Vibration Signals and the Organisation of Labour in Honey Bee Colonies

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A fascinating insight into a means of communication between honey bees

ANYONE WHO has ever looked inside a honey bee colony cannot help but be amazed by the intense, yet peaceful level of activity in the nest (Fig. 1). At any one moment, different groups of workers are cleaning cells, tending brood, building comb, ventilating the nest, grooming and feeding other bees, attending the queen, storing and processing food, and foraging for pollen and nectar.

Many of these activities are interrelated and must be kept in balance with one another. Brood rearing must be adjusted to the availability of pollen and the amount of brood in the nest, in turn, influences the pollen gathering activity by foragers. Similarly, nectar collection must be adjusted to the amount of space available for honey storage which, in turn, requires that the workers that receive and process food and comb builders must be sensitive to the level of foraging success.

Furthermore, many of these activities, as well as the behaviour of the queen, must be coordinated with the annual colony cycle so that swarming occurs early enough in the year to allow the new colony to amass the resources necessary for winter survival.

FINE COORDINATION

How are all of these different activities so finely coordinated? Unlike human societies, a honey bee colony does not have 'central control': there are no leaders or supervisors who oversee the allocation of tasks and monitor worker progress (no annual merit evaluations in the honey bee nest!). Rather, labour in honey bee colonies is organized through a decentralized system of control in which each worker individually decides what to do, and when and how long to do it.

This organisation arises in part through an age-influenced division of labour, in which young bees (nurse bees) engage in brood and queen care, middle-age bees perform the tasks of food storage, food processing and comb building, and older bees leave the nest to gather food. But, how do these different groups of workers coordinate their task performance so that the colony functions as a coherent whole?

Fig 1. Honey bee colony life involves different worker groups that perform different, inter-dependent tasks. Labour is coordinated among workers groups partly by stimuli that arise from brood and food combs, and partly through communication signals that influence individual task decisions

Photos supplied by Stan Schneider

COMMUNICATION SIGNALS

Worker activity is adjusted partly by cues that come from brood and food combs and by worker interactions such as trophallaxis (Fig. 2), which convey information about brood rearing activity and colony food needs. Honey bees also produce a wide variety of communication signals that help to organize labour. Many of these, such as brood pheromone, the waggle dance and the tremble dance, function primarily to coordinate labour within one or a few age groups of workers.

However, honey bees have other communication signals that function in a much broader fashion to influence the activity of virtually all the bees in the nest. These signals, which are called modulatory signals, do not cause a specific response in themselves, but rather alter the likelihood that workers will respond to other signals and cues. Modulatory signals can therefore influence simultaneously many different workers groups and may play an important role in organizing the inter-dependent tasks that are central to colony life.

Fig 2. Trophallaxis in honey bees functions to distribute food among nestmates and is also an important source of information about forage availability and colony food needs

Fig 3. The vibration signal of the honey bee, which consists of a worker rapidly vibrating her body dorso-ventrally for 1–2 seconds while contacting another bee. The signal is a modulatory communication signal, in that it causes a non-specific increase in activity that enhances the performance of many different tasks, depending in part upon the recipient's age

An example of a modulatory signal is the vibration signal (Fig. 3), which I and my students have been studying for over 20 years. We have learned that this signal plays a role in organizing information flow and labour in honey bees and that it is involved in virtually every aspect of colony life. The goal of this article is to summarise the results of some of our research and to explain how we think the vibration signal is involved in shaping colony activities.

CHARACTERISTICS OF THE VIBRATION SIGNAL

The vibration signal is one of the most commonly occurring communication signals in honey bee colonies and can be observed through the year, sometimes at rates of hundreds of signals per hour. There are several features of the vibration signal that make it different from other, better-known honey bee signals, such as the waggle dance and tremble dance. First, whereas the waggle dance and tremble dance are performed only by older bees of foraging age, the vibration signal can be produced by workers of any age. Although the majority of vibration signals are performed by older bees, workers as young as 2–3 days of age can also produce the signal.

Second, whereas waggle dances and tremble dances are 'broadcast' to any worker who chooses to pay attention to them, the vibration signal is directed toward only certain workers chosen from an array of possible recipients. A vibrating bee often produces a long series of signals while roaming throughout large areas of the nest. As she moves through the colony, she contacts and antennates hundreds of different workers, but only some are selected to receive the signal.

