The Use of the Vibration Signal and Worker Piping to Influence Queen Behavior during Swarming in Honey Bees, *Apis mellifera*

Andrew L. Pierce, Lee A. Lewis & Stanley S. Schneider

Department of Biology, University of North Carolina, Charlotte, NC, USA

Abstract

We investigated worker regulation of queen activity during reproductive swarming by examining the rates at which workers performed vibration signals and piping on queens during the different stages of the swarming process. Worker–queen interactions were first examined inside observation hives during the 2–3 wk that preceded the issue of the swarm (pre-swarming period) and then inside the swarm clusters during the period that preceded liftoff and relocation to a new nest site (post-swarming period). Queen court size did not differ between the pre- and post-swarming periods, but workers fed the queens less inside the swarm clusters. Workers performed vibration signals on the queens at increasing rates throughout the pre-swarming period inside the natal nest, but rarely or never vibrated the queen inside the swarm. Piping was performed on the queens during both the pre- and post-swarming periods and always reached a peak immediately before queen flight. During the final 2–4 h before swarm liftoff, queens were increasingly contacted by waggle dancers for nest sites, some of which piped the queen. The vibration signal may operate in a modulatory manner to gradually prepare the queen for flight from the natal nest, and the cumulative effects of the signal during the pre-swarming period may make further vibrations on the queen unnecessary when inside the swarm cluster. In contrast, worker piping may function in a more immediate manner to trigger queen takeoff during both the pre- and post-swarming periods. Workers that vibrate and pipe the queen tend to be older, foraging-age bees. The regulation of queen activity during colony reproduction may therefore be controlled largely by workers that normally have little contact with queens, but help to formulate colony reproductive and movement decisions.

Introduction

Honey bee colonies reproduce through swarming, in which about half the workers and the laying queen leave the natal nest and form a cluster in nearby vegetation. After a new nest cavity has been selected, the entire swarm cluster and the queen must become airborne and move en masse to the chosen site. Failure of the queen to leave the natal nest or relocate to the new nest cavity will result in a failed swarming attempt. Thus, to a large extent, successful colony reproduction in honey bees depends upon the behavior of the queen. A complete understanding of swarming therefore requires knowledge of the mechanisms that workers may use to coordinate queen activity with colony reproductive and movement decisions. Worker–queen interactions in the natal nest preceding swarming have received considerable attention (Allen 1959, 1960; Fletcher 1975; Winston 1987; Schneider 1990, 1991). In contrast,

we know virtually nothing about how workers interact with queens inside swarm clusters.

There are at least two communication signals that workers may use to influence queen activity during the swarming process: the 'vibration signal' and 'wings-together worker piping' (hereafter referred to as worker piping). The vibration signal (sometimes called 'shaking' or the 'shaking signal') consists of a worker rapidly vibrating her body dorso-ventrally for 1–2 s while contacting another bee (Schneider & Lewis 2004). Queens are vibrated only during the 2- to 4-wk period that precedes swarming. Vibration rates increase fairly steadily throughout this pre-swarming period and queens often receive several hundred signals/h during the final days before the swarm leaves the natal nest (Schneider & Lewis 2004). The vibration signal modulates the responsiveness of queens to a variety of stimuli, which may help prepare them for flight from the old nest (Allen 1959; Schneider 1991). However, it is unknown whether workers also perform the signal on queens inside swarm clusters to influence their flight during relocation to a new nest site.

Worker piping consists of a worker pressing her body against the substrate or another bee and activating her wing muscles, which produces a high-pitched sound with a fundamental frequency of approx. 200 Hz (Seeley & Tautz 2001). Piping is performed on workers at high levels in swarm clusters, especially during the final 1–2 h before the cluster becomes airborne and moves to the chosen nest site (Donahoe et al. 2003; Seeley & Visscher 2004; Seeley et al. 2006). Piping causes recipients to warm their flight muscles in preparation for liftoff and is a key component in stimulating the mass flight involved in swarm relocation (Seeley & Tautz 2001). Thus, workers could also potentially use piping to help synchronize the queen's flight activity with colony movements. However, the performance of worker piping on queens has never been investigated.

The purpose of our study was to examine worker–queen interactions during swarming that could enhance the coordination of queen behavior with the different stages of colony reproduction. In particular, we examined the performance of the vibration signal and worker piping on queens during the swarming process. Our basic experimental plan was to compare queen behavior and worker–queen interactions in the natal nest before the departure of the swarm and then inside the swarm cluster before relocation to the new nest cavity. Such pre-swarming/post-swarming

comparisons allowed us to identify mechanisms for the regulation of queen behavior that were common to all stages of colony reproduction, as well as those that were specific for certain aspects of the swarming process.

