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# The Shaking Signal of the Honey Bee Informs Workers to Prepare for Greater Activity

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## Abstract

One of the most conspicuous activities of worker bees inside a hive is the shaking of other workers. This shaking has long been suspected to be a communication behavior, but its information content and function have until recently remained mysterious. Prior studies of the colony-level patterns of the production of the shaking signal suggest strongly that this signal serves to arouse workers to greater activity, such as at times of good foraging. Data from our observations of individual bees bolster the hypothesis that the shaking signal informs workers to prepare for a higher level of activity. We followed foragers in a colony whose only source of 'nectar' was a sugar-water feeder and discovered that when the feeder was left empty for 1–3 d and then refilled, the first bees to find the food initially produced only shaking signals upon return to the hive. It was not until they had completed several trips to the feeder that they began to produce waggle dances. Evidently, the shaking signal and the waggle dance function together to stimulate a colony's foragers to activity.

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## Introduction

A major challenge in studying a behavior that functions as a communication signal is to decipher its message, the information the sender makes available by producing the signal (SMITH 1977). Usually this involves observing individuals and noting what events and activities occur before, during, and after the production of the signal. Once one identifies circumstances of the sender that are consistently associated with the production of the signal, one can make inferences about its message. Sometimes, however, it is difficult to find any consistency among the various contexts in which one sees a signal being produced and then the signal's message remains a mystery.

The history of the study of the shaking signal of the honey bee (Fig. 1) exemplifies the difficulty of determining the message of a behavioral signal. This common and conspicuous behavior of worker bees was repeatedly described more than 50 years ago by HAYDAK (1945), TARANOV & IVANOVA (1946), SCHICK (1953), ISTOMINA-TSVETKOVA (1953), and MILUM (1955), and although all these authors suspected it to be a communication behavior, none could give a clear conclusion about its message. The first

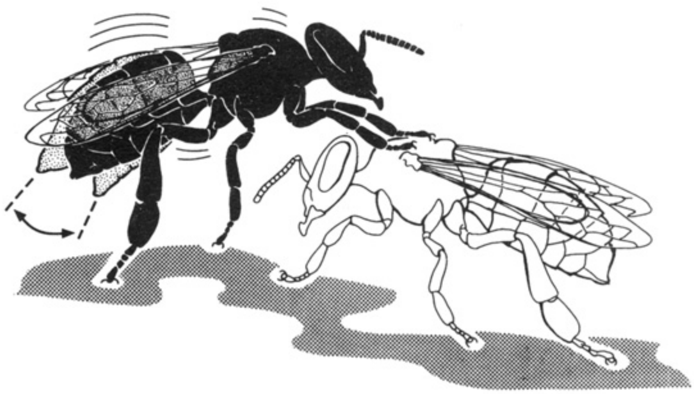


*Fig. 1:* A worker bee producing the shaking signal. Having grasped a nestmate, she vibrates her own body dorsoventrally for 1–2 s at ≈16 Hz. The bee then breaks contact with the shaken bee, crawls across the comb, and usually shakes another bee. Occasionally she will shake the comb rather than another bee. A bee can produce these signals at a rate of 20 or more per min, and can continue doing so for several minutes, hence within one bout of signaling a bee can send her message to numerous nestmates. This communication behavior has received various names including 'dorso-ventral abdominal vibration' (MILUM 1955), 'shaking' (ALLEN 1956), 'jerking dance' (VON FRISCH 1967), 'shaking dance' (GAHL 1975), 'vibratory dance' (FLETCHER 1978a), and 'vibration dance' (SCHNEIDER et al. 1986a). Unfortunately, the original name, dorsoventral abdominal vibration, is a misnomer because a bee producing this signal vibrates the entire body dorsoventrally, not just the abdomen, through flexions of its legs. Likewise, to call this vibration behavior a 'dance' seems improper because, unlike the waggle dance and tremble dance of the honey bee, it is a very brief behavior (just 1–2 s) and so is not suggestive of dancing. For these reasons, perhaps the most appropriate of the various names given to this communication behavior is that coined more than 40 years ago by ALLEN (1956): 'shaking' or 'shaking signal'

systematic observations of shaking, by ALLEN (1956, 1958, 1959a) and HAMMANN (1957), focused on workers shaking queens. These studies did reveal one curious consistency: the only time workers shake their queen is before she must fly out from the hive, either with a swarm or on a mating flight. Based on this fact, ALLEN (1958) suggested that the message of the shaking signal might be 'Prepare for flight' or 'Prepare for greater activity.' This suggestion is supported by the findings of SCHNEIDER (1991) that queens are shaken nearly twice as often when inactive than when active and that, after being shaken, queens show heightened activity, especially increased locomotion. However, observations of workers shaking queens by FLETCHER (1975, 1978a,b) led him to suggest the opposite message for the shaking signal, namely 'Reduce your activity.'