Work done by my former graduate students, Lee Lewis, Kelly Hyland and Tuan Cao, has shown that vibrators do not select recipients based on age; signals are performed on workers of all ages. Rather, vibrators preferentially direct their signals towards less active bees. Although both active and inactive workers can receive the signal, inactive bees are about 20% more likely to be vibrated.

Third, whereas the waggle dance and tremble dance cause specific responses from workers of only certain ages, the vibration signal causes a non-specific response from workers of all ages. The signal elicits a general increase in activity that enhances the performance of a wide variety of tasks depending, in part, on worker age. Young bees that receive the signal spend increased time engaged in brood care, food processing and comb manipulation. Older recipients are more likely to engage in foraging.

Thus, by being directed towards less active bees of all ages and causing a non-specific, modulatory effect, the vibration signal can simultaneously increase the performance of a wide array of tasks, many of which must be adjusted to one another. The generalized nature of the signal therefore makes it well suited to coordinate activity among worker groups that respond to different stimuli and perform different but inter-dependent tasks. In the remainder of this article, we examine how the signal is used in different aspects of honey bee social life.

THE VIBRATION SIGNAL AND FORAGING ACTIVITY

Many of the tasks influenced by the vibration signal are dependent on food availability and one of the primary functions of the signal may be to help balance these

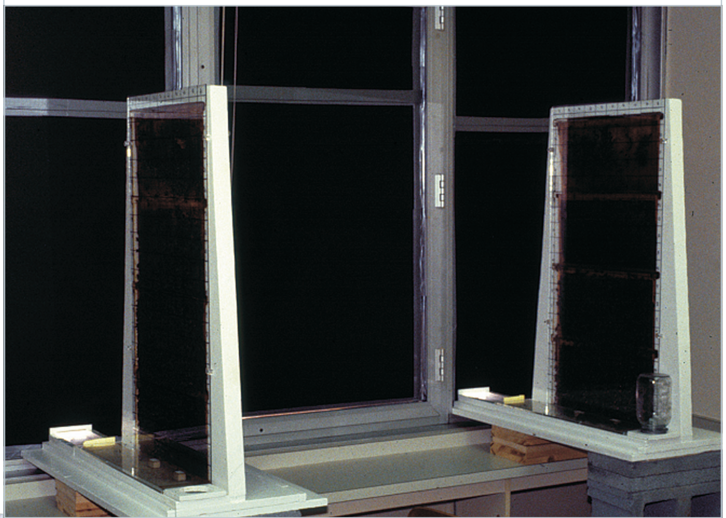

Fig 4. Much of our research on the vibration signal has been conducted using glass-walled observation hives maintained on the campus of the University of North Carolina at Charlotte. Each colony contains a population of tagged bees, which allows us to monitor the behaviour of individual vibrators and recipients of known age

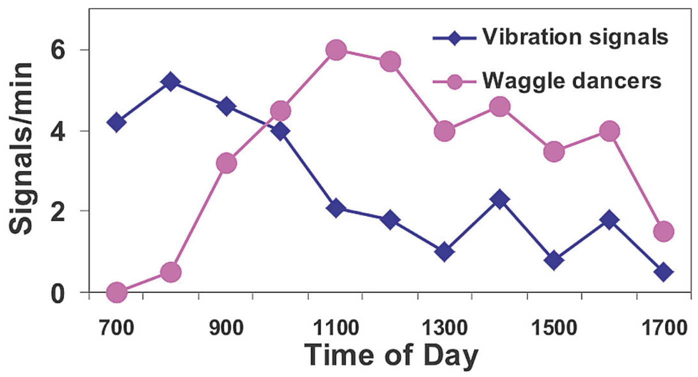

Fig 5. The daily patterns of vibration signal and waggle dance activity. A large peak of vibration signal activity occurs in the early morning before foraging begins for the day. Smaller vibration peaks occur throughout the remainder of the day and often coincide with increases in waggle dance activity

different activities with foraging success. By monitoring the behaviour of tagged workers of known age in observation hives (Fig. 4), we have discovered that most vibration signals are produced by foraging-age bees and that successful food collection stimulates signal performance. Also, vibration signal activity exhibits a distinct daily pattern that fluctuates with changes in a colony's foraging effort (Fig. 5).

