping a recipient with her legs (Schneider and Lewis 2003). Vibration signals are performed throughout the swarming process and may operate in a non-specific, modulatory manner to regulate two main aspects of house hunting (Visscher et al. 1999; Lewis and Schneider 2000, 2001). First, signals performed early in the process may promote scouting and recruitment for nest sites. Some workers that produce vibration signals also perform waggle dances, and recipients of the signal have an increased likelihood of contacting nest-site dancers (Schneider et al. 1998; Visscher et al. 1999; Lewis and Schneider 2000). Second, after consensus has been achieved among waggle dancers, vibration signals may help to prepare the entire swarm for liftoff and movement to the new location. During the liftoff-preparation period, numerous workers perform long series of vibration signals while weaving repeatedly into and out of the cluster. Recipients exhibit heightened locomotion and an increased tendency to fly, so that as liftoff approaches the entire swarm appears to be in motion and this movement culminates in mass flight (Lewis and Schneider 2000). The vibration signal may therefore work in conjunction with waggle dances and worker piping to coordinate several aspects of house hunting, and offers an opportunity to examine how different communication signals interact during collective decision making. However, the precise role of the vibration signal during swarming is unclear (Schneider et al. 1998; Lewis and Schneider 2000; Schneider and Lewis 2003).

We removed vibrating bees from swarm clusters to test two hypotheses for the function of the signal during house hunting. First, if the signal promotes scouting and recruitment, then the removal of vibrators should decrease waggle dance activity and alter the time required to reach consensus for a nest site. Second, if the signal promotes the preparation for mass flight and colony movement, then the removal of vibrating bees should delay swarm liftoff once consensus has been achieved or alter relocation behavior once a swarm becomes airborne.

Methods

Study site and swarm setup

House hunting was investigated from April to June 2002 on the campus of the University of North Carolina at Charlotte. We created artificial swarms from commercially packaged bees, using methods adapted from Lindauer (1955) and Morse and Boch (1971). Each queen was placed in a small cage that was then suspended inside a large, nylon-mesh swarm cage (approximately 60×65×50 cm). The workers were then shaken from the package into the swarm cage and quickly clustered about the queen. We fed the caged bees 50% sucrose solution ad libitum for the next 4–

5 days, after which time copious wax scales had accumulated on the floors of the cages below the clusters. These conditions simulate the preparations associated with natural swarming (Seeley and Buhrman 1999). Artificial swarms behave identically to natural swarms and are frequently used to study house-hunting behavior (Schneider 1995; Schneider et al. 1998; Camazine et al. 1999; Seeley and Buhrman 1999; Lewis and Schneider 2000; Seeley and Tautz 2001)

We estimated the number of bees in each cluster by determining the weight of the swarm cage plus the bees, subtracting the weight of the empty cage, and then dividing by the mean weight of 40 individually weighed workers. All weights were determined immediately after the bees had been introduced into the swarm cages and before we administered sugar solution.

After the clusters had been in the swarm cages for 4–5 days, each was transferred to an observation stand. The caged queen was affixed to a stand and the workers were shaken onto the ground at the base of the stand, whereupon they quickly clustered about the queen. A swarm stand consisted of a 1.5-m pole embedded in a container of cement with two crossed wooden slats at the top to provide a surface for attaching the queen cage and to facilitate cluster formation. Each stand was equipped with a feeder that dispensed 50% sucrose solution ad libitum, to minimize foraging and ensure that waggle dances were performed for nest sites rather than food sources (see also Schneider 1995; Camazine et al. 1999; Seeley and Buhrman 1999; Lewis and Schneider 2000). During each trial of the experiment, we established three swarms simultaneously (see below). The three observation stands were located 30–35 m apart and positioned behind trees or tall shrubs to minimize the drifting of workers among swarms. Swarms were assigned randomly to a stand during each trial to control for possible position effects.

Swarms were established on the observation stands at sunset of the day before the beginning of a trial. Waggle dances for nest sites typically began late the following morning. Once house hunting was underway, we released each caged queen so that she was free to move about normally within the cluster and depart with the swarm.

The swarms chose among nest cavities occurring in buildings and woods surrounding the study site. Additionally, we established ten 20-l pasteboard swarm traps (equipped with pheromone lures) within a 1-km radius around the study site. Such traps are regularly used to attract and capture honey bee swarms (Schmidt et al. 1989; Schmidt and Thoenes 1990) and thus ensured an ample supply of suitable nest sites during our study. Each trap was tied securely in the fork of a tree 2–2.5 m above ground and was well shaded. If a trap became occupied, we transferred the colony and any combs that had been constructed into a 45-l hive box and then remounted the swarm trap in a new location in the study area.