Materials and Methods

Colony Set Up and Maintenance

Worker–queen interactions were monitored in four-frame, glass-walled observation hives maintained on the campus of the University of North Carolina, Charlotte, NC (see Lewis & Schneider 2000; Lewis et al. 2002 for methods of colony set up). The glass walls of the observation hives were marked off in grids of 4×4 cm squares to facilitate monitoring queen behavior. A total of four observation colonies (colonies A–D) were monitored during the spring of 2006. All were fed 50% sucrose solution ad libitum to facilitate rapid growth and all swarmed naturally within 3–6 wk after transfer into the observation hives.

Monitoring Worker–Queen Interactions inside the Natal Nest: Pre-swarming Period

When a colony became crowded with workers, we began to observe the queen periodically throughout the day. After the first observation of the queen receiving a vibration signal from workers, we began to monitor her behavior for 5-min periods four to eight times each day until she left the colony with the swarm. During each 5-min observation period, we recorded the following for each queen, using digital stopwatches when necessary: (1) the number of workers in her court (based on three separate counts); (2) the number of eggs laid; (3) the total time engaged in trophallaxis with workers (mouth-to-mouth receipt of liquid food); (4) the number of vibration signals received; and (5) the number of times that workers performed piping on the queen (colonies B, C and D; worker piping was not monitored in colony A during the pre-swarming period). During the pre-swarming period, we typically could not hear the actual piping sound produced by workers through the glass walls of the observation hives. Piping was therefore identified by the behavior of a worker actively pressing her body or head against the queen, while pulling her wings tightly over her abdomen and arching the abdomen downward in the posture characteristic of worker piping (Seeley & Tautz 2001). The same behavior pattern was

observed in the swarm clusters where we sometimes could also hear piping on the queen when she was inside the queen cage (see below), which verified that our behavioral criteria accurately indicated the performance of worker piping. Subsequently, we determined for each queen during the pre-swarming period daily means for court size, laying rate (eggs/min), the proportion of observation time spent receiving trophallaxis, and the rates at which she received vibration signals (vibration signals/min) and worker piping (pipings/min).

Monitoring Worker–Queen Interactions inside the Swarm Cluster: Post-swarming Period

After a colony swarmed, the swarm was captured in a $56 \times 56 \times 38$ cm screen-mesh swarm cage. The swarm was then transferred to an observation stand that consisted of two 1.6 m support poles embedded in concrete in a plastic tub. A 46×62 cm sheet of 3 mm-thick plexiglass was attached between the top of the support poles. Mounted to the top center of the plexiglass sheet was an 18×9 cm wire-mesh queen cage, which was 1 cm deep. The front of the queen cage, which faced the interior of the swarm cluster, contained a 14×8 cm sheet of queen excluder through which workers, but not the queen, could pass. The depth of the cage allowed only a single layer of workers, such that the queen was visible at all times. In this manner, workers could enter and exit the cage and interact normally with the queen, and the queen could be monitored continuously through the plexiglass sheet while moving freely within a relatively large area inside the swarm. The remainder of the plexiglass sheet outside the queen cage was covered in hardware cloth, to provide a substrate to which workers could cling to form the swarm cluster.

To transfer a swarm to the observation stand, we first introduced the queen into the queen cage through a small hinged opening on the bottom edge of the cage. The workers were then shaken from the swarm cage onto the ground at the base of the observation stand, whereupon they quickly gathered about the queen and formed a swarm cluster. All swarms were transferred to the observation stand between 1800 and 1900 h on the evening before the beginning of a trial.

The selection of a new nest site can sometimes occur quickly, and the entire house-hunting and relocation process can be completed within 24–48 h. Thus, to obtain a complete record of worker–queen interactions, and to insure that we observed queen behavior during the liftoff-preparation periods, we monitored worker–queen interactions continuously from 0700 to 1800 h (subdivided into 30 min periods) each day that a swarm was present on the observation stand. When necessary, we video-recorded queen behavior using a Sony DCR-VX 2000 video camera (Oradell, NJ, USA) and later transcribed the tapes using a Mitsubishi HS U748 VCR (Irvine, CA, USA) with variable-speed playback capabilities. Throughout the time that a swarm was clustered on the observation stand, we paint marked each worker that was observed to perform waggle dances. Most of the worker piping that occurs on swarms is produced by bees that visit and recruit for nest sites (Seeley & Visscher 2003, 2004). By paint marking nest-site dancers, we were able to assess if these same workers also performed piping on the queen. Swarms were provided with 50% sucrose solution ad libitum through a feeder mounted on the observation stand to insure that all dance activity occurred for nest sites rather than food sources (Seeley & Buhrman 1999; Lewis & Schneider 2000).