Small peaks of vibration activity occur throughout the late morning and afternoon hours and coincide with increases in waggle dancing. Because the signal causes increased task performance, these small vibration peaks may help to adjust worker activity to immediate changes in foraging success: in other words, 'increase your activity, the nectar is flowing'.

Additionally, large peaks of vibration activity occur in the early morning hours before food collection begins for the day, but only if a colony has experienced high levels of foraging success for several preceding days. Morning vibration peaks may function to 'prime' the workforce for the upcoming day, based on the success of the past few days. The vibration signal may therefore help to adjust many different colony activities to both short-term and long-term changes in the availability of floral resources.

THE VIBRATION SIGNAL AND COLONY DEVELOPMENT

If the vibration signal helps to adjust honey bee labour to changing conditions, then its use should change as a colony develops and grows. My students, Tuan Cao, Kelly Hyland and Alana Malechuk, examined this possibility by comparing vibration signal behaviour in pairs of observation colonies, one of which contained an established colony and the other a newly founded colony (Fig. 6).

The established colony contained about 10,000 workers and four frames of comb filled with brood and food. The newly founded colony contained a swarm of about 5000 bees and four wooden frames that were empty except for small strips of wax foundation to ensure that combs were built with the proper orientation in the observation hive. The newly founded colonies had to build all their combs 'from scratch' and initially had no brood or food, whereas the established colonies had these resources in abundance. Thus, our experimental methods simulated the conditions experienced by a swarm when it first moves into a nest cavity and allowed us to examine vibration signal behaviour under different energy and labour needs.

When we compared bees that performed vibration signals in the two colony types, we found that the newly founded colonies had greater vibration signal activity, more bees that performed the signal and a more pronounced tendency to focus signalling activity on less active workers.

However, when we compared the behaviour of workers that received the vibration signal in the two colony types, we found no differences. In all cases, vibrated bees spent more time performing a greater number of tasks than did same-age workers that did not receive the signal. But, individual recipients did not work harder in the newly founded colonies compared with recipients in the established colonies. Thus, the vibration signal may influence worker labour in newly founded colonies by stimulating larger numbers of less occupied bees to engage in tasks and these would then work at the same rate as recipients in established colonies. In this manner, the vibration signal may help to adjust the number of workers performing tasks to the labour demands associated with different stages of colony development.

THE VIBRATION SIGNAL AND COLONY REPRODUCTION

Honey bee colonies reproduce through swarming in which the laying queen and about half the workers leave the old nest and move to a new nest cavity. If the laying queen fails to leave the old nest or move to the new nest site, the swarming attempt will fail. Thus, to a large extent, the success of swarming depends upon the behaviour of the laying queen and workers may use the vibration signal to help coordinate her activity with the swarming process.

Laying queens are vibrated only during the 2–4 week period that precedes swarming. By monitoring worker–queen interactions in our observation hives, we have found that laying queens begin to receive vibration signals when a colony becomes very crowded, and that signalling can begin long before the first queen cells are constructed (Fig. 7). Indeed, we now know that the performance of vibration signals on the laying queen is the first indication that a colony is preparing to swarm.

Fig 6. We video recorded the behaviour of tagged bees that performed vibration signals and tagged workers that received vibration signals in established and newly founded colonies, to examine the influence of colony developmental state on signalling activity

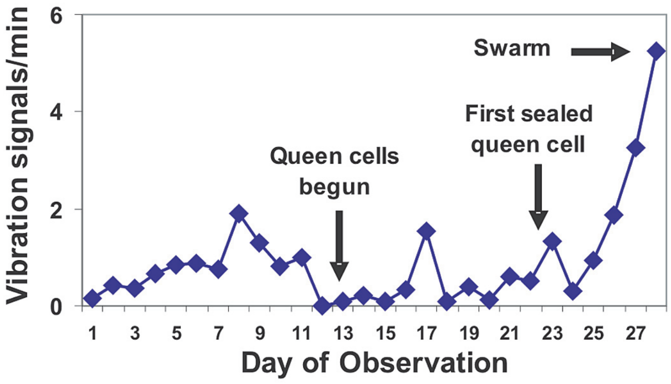

Fig 7. Vibration signals performed per min on a laying queen in a colony during the 28 days preceding swarming. Signalling activity begins on the queen several weeks before swarm departure and often shows a peak in the final days before swarming