Removing vibrating bees and monitoring house-hunting behavior

Swarms were monitored continuously by 5–6 observers from 0700 to 1900 hours each day until departure for a new nest site. In each experimental trial, we compared house-hunting activity among three swarms: a test swarm, a manipulated control (MC) swarm, and an unmanipulated control (UC) swarm. From the test swarm, we removed every vibrating bee observed throughout the house-hunting process. In addition, we paint marked each waggle dancer observed. We recorded each time we removed a vibrating bee that had been previously paint marked as a waggle dancer. The removed vibrating bees were held in small wire-screen cages (40×15×22 cm) supplied with 50% sucrose solution ad libitum and were released when the test swarm achieved liftoff.

The removal of vibrators may have affected more than vibration signal activity on our swarms, because vibrating bees can perform other communication signals associated with house hunting. For example, approximately 20% of bees that produce vibration signals on swarms also perform waggle dances for nest sites (Lewis and Schneider 2000). Therefore, in addition to the vibrating bees that had been paint marked as waggle dancers (the vibrators that were *known* nest-site dancers), we assumed that one-fifth of the vibrators

removed from a test swarm were *potential* dancers for nest sites, even if they had not been marked as waggle dancers before they were observed to vibrate.

We used our MC swarms to control for the effects that the removal of bees had on house-hunting behavior. For each MC swarm, we marked every vibrating bee and waggle dancer observed with distinguishing colors of paint throughout the house-hunting process. We removed one worker from the MC swarm for each vibrating bee removed from the test swarm, as follows. For every four vibrating bees removed from the test swarm, we removed from the MC swarm four randomly selected workers that had not been marked as vibrators or waggle dancers. For every fifth vibrator removed from the test swarm, we removed a paint-marked waggle dancer from the MC swarm. The only exception to this procedure occurred during the first 1–2 h of house hunting, when occasionally there was an insufficient number of waggle dancers on an MC swarm to allow for removal without disrupting or abolishing nest-site recruitment. During these brief periods, for every fifth vibrator removed from the test swarm we removed from the MC swarm one bee that was following or in the immediate vicinity of a waggle dancer. Such bees were considered to be potential nest-site dancers, because they were in the “dance area” of the swarm and could be recruited to nest sites and subsequently perform waggle dances. Finally, for every vibrating bee removed from the test swarm that had been paint-marked as a waggle dancer, we removed one known waggle dancer from the MC swarms. In this manner, by the time the test or MC swarm achieved liftoff, we had removed from each the same total number of workers and an equivalent number of waggle dancers.

We removed no bees from the UC swarm, but marked each vibrator and waggle dancer observed with distinguishing colors of paint. Comparisons between UC and MC swarms allowed us to assess the effects of the removal of bees per se and the removal of a proportion of waggle dancers, and thus to more accurately assess the impact that the removal of vibrating bees had on house-hunting behavior.

We recorded each time a paint-marked vibrator was observed on our test swarms. Because vibrators were marked only on the MC and UC swarms, their appearance on the test swarms could be used as an estimate of drifting among the three swarm types.

We conducted six trials, involving a total of 18 swarms. For each swarm, we used data sheets (organized in hourly blocks) to keep running tallies of the total number of vibrators and waggle dancers marked or removed. At the end of each trial, we determined for each swarm the proportion of workers that performed waggle dances, the proportion that produced vibration signals, and the proportion of vibrating bees that waggle danced for nest sites.

We assessed the following four aspects for each swarm. First, we determined the time required to reach consensus among nest-site dancers. This was defined as the number of hours elapsing between the beginning of a trial and the first observation in which the waggle runs of all dancers were estimated to have the same duration and orientation. It was usually obvious when waggle-run durations of different dancers were the same, although we used digital timers when necessary to compare dance times. Because a swarm often provides a curved dance surface, our estimates of waggle-run orientations were relatively coarse-grained. We may therefore have occasionally classified dancers as indicating the same site, when in reality they were communicating two separate, adjacent sites at similar distances from the swarm. However, achieving consensus among all dancers may not be necessary to initiate liftoff preparations (Seeley and Visscher 2003). Furthermore, in all cases our estimates of consensus were invariably followed by a liftoff attempt. Thus, our methods reliably predicted the beginning of liftoff preparations.

Second, we determined the duration of the liftoff-preparation period. This was defined as the number of minutes elapsing between the first estimate of consensus among waggle dancers and when the swarm became airborne.

Third, we determined whether each swarm maintained continuous, high levels of worker piping during liftoff preparations, defined as the production of ten or more pipes during consecutive

15-s intervals. This amount of piping is consistent with the level that typically occurs during the liftoff-preparation period (Seeley and Visscher 2003). Piping is easily heard (Seeley and Tautz 2001) and can be detected by the unaided ear 4–6 cm from a swarm. Once consensus waggle dancing was estimated to have begun, we conducted one to two 15-s counts of piping every 2–3 min throughout the period of liftoff preparations.