Other systematic investigations of the shaking signal have focused on workers shaking other workers, the most common targets of the shaking signal. And here, too, the information content of the shaking signal remained, until recently, mysterious. ALLEN (1959b) reported that the shaking of workers is often done by foragers and has a positive association with flight activity, but she could not draw any conclusions regarding its information content. Similarly, GAHL (1975) suggested a link between foraging and the production of shaking signals based on his observation that bees that produce shaking signals occasionally switch to performing the waggle dance, but he too could not provide any solid insights into the significance of the shaking signal. The extensive work of SCHNEIDER and his colleagues (SCHNEIDER 1986, 1987, 1989a; SCHNEIDER et al. 1986a,b) has revealed that this signal is produced by bees that have experienced successful foraging, either shortly before producing the signal (which results in shaking after the colony's foraging has begun) or over several days before producing the signal (which results in shaking early in the morning, before the colony's foraging has begun). These findings suggest strongly that the signal, when directed at workers, contains the following piece of information: 'Prepare for greater activity.' This idea derives further support from the finding that foraging-age bees that are shaken have a higher rate of movement and a higher probability of moving to the area near the hive entrance where waggle dances are performed than same-age bees that are not shaken (SCHNEIDER et al. 1986a). Also, when NIEH (in press) compared the behavior of workers before and after they had been shaken, he found that after being shaken many of them moved faster and began to move toward the hive entrance. Furthermore, pre-foraging age workers spend more time actively engaged in work after being shaken than before (SCHNEIDER 1987). Thus it now seems clear that the shaking signal, at least when directed at workers, is involved in priming them to work harder so that the colony can better exploit good foraging opportunities.

In this paper we report findings that reinforce the hypothesis that the shaking signal indicates to worker bees that they should prepare for greater activity. In particular, we report our discovery of a set of circumstances under which foragers will consistently produce shaking signals. We also report an important relationship between the shaking signal and the waggle dance, another of the honey bee's communication signals involved in foraging.

Our study of the shaking signal was stimulated by chance observations made in June 1994 at the Cranberry Lake Biological Station, while investigating the control of water collection by honey bee colonies (KÜHNHOLZ & SEELEY 1997). To study the interaction between water collection and nectar collection, we had a small group of labeled bees from a colony in an observation hive trained to forage at a sugar water feeder, the only source of 'nectar' for this colony. (There is almost no natural forage for bees at the Cranberry Lake Biological station; see Methods.) However, because of vagaries in the weather and breaks in our experiments, the feeder was not filled each day and was often left empty for one or two d. When the feeder was refilled, the labeled foragers revisited it and upon return to the hive they initially produced numerous shaking signals instead of the waggle dances (VON FRISCH 1967) that we expected, though they eventually switched to producing only waggle dances. To determine whether the pattern of events just described is typical, we made further observations on 4 foragers visiting a sugar-water feeder at the Cranberry Lake Biological Station over a 25-d period in July 1994. On some days the feeder was filled, and on others it was left empty. By noting the association between our refilling the feeder and the bees' producing shaking signals, we tested our hypothesis that foragers will produce shaking signals upon finding food following a break in foraging.

## Methods

A group of 10–15 individually labeled bees from a colony housed in an observation hive was allowed to forage at a sugar-water feeder, the only significant source of 'nectar' for the colony. Then the feeder was shut off for 2–4 d. When the feeder was once again filled with food, the first bee to revisit the feeder was chosen as the focal bee for the next 1–3 d of observations. Following each trip to the feeder, the focal bee's behavior inside the observation hive was monitored, and a record was made of her production of shaking signals and waggle runs.

## Study Site

The work was conducted at the Cranberry Lake Biological Station (44°09′N, 74°48′W), located in the Adirondack State Park, Saint Lawrence County, in northern New York State. This study site is surrounded by nearly unbroken forests and lakes, hence there are few natural food sources for bees and it is easy to train bees to forage at a sugar-water feeder. The scarcity of food also makes it possible to control tightly a colony's rate of 'nectar' collection by controlling the number of bees foraging at a feeder, even though the colony's foragers can fly freely from their hive. One indication that natural forage was indeed sparse when the present experiment was performed was the extremely low level of traffic of foragers at the hive entrance whenever the feeder was shut off: only 1 or 2 bees/min into the hive. Also, whenever we stopped providing sugar water at the feeder, the amount of honey stored in the observation hive would steadily decline. But despite the dearth of nectar, the colony was able to gather sufficient pollen to maintain brood rearing.

## Apparatus

A colony of ≈4000 Italian honey bees (*Apis mellifera ligustica*) was housed in a two-frame observation hive (see fig. 4.2 in SEELEY 1995). This hive's entrance was fitted with a wedge that forced all foragers to enter and leave the hive from one side of the comb. Because returning nectar foragers unload their nectar to receiver bees shortly after entering the hive, this wedge established a nectar-unloading area on one side of the lower comb. The hive was housed in a small hut (see fig. 4.3 in SEELEY 1995) situated on the north end of the central field of the biological station.

The feeder was designed to provide a sucrose solution with a constant concentration ad libitum. It consisted of a 50-ml glass jar containing sucrose solution inverted over a slotted plexiglass plate (see fig. 4.5 in SEELEY 1995). This plate-jar combination was placed atop a screened container of anise extract to provide the feeder with scent. Additional scent was provided by mixing 200 μl of anise extract (a 27% solution of essential oil in alcohol) in each litre of sucrose solution. The concentration of this solution was 0.5 mol/l on all d except 7, 8, 19, and 20 July, when it was 2.0 mol/l for the purposes of the experiment described in SEELEY et al.1996. The feeder was positioned in a small clearing 350 m south of the hive, near the bridge over Sucker Brook. Bees were trained to the feeder using standard techniques (VON FRISCH 1967). Fig. 2 shows when we loaded the feeder with sugar solution.