Observations on the queen were continued until the swarm lifted off to move to the chosen nest site. During the first liftoff attempt, the queen was kept inside the queen cage, which caused the swarm to return to the observation stand and re-cluster about the queen. Continuous observations (subdivided into 30 min periods) were then resumed until the second liftoff attempt, during which the queen was released and allowed to relocate with the swarm. By forcing the swarm to engage in two liftoff attempts, we were able to assess if worker–queen interactions changed during the second attempt, to provide further insights into their possible role in coordinating queen behavior with colony movement.

During each 30 min observation period, we conducted three to four separate counts of the number of workers in a court around the queen. We also recorded for each queen: (1) the amount of time spent receiving trophallaxis from workers; (2) the number of vibration signals received; (3) the total number of worker pipings received; (4) the number of marked waggle dancers contacting the queen (defined as entering the queen's court and maintaining antennal contact with the queen for at least 5 s); and (5) number of marked waggle dancers that performed piping on the queen. Subsequently, we determined for each queen, during the first and second liftoff periods, daily means for the proportion of time spent in trophallaxis, and the rates at which she was vibrated, piped, and contacted by waggle dancers.

Data Analysis

We used two approaches to analyze the data for worker–queen interactions during swarming. First, for each queen we compared the different aspects of behavior over all observations during the pre-swarming period and the first and second liftoff attempts during the post-swarming period. For queen court size, we used repeated-measures analysis of variance (SAS Institute 1997) that had two within-subjects factors: the three periods of observation and the different days of observation within each period. The data were square-root transformed prior to analysis to achieve normality (Sokal & Rohlf 1995). Degrees of freedom were estimated by the Satterthwaite method (SAS Institute 1997). For the proportion of time receiving trophallaxis, vibration signals received/min, and worker pipings received/min, we often had numerous zero values during a portion of the pre- or post-swarming periods such that the data could not be transformed to achieve normality. We therefore used Kruskal–Wallis tests (SAS Institute 1997) to compare these variables between the pre-swarming period and the first and second post-swarming liftoff attempts for each queen separately.

Second, we examined the number of workers performing vibration signals and piping on the queen and the number of waggle dancers contacting each queen during the final 2–4 h preceding each swarm liftoff attempt. Worker–queen interactions inside the swarm clusters occurred at high levels only during the final hours when swarms were preparing for liftoff (see Results). By including all observations during the post-swarming periods in our initial analyses, we may have masked the marked increases in worker–queen interactions that occurred during these final hours. We therefore examined the liftoff-preparation periods separately to obtain a more precise description of queen behavior associated with departure for the new nest site.

Mean values are reported as ± 1 SE. All statistical tests were two-tailed. The sequential Bonferroni adjustment (Rice 1989) was used to determine significance levels for the multiple comparisons made between the pre-and post-swarming periods.

Results

During the pre-swarming periods, the four queens were monitored inside the observation hives for 13.5 ± 3.1 d before the issue of the swarms. During the post-swarming periods, the queens were monitored inside the swarm clusters for 2.3 ± 0.5 d before the first liftoff attempt, and 1.7 + 0.3 d before the second liftoff attempt.

Comparisons of Pre- and Post-Swarming Periods

The number of workers in the queen's court did not differ between the pre-swarming period and the post-swarming periods that preceded the first and second liftoff attempts ($F_{2,362} = 2.94$; ns; Table 1). Thus, the queens were surrounded by similar numbers of workers throughout the different stages of the swarming process. However, queen behavior and worker–queen interactions differed markedly between the pre- and post-swarming periods.

The queens continued to lay approx. 1 egg/min throughout the pre-swarming periods (Table 1), and three of the queens (B, C, and D) were observed to lay 0.4–1.2 eggs/min during the final 1–3 h before swarm issue. The swarms built no comb while on the observation stands and thus we observed no egg laying inside the swarm clusters. However, two of the queens (C and D) were observed to open their sting chambers and release one to two eggs, which subsequently dropped into the swarms.