Fourth, we assessed the ability of swarms to move to the chosen nest site after liftoff had occurred. Each swarm was categorized as having disappeared from view within 5 min of becoming airborne, or hovering above the study site for longer than 5 min once liftoff had occurred.

Statistical analysis

We used two-way analyses of variance without replication (Sokal and Rohlf 1995) to compare among the three swarm types and the six trials: swarm size, number of bees that performed vibration signals, number of bees that performed waggle dances, time required to reach consensus, and the duration of the liftoff-preparation period. To adjust for differences in swarm size and the time required to complete house hunting, we expressed the number of bees that performed vibration signals and waggle dances as a proportion of total swarm size per hour of observation. Data were log-transformed when necessary to achieve normality. If the two-way ANOVAs revealed significant differences among the three swarm types, we then performed non-orthogonal, single degree-of-freedom planned comparisons between the test swarms, manipulated controls and unmanipulated controls (Sokal and Rohlf 1995). We used log-likelihood ratio tests (Sokal and Rohlf 1995) to compare the number of swarms of each type that achieved consensus among waggle dancers, maintained continuous piping during the liftoff-preparation periods, and moved out of the study area within 5 min of becoming airborne. We applied the sequential Bonferroni procedure to evaluate significance levels for all statistical tests (Rice 1989). Means are expressed as ± 1 SE.

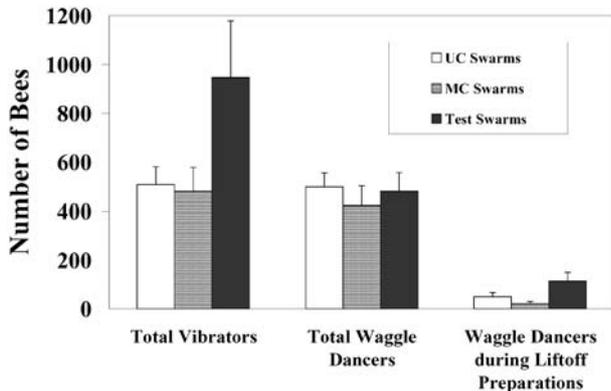
Results

One of the UC swarms lost its queen during the house-hunting process and was eliminated from the study. As a result, we monitored a total of six test swarms, six MC swarms and five UC swarms. The mean number of bees in each cluster (Table 1) did not differ by swarm type ($F_{2,16}=0.42$; $P>0.05$) or trial ($F_{5,16}=1.01$; $P>0.05$). We observed only 3.2 ± 1.3 paint-marked vibrators on each of the test swarms, suggesting that there was little drifting of workers among the different swarms within trials.

On average, we removed 946 ± 232 vibrating bees from each test swarm and the same total number of workers from the MC swarms. We had assumed that 20% of the vibrators removed from the test swarms would be potential nest-site dancers and removed a corresponding number of waggle dancers from each MC swarm (see Methods). However, in the MC and UC swarms only 10% of the paint-marked vibrating bees were observed to perform waggle dances during the house-hunting process (Table 1). Likewise, 10% of the vibrating bees removed from the test swarms had been marked as waggle dancers before they were observed to perform vibration signals (Table 1), although we do not know how many would have performed waggle dances if they had remained on the test swarms. Taken together, these observations

Table 1 The total number of honey bees (*Apis mellifera*), the proportions of workers that performed vibration signals and waggle dances, and the proportion of vibrating bees that produced waggle dances in each of the swarm types

Swarm type	Number of bees	Vibrating bees (% of swarm)	Waggle dancers (% of swarm)	Vibrating bees also marked as waggle dancers (% of vibrating bees)
Test ($n=6$)	13,686.3 \pm 2,159.4	8.0 \pm 2.6	3.8 \pm 0.8	9.8 \pm 1.6
Manipulated control ($n=6$)	11,892.5 \pm 781.6	4.0 \pm 0.7	3.5 \pm 0.6	10.7 \pm 3.1
Unmanipulated control ($n=5$)	11,186.4 \pm 779.5	4.6 \pm 0.8	4.4 \pm 0.4	9.7 \pm 2.3