## The Bees

Approximately 10% of the colony's population consisted of bees that were labeled for individual identification and were of known age. They were obtained by collecting newly emerged bees from a second colony (located 10 km away, on the other side of Cranberry Lake) and were labeled for individual identification with a colored and numbered plastic disk on the thorax (Opalithplättchen, Chr. Graze, Endersbach, Germany) combined with a dot of paint on the abdomen. Unique plastic disk/paint dot combinations were used for each age cohort. Every 3 d, from May 20 to July 19, 50 of these 0-d-old bees were added to the colony.

On all days except two (July 8 and 20, see below), we permitted only 10–15 of the labeled bees to come and go freely from the feeder. All unlabeled bees that tried to forage at the feeder were captured, as were all labeled bees in excess of the 10–15 desired ones. The captured bees were held in perforated plastic bags until the end of the day whereupon they were released at the hive. On July 8 and 20, we did not capture any of the additional bees so that the colony would experience a high influx of 'nectar' (SEELEY et al. 1996). On both days, more than 70 bees visited the feeder.

Whenever the feeder was filled, we noted which individuals visited the feeder during each 30-min interval. These 'roll calls' of the bees served to check on the number of bees foraging at the feeder and to reveal which bees were foraging most steadily.

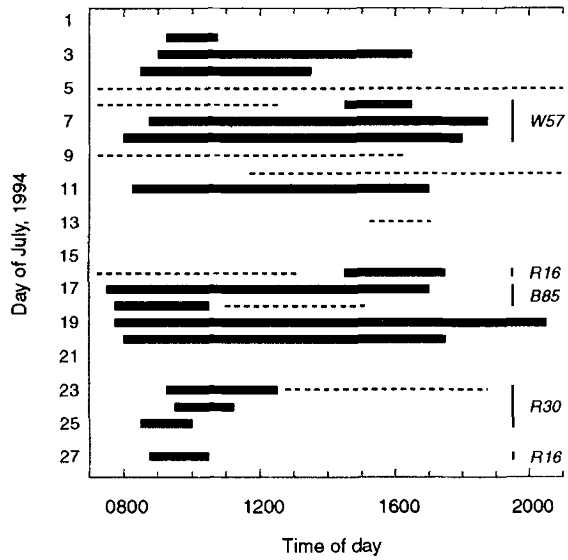



*Fig. 2:* Timetable showing when the feeder was loaded with sugar water (black bars) during the month of July 1994. Dotted lines denote periods of cool or rainy weather, when the bees were unable to fly from their hive. The codes on the righthand side specify the days on which each of the 4 focal bees was observed

## Observation Methods

We gathered data on the production of communication signals by individual foragers by refilling the feeder following an extended shutdown (Fig. 2), noting which labeled bee first rediscovered the newly filled feeder, and then watching this bee every time she returned to the hive with a load of sugar water. When the focal bee left the feeder to return to the hive, an observer at the feeder would alert (via walkie-talkies) a second observer at the observation hive of the bee's impending arrival. Upon seeing her enter the hive's entrance tunnel, the second observer would record the time and the number of shaking signals and waggle runs (of the waggle dance) performed by this bee. When the focal bee exited the hive, the observer at the hive would alert the observer at the feeder, and once the bee had returned to the feeder and had again loaded up with food, the entire cycle of observations would begin anew.

## Statistical Analyses

Measurements are given as the $\bar{X} \pm$ SE. All statistical tests were performed using Student's t-test.

## Results

### Bee Number 1: W57

Bee W57 eclosed on 23 May 1994. She began foraging at the feeder on 26 June, when she was 34 d old. From 26 June to 6 July, the start of our observations on this bee, she visited the sugar water feeder steadily whenever it was loaded with food. She was observed during each of the roll calls conducted on 26, 28, 29, and 30 June, and 2, 3, and 4 July (Fig. 2). Often she was the first bee to arrive at the feeder in the morning.