All monitored worker–queen interactions declined dramatically when comparing the pre- and post-swarming periods. On average, the queens spent approx. 5% of their time receiving trophallaxis from workers during the pre-swarming periods

Table 1: $\bar{x} \pm$ SE court size, proportion of time receiving food, and laying rate for the queens inside the nest before the issue of the swarm and during the periods inside the swarm cluster preceding the first and second liftoff attempts. No egg laying occurred inside the swarm clusters

	Workers in court	% time receiving trophallaxis	Eggs laid/min
Queen A			
Inside nest	11.0 ± 0.53	6.1 ± 1.70	0.8 ± 0.09
First liftoff	9.1 ± 1.03	0.04 ± 0.03	–
Second liftoff	8.1 ± 0.74	0.25 ± 0.12	–
Queen B			
Inside nest	12.4 ± 0.39	6.7 ± 1.60	0.7 ± 0.07
First liftoff	17.4 ± 0.89	0.07 ± 0.075	–
Second liftoff	12.6 ± 0.63	0.06 ± 0.063	–
Queen C			
Inside nest	12.8 ± 0.28	5.6 ± 1.15	0.9 ± 0.07
First liftoff	14.6 ± 0.42	0.39 ± 0.23	–
Second liftoff	12.0 ± 0.51	0.02 ± 0.019	–
Queen D			
Inside nest	13.8 ± 0.50	1.7 ± 0.71	0.5 ± 0.08
First liftoff	16.3 ± 0.59	0.02 ± 0.023	–
Second liftoff	15.1 ± 0.41	0.05 ± 0.036	–

(Table 1). In contrast, queens received food during only approx. 0.1% of the time they were monitored inside the swarm clusters before the first and second liftoff attempts (Table 1). This difference was significant for queens B and C ($\chi^2_2 > 11.8$ for both comparisons; $p < 0.003$), but not for queens A and D ($\chi^2_2 < 4.0$ for both comparisons; $p > 0.13$).

Workers performed vibration signals on the queens in the observation hives throughout the pre-swarming periods. Although the level of signaling activity could vary considerably within and among colonies, it tended to increase throughout the pre-swarming periods, culminating in 2–6 signals/min during the final 2–3 d before swarm issue (Fig. 1). In contrast, workers rarely or never performed vibration signals on the queens inside the swarm clusters ($\chi^2_2 > 15.5$ for all comparisons; $p < 0.0004$; Figs 1 and 2).

Piping was performed on the queens during all stages of the swarming process. Workers often produced a series of pipes, which consisted of repeatedly pressing the body or head against the queen, each time assuming the characteristic posture of piping. During the pre-swarming periods, piping on the queen began 6–10 d before swarming and then increased fairly steadily, culminating in a pronounced peak of activity on the day of swarm issue (Fig. 1). Indeed, the highest rates of piping were always observed immediately before swarm issue, when the queens received 8–19 pipes/min. Queen D received increased piping activity on day 7 of observation, 2 d before successful swarm issue (Fig. 1). The colony attempted to swarm on day 7 but the queen failed to leave the hive, resulting in the workers returning to the nest. Queen C received increased piping 5 d before swarm issue (Fig. 1).
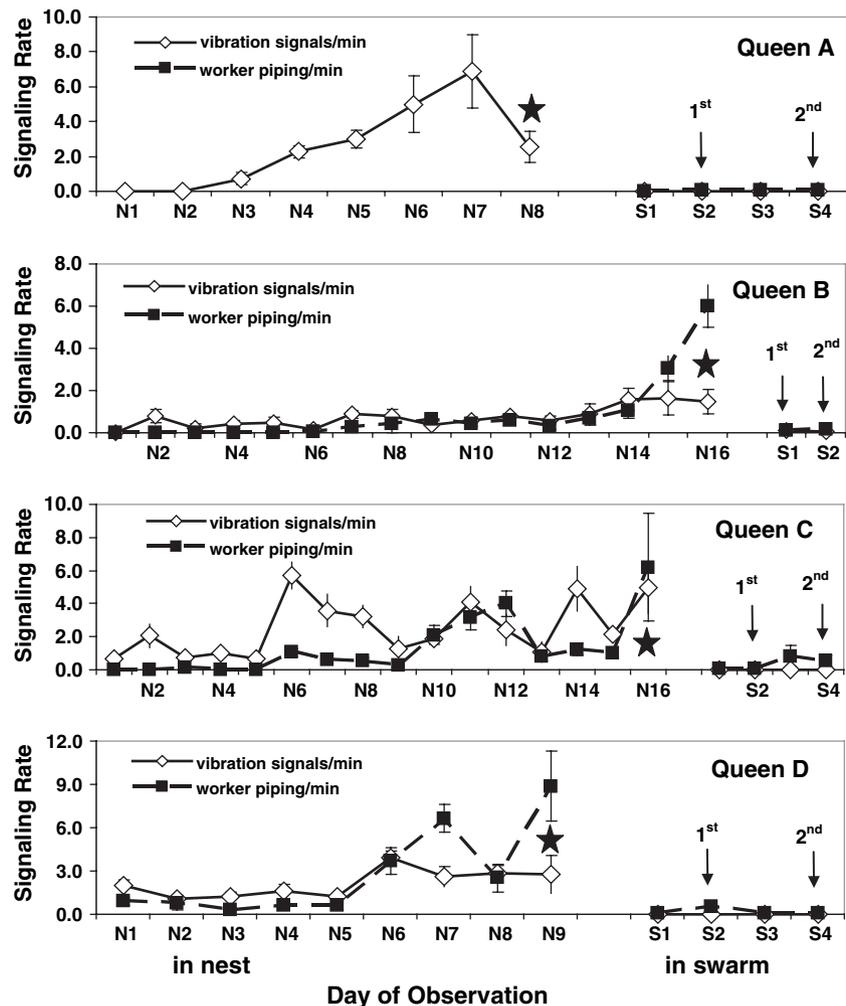
Fig. 1: $\bar{x} \pm$ SE rate at which the queens received vibration signals and worker piping each day during the pre-swarming period while in the nest (N) and during the post-swarming period in the swarm cluster (S). Worker piping was not monitored during the pre-swarming period for queen A. ★ Day of swarm issue from the natal nest; 1st and 2nd indicate the first and second liftoff attempts by each swarm