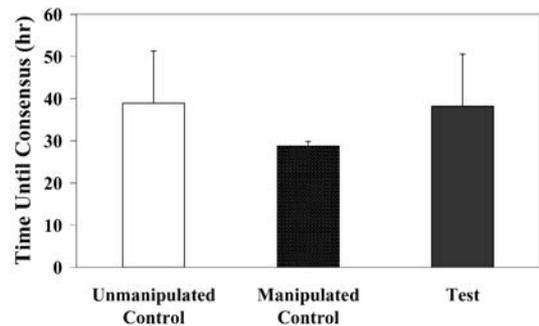
**Fig. 1** Mean \pm SE total number of vibrators, waggle dancers, and waggle dancers during the liftoff-preparation periods that were observed for the unmanipulated control (UC) swarms, manipulated control (MC) swarms, and the test (Test) swarms of the honey bee (*Apis mellifera*). For statistical analyses, we adjusted for differences in swarm size and observation times so that values were expressed as the rate at which bees performing the different signals were observed on the swarms

suggest that we may have removed more nest-site dancers than necessary from the MC swarms to control for the effects of our manipulations on waggle-dance activity.

All swarms reached consensus in waggle dancing, maintained high, continuous levels of piping throughout the liftoff-preparation periods, and eventually achieved liftoff and movement to the chosen nest site. Our manipulations, therefore, did not ultimately prevent the selection of a nest site and colony relocation. The removal of vibrating bees, however, did affect several aspects of the house-hunting process.

Vibrator removal and number of vibrating bees

There was a significant difference among the three swarm types in the number of vibrating bees observed ($F_{2,16}=6.63$; $P=0.0170$; Fig. 1). When adjusted for differences in swarm size and observation duration, the number of vibrating bees removed from the test swarms was on average 1.75 times greater than the number marked on the MC swarms ($F_1=9.56$; $P=0.0129$; Fig. 1). Indeed, workers producing vibration signals accounted for 8% of the test swarms, but only about 4–5% of the control swarms (Table 1) and the MC and UC swarms did not differ in the

**Fig. 2** Mean \pm SE number of hours required to achieve consensus among nest-site dancers for the three swarm types

number of vibrators marked ($F_1=0.07$; $P=0.8026$; Fig. 1). Because we adjusted our values for differences in observation duration, the greater number of vibrating bees did not occur simply because the test swarms remained on the observation stands for longer periods of time. Rather, the rate at which new bees began to perform vibration signals was higher on the test swarms compared to the MC and UC swarms.

Vibrator removal and waggle dance activity

The removal of vibrating bees did not influence the aspects of waggle dance behavior that we examined. Marked waggle dancers comprised 3–4% of all swarms (Table 1) and the three swarm types did not differ in the total number of dancers observed when adjusted for swarm size and observation duration ($F_{2,16}=0.50$; $P=0.6221$; Fig. 1). The three swarm types also did not differ in the time required to reach consensus ($F_{2,16}=0.43$; $P=0.6615$; Fig. 2). These patterns were consistent among trials (for all comparisons: $F_{5,16}<2.62$; $P>0.10$). The fact that the MC and UC swarms did not differ in waggle dance activity suggested that nest-site selection was not affected by the removal of workers per se or the removal of a proportion of waggle dancers.

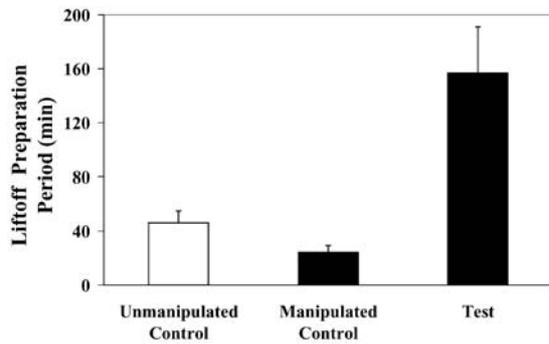


Fig. 3 Mean \pm SE duration of the liftoff-preparation periods for the three swarm types

Vibrator removal, swarm liftoff preparations and movement

The removal of vibrating bees had three effects on swarm liftoff activity. First, it increased the time required to prepare for liftoff. There was a significant difference in the duration of the liftoff-preparation periods among the three swarm types ($F_{2,16}=12.37$; $P=0.0026$; Fig. 3). This difference arose because the liftoff-preparation periods for the test swarms were on average 7.5 times greater than those observed for the MC swarms ($F_1=24.10$; $P=0.0008$; Fig. 3), and this pattern was consistent among trials ($F_{5,16}=0.73$; $P=0.6164$). In comparison, the liftoff-preparation periods for the MC and UC swarms did not differ ($F_1=2.50$; $P=0.1481$; Fig. 3).