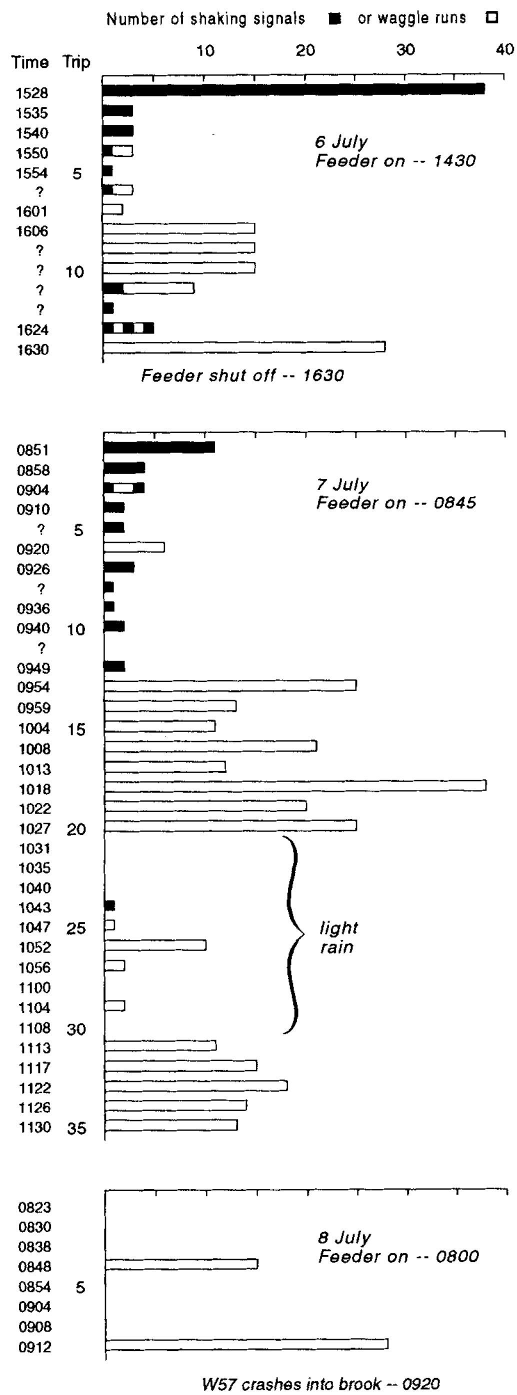
At 1430h on 6 July we reloaded the feeder with sugar solution, thus ending a 49-h period during which we had purposefully left the feeder empty. (The feeder had been shut off at 1330h on 4 July, then it had rained throughout 5 July. The rain continued on the morning of 6 July, but by 1330h the rain clouds had passed and the sun had begun to shine.) As usual, W57 was the first bee to visit the feeder and so she became our focal bee. After imbibing a load of the sugar solution, she returned to the hive at 1528h, quickly found a receiver bee who unloaded her, and then began producing shaking signals while walking about on the comb. She produced 38 signals in quick succession, after which she left the hive and flew back to the feeder. Following her next two trips to the feeder she again produced only shaking signals, though many fewer (just 3) on each return to the hive (Fig. 3). After her fourth foraging trip, she produced one shaking signal by shaking the receiver bee, then produced two waggle runs, and finally rushed out of the hive. She behaved similarly after her next two trips to the feeder (Fig. 3). It was only after her sixth foraging trip that she ceased producing shaking signals and began producing just waggle runs. And it was not until after her eighth trip to the feeder, nearly 40 min after she had begun exploiting the feeder that day, that she produced a strong waggle dance with 15 consecutive waggle runs. For the remainder of the day, she produced mostly waggle runs, though she did produce a few more shaking signals after trips 11, 12, and 13, usually mixing them with waggle runs (Fig. 3).

On the morning of the next day, 7 July, bee W57 arrived at the feeder shortly after it was refilled at 0845 and began a pattern of steady foraging which continued until the feeder was shut off at 1845h. We recorded her behavior inside the observation hive following her first 35 trips to the feeder. As is shown in Fig. 3, she generated a pattern of communication signals broadly similar to that of the previous day. The first two trips to the feeder were followed by shaking signals only. And during the first hour of exploiting the feeder, in which time the bee visited the feeder 12 times, she produced mainly shaking signals inside the hive (30 shaking signals and 8 waggle runs). Only after completing these 12 trips did she begin to perform strong waggle dances and so produce numerous waggle runs. Her next 7 foraging trips, numbers 13–20, were followed by numerous (11–28) waggle runs but no shaking signals. After the next 10 visits to the feeder, trips 21–30, her production of waggle runs dropped markedly, most likely because the sky had filled with dark clouds and a light rain was falling. Then, when the sky cleared and the rain stopped, she began to again produce many waggle runs each time she returned to the hive with a load of food (trips 31–35). It should be noted too that after her first hour of foraging this day, she produced just one shaking signal.

On the morning of 8 July, bee W57 was slow to appear at the feeder in the morning and when she finally did appear she acted as if she were worn out. At 0920h, she lifted off from the feeder to fly home but flew weakly and crashed into the stream beside the feeder. She died shortly thereafter. That morning she managed to complete 8 trips to the feeder, 2 of which were followed by waggle runs. She produced no shaking signals.

**Bee Number 2: R16**

Bee R16 eclosed on 1 June 1994. She began foraging at the feeder on 2 July, when she was 31 d old. From 2 to 11 July, the start of our observations on this bee, she visited



Number of shaking signals ■ or waggle runs □
Time
Trip
10
20
30
40
1528
1535
1540
1550
1554
5
?
1601
1606
?
?
10
?
?
1624
1630
6 July
Feeder on -- 1430
Feeder shut off -- 1630
0851
0858
0904
0910
?
5
0920
0926
?
0936
0940
10
?
0949
0954
0959
1004
15
1008
1013
1018
1022
1027
20
1031
1035
1040
1043
1047
25
1052
1056
1100
1104
1108
30
1113
1117
1122
1126
1130
35
7 July
Feeder on -- 0845
light rain
0823
0830
0838
0848
0854
5
0904
0908
0912
8 July
Feeder on -- 0800
W57 crashes into brook -- 0920

the feeder steadily whenever it was loaded with food. In particular, she was observed at the feeder during each of the roll calls conducted on 2, 3, 4, 6, 7, 8, and 11 July.