The colony did not attempt to swarm on this day and we do not know the reason for the increased signaling activity.

Workers also performed piping on the queens inside the swarm clusters (Fig. 1). However, when viewed over all 30-min observation periods preceding the first and second liftoff attempts, the piping rates on queens inside the swarms were typically 5–30 times less than those observed inside the observation hives during the pre-swarming periods ($\chi_2^2 > 9.5$ for all comparisons; p < 0.008; Figs 1 and 2). The low overall piping rates during the post-swarming periods resulted in part because workers began to pipe the queens only during the final 2–4 h before swarm liftoff. To fully assess the role of worker piping on queen behavior during swarm relocation, it was therefore necessary to examine worker–queen interactions during the final hours before liftoff.

Worker–Queen Interactions during Liftoff Preparations

Fig. 3 illustrates the worker–queen interactions that were observed during the final six to nine 30 min
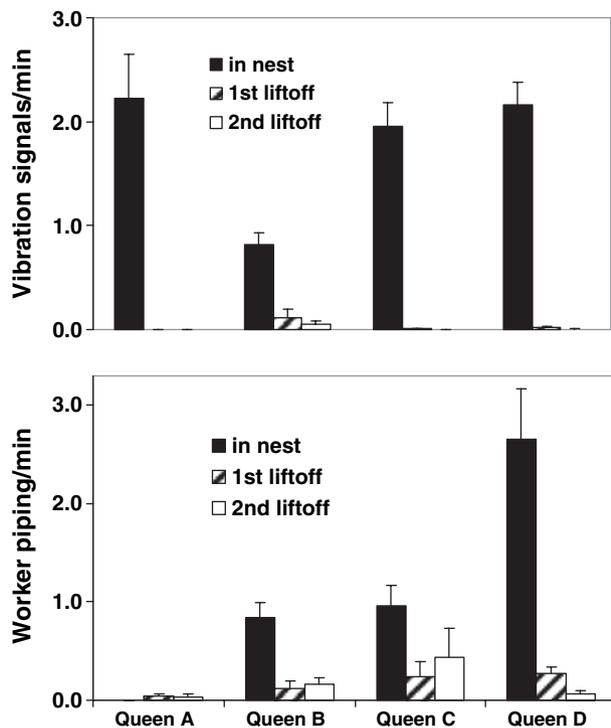
Fig. 2: $\bar{x} \pm$ SE rate at which the queens received vibration signals and worker piping over all observation periods during the pre-swarming period inside the nest and the post-swarming periods preceding the first and second liftoff attempts. Worker piping was not monitored during the pre-swarming period for queen A

observation periods that preceded each liftoff attempt by our four swarms. The graphs reveal four main aspects of worker interactions with the queens during the liftoff-preparation periods.

First, queens received no vibration signals from workers prior to liftoff. Second, workers could perform piping on the queen throughout the final 2–4 h period, and there was always a pronounced increase in piping activity on the queen 30–60 min before the swarm became airborne. Third, as liftoff approached the queens were contacted increasingly by marked waggle dancers for nest sites. These dancers actively forced their way through the queen's court, antennated her for an average of 17.3 ± 1.70 s, then left the court and moved rapidly through the swarm. The number of contacts by marked nest-site dancers increased fairly steadily throughout the final 2–4 h and typically culminated in a peak immediately before liftoff. Fourth, some of the nest-site dancers performed piping on the queen. On average, pipes performed by known waggle dancers accounted for $30.1 \pm 17.03\%$ of the total piping activity on the queens during the liftoff-preparation periods.