The test swarms maintained levels of waggle dancing and piping activity during the liftoff-preparation periods that did not differ from those observed for the MC and UC swarms. All swarms had 15–20 waggle dancers simultaneously indicating one site throughout the liftoff-preparation periods, and the three swarm types did not differ in the rate at which new waggle dancers for the selected site were marked during these periods ($F_{2,12}=0.23$; $P=0.8036$; Fig. 1). Similarly, all swarms exhibited continuous piping activity and each eventually produced 25 or more pipes per 15 s count. Most importantly, the test swarms maintained these high levels of consensus dancing and piping throughout the 1.5–3 h that comprised their liftoff-preparation periods. The longer liftoff-preparation periods for the test swarms therefore did not result from the inability to generate and maintain the elevated levels of waggle dancing and piping typically associated with liftoff behavior.

Second, in addition to extending the liftoff-preparation period, the removal of vibrators could cause the termination of liftoff attempts. In three of our trials, the test swarms clearly showed a prolonged period of liftoff preparations, in which they exhibited high levels of consensus waggle dancing and continuous worker piping for several hours, throughout which time we continued to remove vibrating bees. In each of the three swarms, waggle dancing for the chosen site and worker piping eventually declined and the liftoff preparations were

aborted. In contrast, we never observed an aborted liftoff attempt in the six MC swarms, despite the removal of the same total number of bees and similar proportions of nest-site dancers ($G_1=5.178$; $P=0.0229$).

One of the aborted liftoff attempts occurred at 1745 hours, following a 3-h period of consensus dancing and continuous piping, at the end of which a storm blew in. This aborted attempt may have been influenced by deteriorating weather conditions. However, the other two aborted liftoff attempts occurred at 1300 and 1645 hours, respectively, on sunny, warm days. In comparison, 54% of the liftoffs by the two types of control swarms occurred during these hours and 40% of liftoffs by the UC occurred after 1820 hours. The aborted liftoff attempts by the test swarms therefore did not occur solely because our manipulations prolonged liftoff-preparations until it was too late in the day to complete the house-hunting process. Rather, the removal of vibrating bees specifically may have caused the termination of liftoff attempts. The three test swarms that aborted liftoff attempts reestablished consensus dancing and worker piping the following morning and eventually reached liftoff, even though we continued to remove vibrators. Thus, while the removal of vibrating bees could delay and sometimes terminate liftoff, it could not permanently prevent it.

A third effect that the removal of vibrators had on liftoff activity was that in some instances it may have interfered with a swarm's ability to relocate to the new nest site once liftoff had been achieved. In two of our trials, the test swarms reached liftoff after a prolonged period of consensus dancing and piping, but appeared to be unable to move en masse to the selected site. One swarm hovered above the study site for approximately 20 min before settling in a nearby tree. The second began moving in the direction indicated by its nest-site dancers, but progression was halting and we could easily keep pace with the swarm while walking slowly. After approximately 15 min, the swarm returned to the observation stand and re-clustered. In both cases, the queen departed with the swarm and as far as we could determine remained airborne throughout the attempts to relocate. Furthermore, all MC and UC swarms had disappeared from view in less than 5 min of achieving liftoff and their queens had been treated in a manner identical to the test swarm queens. We did not continue to remove vibrators from the two test swarms once they had re-clustered, because all manipulations were terminated once mass liftoff began. After re-clustering, both test swarms reinitiated house hunting and we observed numerous vibrating bees and waggle dancers, yet each swarm required 12–24 h before it lifted off again and moved to the chosen site. The difference in the number of test versus MC swarms that exhibited altered relocation behavior approached significance ($G_1=3.175$; $P=0.0748$). These observations raise the possibility that, in addition to influencing the speed with which liftoff preparations were completed, the removal of vibrating bee may also have affected the ability of some swarms to successfully move to a new nest site.

Discussion

The removal of vibrating bees from our test swarms more than quadrupled the time required to complete liftoff preparations, contributed to aborted liftoff attempts, and may have adversely affected the ability of some swarms to move to the chosen site after they became airborne. These results are consistent with the hypothesis that during house hunting the vibration signal functions to promote liftoff and movement by the entire swarm once a nest site has been selected. However, bees that perform vibration signals can be involved in several other aspects of house hunting (Schneider et al. 1998; Visscher et al. 1999; Lewis and Schneider 2000; Seeley and Tautz 2001). This raises the possibility that the changes in the behavior of our test swarms may have occurred, not because of altered vibration signal activity per se, but rather because the removal of vibrating bees affected other activities necessary for liftoff and movement. Thus, at least four alternate explanations must be considered to fully evaluate our results.