At 1430h on 16 July we reloaded the feeder with sugar solution, thus ending a 117.5-h period during which we had left the feeder empty on purpose. (We intended to leave the feeder off on 12–15 July. Rain during the morning and early afternoon of 16 July prevented us from refilling the feeder until mid afternoon, by which time it was sunny and warm.) Despite this nearly 5-d long break in the presence of food at the feeder, a bee, R16, arrived at the feeder only 20 min after we had reloaded it. This bee became our next focal individual. As is shown in Fig. 4, this bee completed 27 trips to the feeder before we shut it off at 1730. On her first return to the hive with a load of food, she produced only shaking signals (26 total). Her next trip to the feeder was followed by a mixture of shaking signals and waggle runs. But after this, nearly every trip was followed by the production of waggle runs only. Only at the very end of the day did she again produce shaking signals, and even then their numbers were low, at most 2 per return to the hive.

### Bee Number 3: B85

Bee B85 eclosed on 10 June 1994. She began foraging at the feeder on 11 July, when she was 31 d old. Like W57 and R16, she foraged steadily at the feeder whenever it was loaded with food.

At 0730h on 17 July we reloaded the feeder with sugar solution and expected to resume our data collection from the previous afternoon by watching bee R16. However, the bees were slow to begin foraging this morning, probably because the day started out quite cool, and the first bee to appear at the feeder, B85, did not arrive there until 0901h. We decided to watch this bee until R16 appeared. But because R16 did not show up at the feeder until 0952h, by which time we had gathered much data on B85, we stayed with this bee.

Our new focal bee, B85, showed the same general pattern of signal production as the previous two bees. She produced only shaking signals after each of her first 5 trips to the feeder on 17 July, and then produced only waggle runs after later trips that day (Fig. 5). We stopped following this bee once she had completed 20 trips to the feeder. The bee B85 differed from the previous two bees in that she did not mix the two types of signal during a single in-hive period. Also, she was the strongest producer of shaking signals that we had seen to date, performing 67 shaking signals after her second foraging trip. In relation to this, it may be significant that most of the bees inside the hive were inactive, just sitting quietly on the combs, at the beginning of this cool morning. When B85 returned to the hive after her first few trips to the feeder, there was no traffic of bees in the entrance

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*Fig. 3:* The production of shaking signals and waggle runs after each trip to a feeder by the bee W57. Each horizontal bar denotes the number of shaking signals (filled portion) or waggle runs (open portion), or both, that she produced after a given foraging trip. For cases where both types of signal were produced, the bar indicates the precise order of their production. For example, after the fourth foraging trip on 6 July, the bee produced first one shaking signal and then two waggle runs. The times listed on the left indicate when the bee entered the hive following each of her trips to the feeder

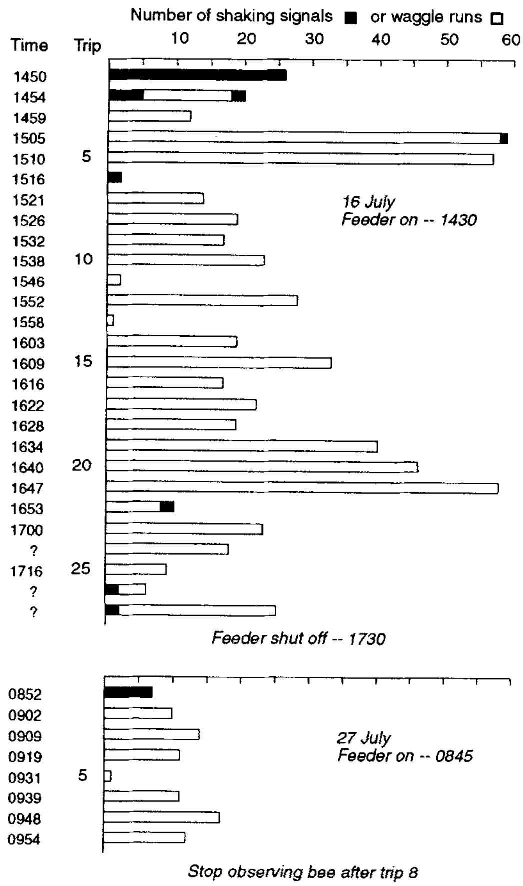


*Fig. 4:* The production of shaking signals and waggle runs after each trip to a feeder by the bee R16. Details as in Fig. 3

tunnel, there were no bees performing waggle dances in the hive, and the dance floor area inside the entrance was congested with virtually immobile bees, probably foragers.

The next morning we reloaded the feeder at 0745h and B85 was again the first bee there. As is shown in Fig. 5, we recorded her in-hive behavior following each of her first 10 trips to the feeder. She produced no signals after each of her first 3 trips, and after the next 7 trips she produced only waggle runs. We stopped recording her behavior after trip number 10 because by then dark rain clouds were filling the sky and heavy rain seemed imminent. Torrential rains began at 1100h.