The laying queen is vibrated at a variable but increasing rate throughout the swarm preparation period and she can receive several hundreds of signals an hour during the final days before swarm departure. Exactly how the vibration signal affects the queen is unclear, but most evidence suggests it helps to gradually prepare her for flight. During swarming preparations, a laying queen receives more vibration signals when she is inactive than active and responds by walking or running. At the same time, workers begin to feed her less. The combination of increased movement and reduced food intake results in a noticeable 'slimming' of the queen that may get her ready for flight and ensure that she will leave the nest with the swarm.

INFLUENCING VIRGIN QUEENS

Workers also use the vibration signal to influence the behaviour of virgin queens. During swarming (and queen supersedure), workers raise virgin queens in specially constructed queen cells. Once emerged, some virgin queens may depart in afterswarms with portions of the workers. Usually, however, virgin queens remain in the nest and attempt to destroy rivals who have not emerged and are still within queen cells. They will also engage other emerged queens in fights to the death (Fig. 8). The end result is a single surviving virgin queen that takes mating flights and becomes the new laying queen of the colony.

Workers can perform vibration signals on virgin queens throughout the period when they are battling one another. However, workers do not treat all virgin queens the same. Some may be vibrated hundreds of times an hour while others receive few or no signals. Virgin queens that are vibrated at higher rates kill more of their rivals and are more likely to become the new laying queens of their colonies. Workers may therefore use the signal to promote the survival of certain queens and this could happen in two ways.

First, virgin queens sometimes respond to vibration signals by producing a sound called 'piping', which may communicate their presence to other queens in the colony and delay the emergence of rivals still in their queen cells. By stimulating piping, the vibration signal might help a virgin queen eliminate her rivals while they are incapable of fighting back!

Second, virgin queens are often vibrated at very high rates when approaching a rival and they may respond with a brief burst of running that removes them from the potential battle. Workers could therefore use the signal to interrupt and prevent battles, perhaps until a queen has greater maturity and fighting ability. Thus, the vibration signal may give workers a degree of control over the behaviour of virgin queens and help to determine which queen will inherit the nest.

THE VIBRATION SIGNAL AND HOUSE HUNTING BY HONEY BEE SWARMS

After a swarm leaves the old nest, it forms a cluster in nearby vegetation and workers search for a new nest site (Fig. 9). Initially, many different nest sites are investigated, but eventually the choices are winnowed down until there is a single selection. Once a site has been selected, the entire swarm must become airborne and move as a group to the chosen site. How does a swarm of up to 10,000–12,000 bees accomplish such remarkable decision making and coordinated mass movement? We now know that the 'house hunting' process involves an intricate interaction of

Fig 8. Emerged virgin queens often battle to the death until there is a sole survivor who becomes the new laying queen of the colony. Workers can perform vibration signals on virgin queens at very high rates and this may help to determine the outcome of queen fights

Courtesy Kenneth Lorenzen

Fig 9. After a swarm forms a cluster, scouts communicate the location of new nest sites by performing waggle dances on the swarm surface. Typically, when all dancers are indicating the same site, the swarm begins lift off preparations to move to the chosen location. These preparations involve two additional signals, the vibration signal and worker piping

Fig 10. Worker piping consists of a bee pressing her body against the substrate or another bee and producing a high-pitched sound. Piping is produced at high rates during the lift off-preparation period and causes recipients to warm their flight muscles

Fig 11. We video recorded queen behaviour inside swarm clusters by creating experimental swarms on an observation stand that had a clear plastic back. In this way, we could study how workers interact with the queen when a swarm is preparing to lift off and move to a new nest site

Courtesy Dr Tom Seeley

at least three different communication signals: the waggle dance, the vibration signal, and 'worker piping'.

Scout bees perform waggle dances on the surface of the swarm cluster to communication the distance and direction to potential nest cavities. At first, dances are performed for many different sites, but usually all waggle dance activity becomes focused gradually on a single site, which is the new cavity to which the swarm will relocate. About the time that the waggle dancers have reached a consensus for a nest site, the swarm begins to prepare for lift off and mass movement, and this involves the vibration signal and worker piping.