First, because some vibrating bees perform waggle dances on swarms (Schneider et al. 1998; Visscher et al. 1999; Lewis and Schneider 2000), their removal may have interfered with the ability to complete the process of selecting a nest site. This, in turn, may have prolonged liftoff preparations and caused some liftoff attempts to be aborted. However, this explanation seems unlikely. Our swarms did not differ in the overall levels of waggle dance activity, the time required to reach consensus for a nest site, or the rate at which new dancers for the chosen site were marked during the liftoff-preparation periods, regardless of whether we removed vibrators, waggle dancers, randomly selected workers, or no bees. Indeed, the test swarms maintained for several hours the same high levels of consensus dancing observed for the MC and UC swarms, despite the continued removal of vibrators throughout these periods. Furthermore, we removed as many (and possibly more) nest-site dancers from the MC swarms as from the test swarms. Yet, we never observed an aborted liftoff attempt by the MC swarms and their liftoff-preparation periods did not differ from the UC swarms, from which no bees were removed. These observations suggest that the altered behavior of the test swarms did not result primarily from a compromised ability to maintain the levels of consensus dancing that normally precede liftoff.

Second, if vibrating bees pipe, then their removal may have hindered the ability of the test swarms to generate the level of piping activity necessary to stimulate flight. This could have prolonged liftoff preparations and contributed to the termination of some liftoff attempts. However, we never observed piping by the marked vibrators on our MC and UC swarms. Most pipers are nest-site scouts (Seeley and Visscher 2003) which have a relatively high likelihood of switching between waggle dancing and piping, but a much lower probability of producing vibration signals (Seeley and Tautz 2001). Furthermore, the removal of vibrating bees from our test

swarms had no effect on the level of piping activity detected during the liftoff-preparation periods. All of our swarms maintained high, continuous levels of piping and each eventually produced in excess of 25 pipes/15 s during the liftoff-preparation periods. In particular, the test swarms produced 25 or more pipes/15 s continuously for 1.5–3 h, suggesting that their total cumulative amounts of piping were far greater than those of the MC and UC swarms. Yet, their liftoff-preparation periods were on average 7 times longer. We monitored piping using the unaided ear and may have detected greater piping activity if we had used microphones and recording equipment. However, the levels of piping that we detected were consistent with those previously reported using recording devices (Seeley and Visscher 2003). While we cannot rule out an association between the vibration signal and piping at this time, there is little evidence to suggest that the altered liftoff behavior of the test swarms arose from the inadvertent removal of pipers.

Third, once a swarm becomes airborne, some bees (presumably scouts) lead the colony to the chosen nest site. If these scouts perform vibration signals, then we would have removed them, which could have contributed to the inability of two of our test swarms to relocate successfully after they achieved liftoff. However, scouts may have only limited involvement in vibration signal production. Lewis and Schneider (2000) found that only 4–11% of scouts visiting nest boxes produced vibration signals when returning to the swarms, and that these scouts accounted for only 1–4% of the total vibrators marked throughout the house hunting process. Similarly, Visscher et al (1999) suggested that most vibrators on swarms were not nest-site scouts. Thus, while the association between scouting and the vibration signal is not well understood, the available evidence suggests that the removal of vibrating bees probably had little effect on the number of scouts available to lead the test swarms after liftoff. On the other hand, if the small number of scouts that vibrate are the bees that lead swarms, then this would further underscore the importance of vibrating bees (and by inference vibration signals) in swarm liftoff and movement.

A fourth possible explanation for our results is that the removal of vibrating bees reduced the number of workers that perform buzz running, which could have prevented the final break up of the clusters and delayed departure. However, the importance of buzz running in initiating swarm liftoff is unclear (Camazine et al. 1999). Furthermore, buzz running may be produced primarily by scouts (Seeley and Tautz 2001), and vibrating bees have never been reported to perform this signal (Lewis and Schneider 2000).

Collectively, these observations suggest that, while our manipulations undoubtedly resulted in the removal of some nest-site dancers, pipers, scouts and perhaps buzz runners from the test swarms, these effects alone were not sufficient to account for the observed changes in liftoff behavior. Our results must be interpreted cautiously, however, because we could not control precisely for all

the effects that our manipulations may have had on house hunting. Nevertheless, a more parsimonious explanation for our observations is that the removal of vibrating bees altered liftoff preparations and swarm movement through a direct effect on vibration signal activity.