### Bee Number 4: R30

Bee R30 eclosed on 1 June 1994. She began foraging at the feeder late in the day on 16 July, when she was 45 d old. Despite her age, she foraged vigorously, visiting the feeder

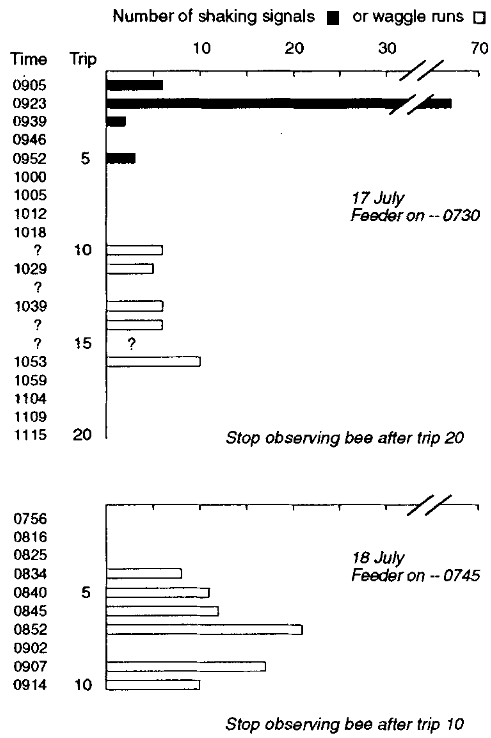


*Fig. 5:* The production of shaking signals and waggle runs after each trip to a feeder by the bee B85. Details as in Fig. 3

steadily whenever it was loaded with food. She was observed during each of the roll calls on 17, 18, 19, and 20 July.

At 0915h on 23 July we reloaded the feeder with sugar solution, thus ending a 64-h period during which we had left the feeder empty. Although the day started sunny and warm, most of the bees inside the observation hive were still extremely quiet, virtually motionless, perhaps because there had been little or no food to collect during the previous two d. At 0919h, one of the bees with experience at the feeder, R30, left the hive; she arrived at the feeder at 0920h. Since she was the first bee to appear there, she became our focal bee. At 0922h she left the feeder and at 0924h she was sighted in the entrance tunnel of the observation hive. Immediately upon entering the hive, she began to produce shaking signals at an extremely high rate. She shook 33 bees in her first 92 s (22 shakings/min) inside the hive. Following this, she quickly unloaded her food to two receiver bees simultaneously, then shook 16 more bees, and finally rushed out of the hive. As is shown in Fig. 6, bee R30 generated a pattern much like the previous 3 bees, producing only shaking signals after each of her initial 8 trips to the feeder, then producing a mixture of shaking signals and waggle runs after most of her next 18 foraging trips, and finally producing only waggle runs after each of her last 7 trips to the feeder.

Around 1200h the sky filled with dark clouds, the temperature began to drop, and so

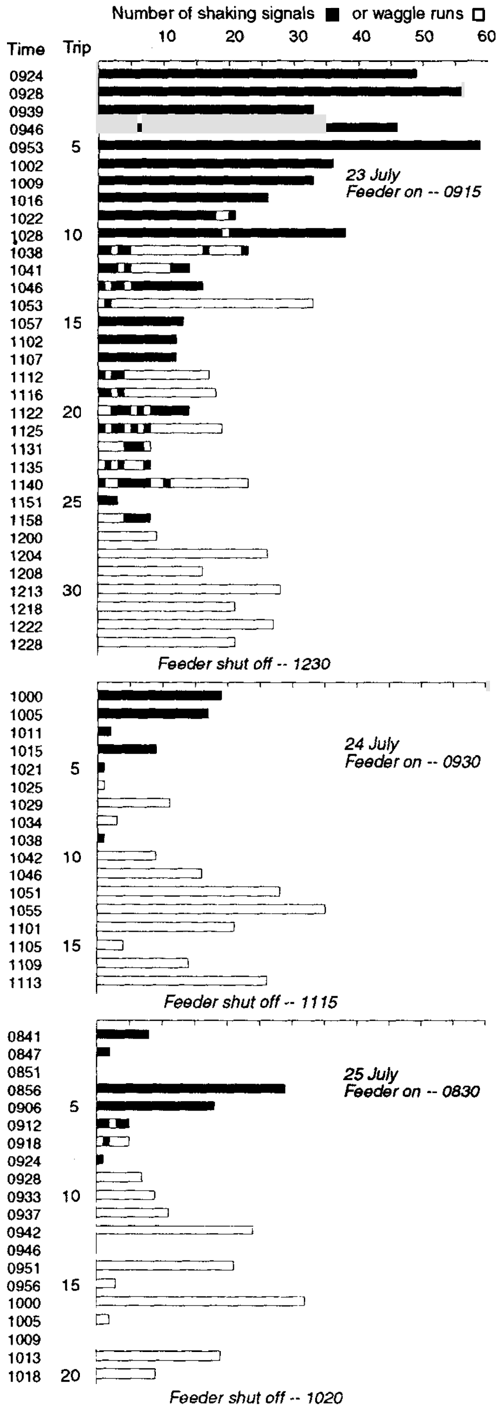


*Fig. 6:* The production of shaking signals and waggle runs after each trip to a feeder by the bee R30. Details as in Fig. 3

rain seemed imminent. Because we wanted to watch R30 more the next day, we did not want to endanger her by inducing her to forage during a rainstorm. So at 1230, after watching her behavior throughout 33 foraging trips, we shut off the feeder.