Comparisons of First and Second Liftoff Attempts

None of the monitored aspects of queen behavior or worker–queen interactions differed between the periods preceding the first and second liftoff attempts by the swarms (for all comparisons, p > 0.05; Table 1; Figs 2 and 3). Thus, we found no evidence that the failure of a queen to depart with the swarm resulted in altered worker–queen interactions during the re-clustering period preceding the second liftoff attempt.

Discussion

Workers interacted with the queens throughout the swarming process in a manner that may have influenced queen behavior. In particular, workers may have used the vibration signal and piping to help coordinate queen activity with the different stages of colony reproduction. However, the extent to which the two signals were used varied markedly between the pre- and post-swarming periods.

During the pre-swarming periods, the vibration signal was the most frequent and noticeable interaction that workers had with the queens. The queens were vibrated throughout the 2–3 wk that preceded swarming and increased vibration rates were always observed during the final 2–3 d before swarm issue.
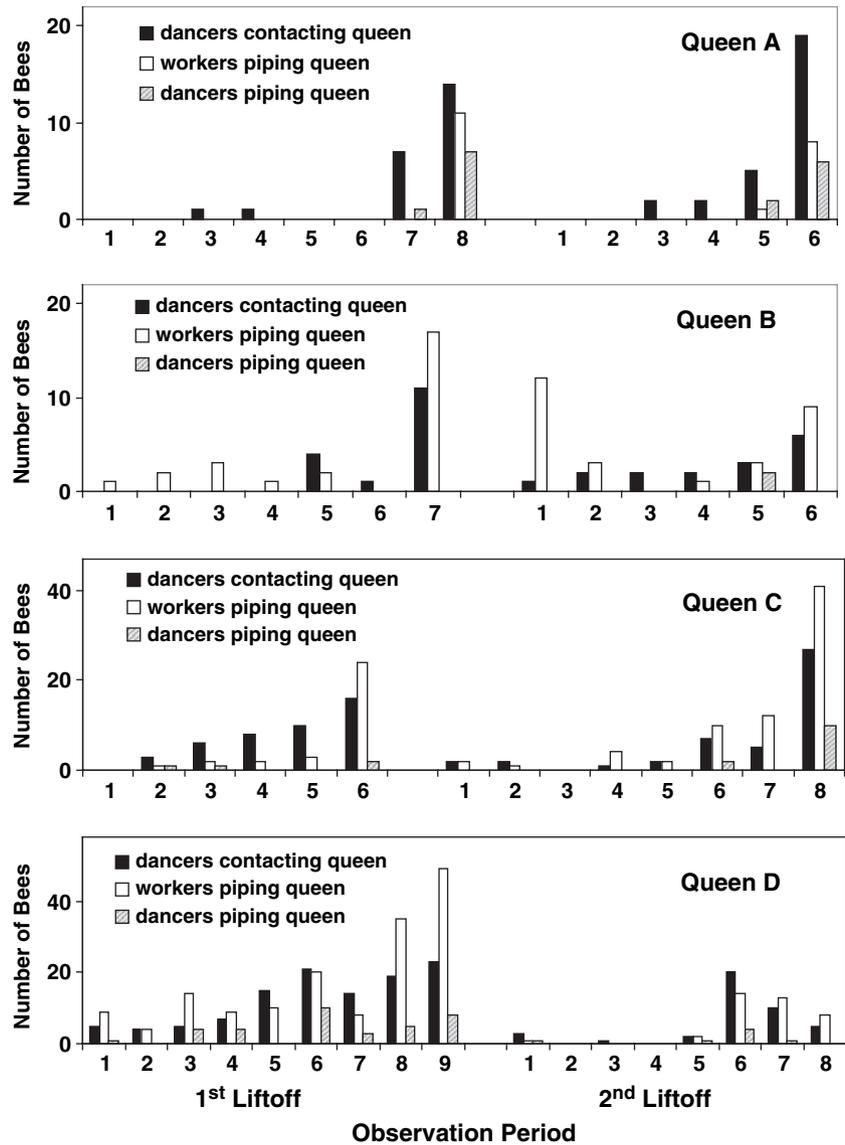
Fig. 3: The number of workers and marked nest-site dancers that contacted and piped the queen during the final 30-min observation periods preceding the first and second liftoff attempts by each swarm

Similar patterns of vibration signal activity on queens have been previously reported (Allen 1959; Fletcher 1975; Schneider 1991). In contrast, workers rarely or never performed vibration signals on the queens inside the swarm clusters during the post-swarming period. This result was surprising, because vibration signals are performed on workers in swarms, especially during the liftoff-preparation period, and may enhance the speed and efficiency with which the entire cluster becomes airborne and moves to the new nest site (Lewis & Schneider 2000; Donahoe et al. 2003). Thus, although the signal may influence worker activity during swarm relocation, its effects on queen behavior are restricted entirely to the pre-swarming period inside the natal nest.