While removing vibrating bees delayed liftoff, all test swarms ultimately completed the house-hunting process. However, this occurred only after prolonged periods of consensus dancing and piping, throughout which time we continued to remove vibrators. Perhaps the effects of the limited number of signals produced by vibrators before removal accumulated gradually until some threshold of signaling was finally reached. Also, the sustained, high levels of consensus dancing and piping may have compensated for the reduction in vibrators and eventually stimulated liftoff. Either way, these observations suggest that a primary role for the vibration signal during house hunting is to increase the speed and efficiency with which liftoff occurs, and this could happen in two ways. The signal could facilitate liftoff directly, by eliciting greater movement and flight in recipients (Lewis and Schneider 2000). Additionally, the signal could influence liftoff indirectly, by enhancing responsiveness to nest-site dances, piping, scouts and buzz running. The heightened locomotion caused by vibration signals could increase contact with workers performing other signals, so that the threshold stimulation for liftoff is more quickly reached (Schneider et al. 1998; Lewis and Schneider 2000). The signal could also lower response thresholds to other signals so that less stimulation is required to achieve liftoff (Lewis and Schneider 2000). By operating in a modulatory manner (Schneider 1987; Nieh 1998; Painter-Kurt and Schneider 1998; Schneider and Lewis 2003), the vibration signal may therefore help to coordinate mass flight of a swarm by generating a non-specific increase in activity that helps to integrate the effects of the suite of signals associated with liftoff preparations. Indeed, the removal of vibrating bees may have stimulated signal performance by other workers, resulting in new vibrators being marked at higher rates on the test swarms. The removal of vibrators may therefore have elicited a compensatory action to achieve some necessary level of stimulation for liftoff.

We found no evidence to support the hypothesis that the vibration signal promotes scouting and recruitment for nest sites. The test and control swarms did not differ in the total number of waggle dancers observed, the time required to reach consensus for a specific site, or the rate at which new dancers for the chosen site were marked during the liftoff-preparation periods. The removal of vibrating bees therefore had no observable effect on the aspects of recruitment and nest-site selection that we examined. These results were surprising, because vibration signals are performed throughout the nest-site selection process, nest-site dancers can intermix vibration signals and waggle dances, and vibrated recipients respond with an increased likelihood of contacting waggle dancers and flying from the swarm (Schneider et al. 1998; Visscher et al. 1999; Lewis and Schneider 2000).

Furthermore, we cannot explain fully why the removal of a proportion of waggle dancers from the MC swarms had no influence on house hunting. Perhaps the limited number of nest-site dancers removed from the MC swarms could be easily replaced by other dancers, so that there were no noticeable effects on waggle dance activity. Nevertheless, while the removal of vibrating workers and a portion of nest-site dancers did not influence the aspects of waggle dancing that we monitored, it may have affected the number of nest sites investigated and how scouts distributed themselves throughout the environment. We are currently mapping the sites investigated by scouts from test and MC swarms to examine in more detail the effect that the vibration signal may have on the selection of nest sites during house hunting.

Signals that function similarly to the vibration signal are often associated with group movements in social animals, and have been described for such diverse species as ants (Hölldobler and Wilson 1978; Hölldobler et al. 1996; Maschwitz and Schönegge 1983), wild geese (Darling 1938), swans (Black 1988), wolves (Harrington and Mech 1978), African wild dogs (Estes and Goodard 1967), dolphins (Janik and Slater 1998), sperm whales (Weilgart and Whitehead 1993) and golden lion tamarins (Boinski et al. 1994). These signals sometimes act as “catalysts” (sensu Robson and Traniello 1999), in that they cause a general increase in activity or arousal that helps to coordinate responses to other specific signals and cues that initiate departure and maintain group cohesion during travel. Modulatory communication signals may therefore play central roles in directing information flow and integrating behavior during the collective decisions that organize relocation events in many group living species.

Acknowledgements We thank T.D. Seeley and three anonymous reviewers for helpful comments on the manuscript. We give special thanks to A. Afflerbach, K. Sweeny, P.M. Gross, and V. Williams for their many hours of observation at the swarms. The project was funded by a Faculty Research Grant from the University of North Carolina at Charlotte awarded to S.S. Schneider. The experiments conducted in this study comply with current animal welfare laws of the U.S.A.

References

- Beshers SN, Robinson GE, Mittlethal JE (1999) Response thresholds and division of labor in insect colonies. In: Detrain C, Deneubourg JL, Pasteels JM (eds) Information processing in social insects. Birkhäuser, Berlin, pp 115–139
- Black JM (1988) Preflight signaling in swans: a mechanism for group cohesion and flock formation. *Ethology* 79:143–157
- Boinski S, Moraes E, Kleiman DG, Dietz JM, Baker AJ (1994) Intra-group vocal behaviour in wild golden tamarins, *Leontopithecus rosalia*: honest communication of individual activity. *Behaviour* 130:53–75
- Camazine S, Visscher PK, Finley J, and Vetter RS (1999) House-hunting by honey bee swarms: collective decisions and individual behaviors. *Insectes Soc* 46:348–360