On the morning of the next day, 24 July, the weather was warm and sunny. At 0830h we began watching inside the observation hive and found R30 already producing shaking signals. Over the next 32 min she shook other bees 102 times. At 0902h she left the hive and arrrived at the empty feeder at 0905h. There she briefly probed the slots in the feeder for food but found none (the feeder was not refilled on this day until 0930) and soon flew away. At 0913 she crawled inside the observation hive and began producing more shaking signals. By 0930h she had produced 97 shaking signals at a rate of 5.7 shakings/min, never leaving the hive. Between 0930h and 0956h she remained inside the hive, walking slowly about and shaking other bees 32 more times. Finally, at 0956h, she flew from the hive and discovered the refilled feeder. After loading up and flying home, she began to generate the same pattern of communication signals as she did the previous day, at first producing only shaking signals but eventually producing only waggle runs (Fig. 6).

It seemed that R30 was less motivated to produce shaking signals after finding food on this day relative to the previous day. This change is seen by comparing between the 2 days the number of shaking signals that she produced after her early foraging trips that were followed by shaking signals only. On 23 July she produced $42 \pm 12$ shakings/trip ($n = 8$ trips), but on 24 July she produced only $10 \pm 8$ shakings/trip ($n = 5$ trips) ($p < 0.001$ for the difference between the means of the 2 d). In contrast, it seemed that her motivation to produce waggle runs after finding food was the same on both days. Consider her later foraging trips that were followed by waggle runs only. On 23 July she produced $21 \pm 7$ waggle runs/trip ($n = 7$ trips) and on 24 July she produced $19 \pm 10$ waggle runs/trip ($n = 8$ trips) ($p > 0.50$ for the difference between the means of the 2 d).

We shut off the feeder early (at 1115h) on 24 July to improve our chances of watching R30 on the following day. Because she was already quite old, 53 d, we feared that she might die before the day was out if we let her forage steadily for the rest of the day.

On the morning of 25 July we began our observations of R30 inside the observation hive at 0630h, thus long before the feeder was reloaded at 0830h and well before the first bee from the colony returned with food from a natural food source (at 0718h the first forager returned with small loads of pollen). We saw that at 0630h R30 was already producing shaking signals inside the hive. Between 0630h and 0700h, she remained inside the hive and produced 230 shaking signals, many of them rather feebly performed, at a rate of 7.7 shakings/min. Over this time period we also observed 8 other bees from the feeder producing shaking signals. Between 0700h and 0730h, R30 gradually slowed down her production of shaking signals, and by 0736h she was sitting motionless in the hive. At 0739h she began to groom herself and at 0743h she exited the hive, presumably to inspect the feeder, which was still empty. She returned to the hive at 0746h and began to groom herself. By 0747h she had begun once again to produce shaking signals, but now her signals were neither vigorous nor frequent; the average rate between 0748h and 0800h was just 1.6 shakings/min. At 0800h R30 was again motionless, but at 0834h she again exited the hive and on this trip she discovered the newly filled feeder, arriving there at 0836h.

Her pattern of communication behavior on this day was the same as on the previous two days: shaking signals only after the early (first 5) foraging trips, then a few trips after which the bee produced a mixture of shaking signals and waggle runs, and finally numerous trips after which she produced only waggle runs. We shut off the feeder at 1020, by which time R30 had completed 20 trips to the feeder. Over the next 15 min she made two more trips to the feeder, returning to the hive at 1023h and 1033h, but after both trips she produced no communication signals.

### Bee Number 2: R16 (again)

As stated earlier, bee R16 eclosed on 1 June 1994 and began foraging at the feeder on 2 July, when she was 31 d old. She visited the feeder steadily whenever it was loaded with food during the period 2–15 July. We watched this bee closely on 16 July (Figs 2 and 4) and expected to do so again on 17 July, but this d she was slow to return to the feeder and so we switched to the bee B85. Nevertheless, R16 continued to forage steadily at the feeder and was registered in nearly all the roll calls made whenever the feeder was loaded with food on 17–26 July. By the time she again became our focal bee on 27 July, she was 56 d old.

At 0845 on 27 July we reloaded the feeder with sugar solution, thus ending a 46.5- h period during which we had left the feeder empty. We hoped to watch the bee R30 some more, to see if the experience of renewed foraging after a long break would cause her to produce large numbers of shaking signals, as she had done on 23 July following a similar break in foraging. Unfortunately, R30 never reappeared at the feeder on 27 July. So we recorded the communication behavior of R16 instead, since she was the first bee to discover the refilled feeder. As is shown in Fig. 4, this bee behaved in the familiar pattern, performing only shaking signals after her first trip to the feeder, but then performing only waggle runs after her later trips.

## Discussion

### The Circumstances of Shaking Signal Production

We observed closely 4 focal bees to test our hypothesis that foragers will produce shaking signals upon finding food following a break in foraging. As is shown in Figs 3–6, we found that all 4 focal bees, upon finding the feeder refilled after being empty for several days, produced only shaking signals upon return to the hive. Moreover, we found that all 4 bees produced shaking signals primarily in association with the first several trips (9.1 $\pm$ 3.2, range 1–26) to the newly refilled feeder. On later trips, all 4 focal bees switched to producing primarily waggle dances. Finally, we found that the focal bees produced shaking signals at the start of their foraging on 8 of the 10 d on which we monitored their behavior (see below for a discussion of what was different about the 2 d when the bees did not produce shaking signals).