Work done by my students, Lee Lewis and Kelly Donahoe, revealed that workers perform vibration signals throughout the house hunting process, but the signal reaches a crescendo during the final 1–2 hours before lift off. At this time, many workers perform long series of signals while weaving in and out of the swarm cluster. Recipients respond to the signal with increased movement, such that as lift off approaches the entire surface of the swarm appears to be in motion. Simultaneously, some workers (primarily the nest site dancers) begin to produce a high-pitched sound called 'worker piping' (Fig. 10), which has been studied extensively by Professor Tom Seeley at Cornell University.

Piping causes recipients to warm their flight muscles in preparation for flight. There is always a pronounced increase in piping immediately before lift off, and piping may be the signal that finally triggers the flight of the swarm cluster. Thus, successful house hunting involves the waggle dance, to select a specific nest site, worker piping, to trigger the flight necessary for mass lift off, and the vibration signal, to activate the swarm and modulate responsiveness to the other signals that regulate swarm movement.

THE ROLE OF THE VIBRATION SIGNAL IN MAKING THE SWARM LIFT OFF

We tested the role of the vibration signal in this suite of communication behaviours by removing vibrators from swarm clusters. We found that removing the vibrators did not prevent a swarm from eventually achieving lift off, but it increased the time required for lift off preparations by seven times, even though there were continuous high levels of waggle dancing and worker piping throughout these extended lift off periods.

Furthermore, even after achieving lift off, some of our experimental swarms were unable to relocate to the chosen site. Thus, by causing increased activity that may enhance responsiveness to the other signals involved in house hunting, the vibration signal may promote a speedy and accurate lift off decision.

We have also examined how workers interact with the queen inside the swarm cluster. Although much research has been devoted to how workers interact with a queen before the swarm leaves the nest, we know virtually nothing about worker–queen interactions in the swarm cluster.

My undergraduate Honours student, Andrew Pierce, set up swarms on special observation stands that allowed us to film the queen's behaviour through a clear plastic sheet so that we could monitor worker–queen interactions while a swarm was searching for a new nest site (Fig. 11). The queen was confined inside a cage made of queen excluder attached to the plastic back so that we could continually track her behaviour throughout the swarming process.

To our surprise, we found that workers rarely or never performed vibration signals on the queen inside the swarm cluster. Thus, the vibration signal, which is such a prominent part of worker–queen interactions during swarm preparations inside the nest, plays no role in ensuring that the queen takes flight during swarm lift off and movement to a new nest site. Equally surprising, we found that workers performed piping on the queen inside the swarm cluster, especially during the final hour before lift off. This was the first time that worker piping on the queen had ever been reported. Thus, workers may use piping to trigger flight in queens, in a similar way to how it is used to trigger flight in workers during swarm movement.

If workers perform piping on the queen inside the swarm cluster, do they also perform it on the queen before the swarm leaves the old nest?

When we re-examined worker–queen interaction prior to swarm departure from the nest, we were astonished to find that workers do indeed perform piping on the queen at very high levels immediately before the swarm departs. Thus, workers may use two signals to prepare the queen for swarming: the vibration signal, which gradually prepares her to leave the nest, and worker piping, which may be the final trigger for flight with the swarm.

However, why are both the vibration signal and worker piping necessary to stimulate queen flight from the old nest, but only piping seems to be needed to stimulate her to fly with the swarm cluster to the new nest site? We do not know. Perhaps if the vibration signal helps to prepare the queen for flight, then once she has the capability to fly from the old nest, further preparations for flight are unnecessary. Our future research will focus on attempting to tease apart the roles of the different communication signals and how they interact to influence queen and worker behaviour.

CONCLUSIONS

In conclusion, we have found that the vibration signal influences many aspects of honey bee colony life. By operating in a non-specific modulatory manner, this one signal can affect the behaviour of laying queens, virgin queens and workers of all ages. Furthermore, our studies of house hunting and worker–queen interactions during swarming have revealed that the vibration signal often works in conjunction with other signals to help formulate colony-level decisions.

Despite over 20 years of research on the vibration signal, much remains to be learned about this communication behaviour. However, the vibration signal provides a wonderful tool for gaining fascinating insights into the remarkable complexity of honey bee behaviour and social life. ◆

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