- Camazine S, Deneubourg J-L, Franks NR, Sneyd J, Theraulaz G, Bonabeau E (eds) (2001) Self-organization in biological systems. Princeton University Press, Princeton, N.J.
- Darling FF (1938) Bird flocks and the breeding cycle. Cambridge University Press, Cambridge, Mass.
- Esch H (1967) The sounds produced by swarming honey bees. *Z Vergl Physiol* 56:408–411
- Estes RD, Goodard J (1967) Prey selection and hunting behavior of the African wild dog. *J Wildl Manage* 31:52–70
- Gordon DM (1996) The organization of work in social insect colonies. *Nature* 380:121–124
- Harrington FH, Mech LD (1978) Howling at two Minnesota wolf pack summer homesites. *Can J Zool* 56:2024–2028
- Hölldobler B, Wilson EO (1978) The multiple recruitment systems of the African weaver ant *Oecophylla longinoda* (Latreille) (Hymenoptera: Formicidae). *Behav Ecol Sociobiol* 3:19–60
- Hölldobler B, Janssen E, Bestmann HJ, Leal IR, Oliveira PS, Kern F, König WA (1996) Communication in the migratory termite-hunting ant *Pachycondyla* (= *Termitopone*) *marginata* (Formicidae, Ponerinae). *J Comp Physiol A* 178:47–53
- Janik VM, Slater PJB (1998) Context-specific use suggests that bottlenose dolphin signature whistles are cohesion calls. *Anim Behav* 56:829–838
- 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
- Lewis LA, Schneider SS (2001) Factors influencing the selection of recipients by workers performing vibration signals in colonies of the honeybee, *Apis mellifera*. *Anim Behav* 63:361–367
- Lindauer M (1955) Schwarmbienen auf Wohnungssuche. *Z Vergl Physiol* 37:263–324
- Martin P (1963) Die Steuerung der Volksteilung beim Schwärmen der Bienen. Zugleich ein Beitrag zum Problem der Wanderschwärme. *Insectes Soc* 10:13–42
- Maschwitz U, Schönege P (1983) Forage communication, nest moving recruitment, and prey specialization in the oriental ponerine *Leptogenys chinensis*. *Oecologia* 57:175–182
- Morse RA, Boch R (1971) Pheromone concert in swarming honey bees (Hymenoptera: Apidae). *Ann Entomol Soc Am* 64:1414–1417
- Nieh JC (1998) The honey bee shaking signal: function and design of a modulatory communication signal. *Behav Ecol Sociobiol* 42:23–36
- Painter-Kurt S, Schneider SS (1998) Age and behavior of honey bees, *Apis mellifera* (Hymenoptera: Apidae), that perform vibration signals on workers. *Ethology* 104:457–473
- Rice WR (1989) Analyzing tables of statistical tests. *Evolution* 43:223–225
- Robson SK, Traniello JFA (1999) Key individuals and the organization of labor in ants. In: Detrain C, Deneubourg JL, Pasteels JM (eds) Information processing in social insects. Birkhäuser, Berlin, pp 239–259
- Schmidt JO, Thoenes SC (1990) The efficiency of swarm traps: what percent of swarms are captured and at what distance from the hive. *Am Bee J* 130:811–812
- Schmidt JO, Thoenes SC, Hurley R (1989) Swarm traps. *Am Bee J* 129:468–471
- Schneider SS (1987) The modulation of worker activity by the vibration dance of the honey bee, *Apis mellifera*. *Ethology* 74:211–218
- Schneider SS (1995) Swarm movement patterns inferred from waggle dance activity of the neotropical African honey bee in Costa Rica. *Apidologie* 26:395–406
- Schneider SS, Lewis LA (2003) Honey bee communication: the “tremble dance”, the “vibration signal” and the “migration dance.” In: Webster T (ed) Monographs in honey bee biology. Northern Bee Books, Hebden Bridge, West Yorkshire, UK (in press)
- Schneider SS, Visscher PK, Camazine S (1998) Vibration signal behavior of waggle-dancers in swarms of the honey bee, *Apis mellifera* (Hymenoptera: Apidae). *Ethology* 104:963–972
- Seeley TD, Buhrman SC (1999) Group decision making in swarms of honey bees. *Behav Ecol Sociobiol* 45:19–31
- Seeley TD, Tautz J (2001) Worker piping in honey bee swarms and its role in preparing for liftoff. *J Comp Physiol A* 187:667–676
- Seeley TD, Visscher PK (2003) Choosing a home: how the scouts in a honey bee swarm perceive the completion of their group decision making. *Behav Ecol Sociobiol* (in press)
- Sokal RR, Rohlf FJ (1995) Biometry. Freeman, New York
- Visscher PK. (2003) How self-organization evolves. *Nature* 421:799–800
- Visscher PK, Camazine S (1999) Collective decisions and cognition in bees. *Nature* 397:400
- 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
- Weilgart L, Whitehead H (1993) Coda communication by sperm whales (*Physeter macrocephalus*) off the Galápagos Islands. *Can J Zool* 71:744–752