We do not fully understand why queens are vibrated at such markedly different rates in the pre- and post-swarming periods. However, the difference may reflect, in part, the level of preparation needed by a queen to achieve flight during the different stages of colony reproduction. The vibration signal does not stimulate flight directly, but rather modulates responsiveness to a variety of stimuli that may help to gradually prepare queens to leave the nest (Schneider et al. 2004; Schneider & Lewis 2004). Queens respond to the vibration signal primarily with increased locomotion (Schneider 1991). During the pre-swarming period when workers are vibrating the queen, they also feed her less and her laying activity declines (Allen 1960; Schneider 1990, 1991). In combination, the greater movement elicited by the

vibration signal, reduced food intake, and lower egg production result in weight loss that may gradually prepare the queen to take flight and leave the nest with the swarm (Allen 1959; Schneider 1991; Schneider & Lewis 2004). Because a queen in a swarm cluster is already capable of flight, additional vibration signal activity may be unnecessary, especially as her egg laying ceases and workers further reduce her food intake. An association between the vibration signal and preparation for queen flight is also suggested by the observations that virgin queens can be vibrated at high rates before taking mating flights, but workers cease vibrating them after egg laying begins and resume signaling activity only later when the colony prepares for reproductive swarming (Fletcher 1978; Schneider 1991; Schneider & Lewis 2004).

In addition to influencing flight activity, the modulatory effects of the vibration signal may also modify several other aspects of queen behavior during the pre-swarming period. For example, queens respond to the signal, not only with heightened locomotion, but also with increased cell inspection activity and oviposition behavior (Schneider 1991). The signal may therefore help maintain egg laying activity during the pre-swarming period, as well as prepare the queen to attend to stimuli associated with leaving the natal nest. Thus, the vibration signal may help coordinate several aspects of queen behavior with swarming preparations in the natal nest, and the effects of the signal on flight preparations may be sufficient to obviate the need for further vibrating of the queen after swarming has occurred. The vibration signal may also modulate virgin queen behavior during queen replacement in honey bee colonies (Schneider 1991; Schneider et al. 2001). Similarly, workers of the ant, *Pachycondyla marginata*, use vibration-like, modulatory signals to regulate queen behavior during colony emigrations to new nesting locations (Hölldobler et al. 1996).

Our study is the first to report the performance of worker piping on queens, which occurred during all stages of the swarming process. During the pre-swarming period, the queens were piped for several days before swarming, but the greatest piping activity always occurred immediately before a swarm attempt. Workers did not perform piping on the queens throughout most of the post-swarming periods. However, during the final 2–4 h before liftoff, workers piped the queens at increasing rates, culminating in peaks of piping activity immediately before the swarm became airborne. These observations are consistent with the proposed function of worker piping, namely that it causes recipients to warm their flight muscles in preparation for takeoff (Seeley & Tautz 2001). Thus, during both swarm issue and relocation to a new nest site, workers may use piping to synchronize the initiation of queen flight with the mass flight of the colony. However, piping can also occur on queens at high levels several days before swarm departure (Fig. 1), which suggests that the signal may also influence other aspects of queen behavior in addition to flight initiation.

During the pre-swarming period, the vibration signal and piping may work together to prepare a queen to leave the natal nest. The vibration signal may help to gradually prepare the queen physiologically for flight, whereas piping may function primarily to trigger immediate departure with the swarm. Similarly, the vibration signal may interact with piping in swarm clusters to organize the mass liftoff of workers (Donahoe et al. 2003). However, we cannot fully explain why both signals may be necessary for the liftoff of workers when a swarm moves to a new nest site, whereas only piping is used to stimulate the liftoff of queens during swarm relocation.

An unexpected finding in our study was that during the liftoff-preparation periods in swarm clusters, the queens were contacted increasingly by nest-site dancers. Some of the nest-site dancers performed piping on the queens, which is consistent with previous reports that most of the piping on swarms is produced by nest-site scouts and recruits (Seeley & Visscher 2003, 2004). However, the majority of the nest-site dancers simply antennated the queens briefly and then resumed moving rapidly through the clusters. The function of these contacts between dancers and queens is unknown. Dancers for nest sites and bees that perform piping are typically older, foraging-age workers (Gilley 1998). Similarly, most vibration signals performed on queens during the pre-swarming period are produced by foraging-age bees (Painter-Kurt & Schneider 1998). Taken together, these observations suggest that the regulation of queen behavior during the swarming process may be handled largely by older workers that normally have little contact with queens, but which participate in selecting nest sites and preparing the colony for collective movements.

Acknowledgements

Literature Cited

Allen, M. D. 1959: The occurrence and possible signifi-cance of the 'shaking' of honeybee queens by the workers. Anim. Behav. **7**, 66—69.

Allen, M. D. 1960: The honey bee queen and her attend-ants. Anim. Behav. **8**, 201—208.

Donahoe, K., Lewis, L. A. & Schneider, S. S. 2003: The role of the vibration signal in the house-hunting pro-cess of honey bee (*Apis mellifera*) swarms. Behav. Ecol. Sociobiol. **54**, 593—600.

Fletcher, D. J. C. 1975: Significance of dorsoventral abdominal vibration among honey-bees (*Apis mellifera* L.). Nature **256**, 721—723.

Fletcher, D. J. C. 1978: The influence of vibratory dances by worker honeybees on the activity of virgin queens. J. Apic. Res. **17**, 3—13.

Gilley, D. C. 1998: The identity of nest-site scouts in hon-eybee swarms. Apidologie **29**, 229—240.

Hölldobler, B., Janssen, E., Bestmann, H. J., Leal, I. R., Oliveira, P. S., Kern, F. & König, W. A. 1996: Commu-nication in the migratory termite-hunting ant *Pachycon-dyla* (=*Termitopone*) *marginata* (Formicidae, Ponerinae). J. Comp. Physiol. A **178**, 47—53.

Lewis, L. A. & Schneider, S. S. 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, L. A., Schneider, S. S. & Debrandi-Hoffman, G. 2002: Factors influencing the selection of recipients by workers performing vibration signals of the honeybee, *Apis mellifera*. Anim. Behav. **63**, 361—367.

Painter-Kurt, S. & Schneider, S. S. 1998: Age and behavior of honey bees, *Apis mellifera* (Hymenoptera: Apidae), that perform vibration signals on queens and queen cells. Ethology **104**, 475—485.

Rice, W. R. 1989: Analyzing tables of statistical tests. Evolution **43**, 223—225.

SAS Institute 1997: SAS/STAT Software: Changes and Enhancements through Release 6.12. SAS Institute, Inc., Cary, NC.

Schneider, S. S. 1990: Queen behavior and worker–queen interactions in absconding and swarming colon-ies of the African honey bee, *Apis mellifera scutellata* (Hymenoptera: Apidae). J. Kansas Entomol. Soc. **63**, 179—186.

Schneider, S. S. 1991: Modulation of queen activity by the vibration dance in swarming colonies of the Afri-can honey bee, *Apis mellifera scutellata* (Hymenoptera: Apidae). J. Kansas Entomol. Soc. **64**, 269—278.

Schneider, S. S. & Lewis, L. A. 2004: The vibration signal, modulatory communication and the organization of labor in honey bees, *Apis mellifera*. Apidologie **35**, 117—131.

Schneider, S. S., Painter-Kurt, S. & DeGrandi-Hoffman, G. 2001: The role of the vibration signal during queen competition in colonies of the honeybee, *Apis mellifera*. Anim. Behav. **61**, 1173—1180.

Schneider, S. S., Lewis, L. A. & Huang, Z. Y. 2004: The vibration signal and juvenile hormone titers in worker honeybees, *Apis mellifera*. Ethology **110**, 977—985.

Seeley, T. D. & Buhrman, S. C. 1999: Group decision making in swarms of honey bees. Behav. Ecol. Socio-biol. **45**, 19—31.

Seeley, T. D. & Tautz, J. 2001: Worker piping in honey bee swarms and its role in preparing for liftoff. J. Comp. Physiol. A **187**, 667—676.

Seeley, T. D. & Visscher, P. K. 2003: Choosing a home: how the scouts in a honey bee swarm perceive the completion of their group decision making. Behav. Ecol. Sociobiol. **54**, 511—520.

Seeley, T. D. & Visscher, P. K. 2004: Group decision mak-ing in nest-site selection by honey bees. Apidologie **35**, 101—116.

Seeley, T. D., Visscher, P. K. & Passino, K. M. 2006: Group decision making in honey bee swarms. Amer. Sci. **94**, 220—229.

Sokal, R. R. & Rohlf, F. J. 1995: Biometry. W. H. Free-man, New York.

Winston, M. L. 1987: Honey Bee Biology. Harvard Univ. Press, Cambridge, MA.