Taken together, our results indicate one set of circumstances under which forager bees will consistently produce shaking signals.: (1) the forager has just entered her hive with a load of food gathered at a desirable food source; (2) she and the other foragers in her colony recently have experienced a dearth of forage; and (3) she is one of the first foragers to again find a good source of food, hence most of the other foragers are still inactive (not engaged in foraging) in the hive. It is not clear how important each of these circumstances is in stimulating a forager to produce shaking signals. Solving this mystery will require experiments in which the various conditions are varied independently and their effects on shaking signal production are measured. Certain details of our findings, however, suggest that the second circumstance – the recent experience of a lack of forage – is indeed important. Among the 10 d on which we made observations, there were 2 exceptional d (8 and 18 July) on which the focal bee did not produce any shaking signals at the start of her foraging activity. And one difference between these 2 d and the other 8 d when the focal bees did produce shaking signals is that both of these days followed days when food was provided at the feeder for the entire day, whereas the other 8 d followed days when food was provided at the feeder for only part of the day or not at all (Fig. 2). It appears therefore that the experience of resuming foraging after a period of dearth is important in motivating a forager to produce shaking signals.

The circumstances just discussed are certainly not the only ones under which worker bees will produce shaking signals. Several authors (ALLEN 1959b; SCHNEIDER et al. 1986a; NIEH 1997) have reported that foragers will perform shakings even when they are not actively engaged in exploiting a food source, such as early in the morning when it is still too dark or too cool for bees to fly from the hive. As described above, we too observed this phenomenon with the bee R30, who produced several hundred shaking signals before leaving the hive on the morning of 25 July. Also, it is well known that worker bees will produce shaking signals outside the context of foraging, when they direct their shakings at the queen in connection with swarming and mating flights (TARANOV & IVANOVA 1946; ALLEN 1956, 1958, 1959a; HAMMANN 1957; FLETCHER 1975, 1978a,b; SCHNEIDER 1989b). Thus it is clear that several very different sets of experiences can stimulate bees to produce shaking signals.

The phenomenon of animals producing one type of communication signal in a broad range of activities is not uncommon (SMITH 1977), and one of the best examples of this involves another of the honey bee's signals, the waggle dance. Worker bees produce this signal in association with collecting food (nectar or pollen), fetching water, gathering resin (VON FRISCH 1967), and choosing a new nest site (LINDAUER 1955). Any one type of signal, however, must have a constant message if it is to convey unambiguous information to its recipients. We can see this constancy of message in the waggle dance, for regardless of the activity that a dancing bee is engaged in, the message of her dance is the same: a good place (for food, water, resin, or a home) is located at a specific distance from the hive and in a specific direction from the sun. It seems likely that there is also just one message expressed by the shaking signal even though it is produced in various circumstances.

### The Message of the Shaking Signal

What information is made available by the shaking signal? Given the results reported here, we suggest that this signal informs other workers that it is time to prepare for greater activity. This message is consistent with the circumstances under which we repeatedly saw bees producing the shaking signal, namely the renewal of a profitable foraging opportunity following a period of food dearth. Under these circumstances many bees (probably the colony's foragers) were standing virtually motionless in the peripheral regions of the hive, presumably resting and minimizing their consumption on the colony's food reserves. Given their location and low mobility, it seems that most of these bees would have difficulty knowing when there is again desirable food to be gathered if there were no signals to give them this news. We suggest that the shaking signal helps to provide them with this information. Our hypothesis regarding the message of the shaking signal is further supported by our discovery of a shift from producing the shaking signal to producing the waggle dance during the first hour or so after a forager finds a rich new food source. This shift leads us to suggest that the shaking signal and the waggle dance function as complementary communication devices that work together to arouse a colony's foragers to greater activity, with the first telling foragers to *prepare* to work, and the second telling them precisely *where* to work.

Our interpretation of the information content of the shaking signal is consistent with most of the previous findings regarding this behavior in the context of worker-worker communication. Most notably, SCHNEIDER et al. (1986a) report that foraging-age bees (but not younger bees) that have received the shaking signal become more active in the hive and tend to move into the 'dance floor', the region of the combs near the hive entrance where waggle dances are performed. Likewise, NIEH (1997) reports that workers (ages unknown) move faster after being shaken than before, and that after being shaken their travel is oriented toward the hive entrance whereas before being shaken it shows a random orientation. ALLEN (1959b) also looked for a response to the shaking signal but did not detect any. This is probably because she followed each shaken bee only briefly, just 5 min on average, and shaken bees respond rather slowly to this signal. Both SCHNEIDER et al. (1986a) and NIEH (in press) had to follow each shaken bee for at least 30 min to detect the response. Thus the recipients of the signal behave in a way that is consistent with our proposed message, i.e. they slowly become more mobile and often they move into the 'dance floor'. Moreover, ALLEN (1959b), GAHL (1975), and SCHNEIDER (1986, 1989a) report observing foragers that interspersed shaking and waggle dancing. Their reports confirm our finding that sometimes a forager will combine the two types of signal and this lends further credibility to our suggestion that the two types of signal function together to boost a colony's foraging activity. SCHNEIDER et al. (1986a 1986b) and NIEH (in press) also report that worker bees, presumably foragers, will also begin to produce shaking signals in the hive in the early morning even before any foragers have flown from the hive, as we observed for one bee, R30. Can this phenomenon be reconciled with our proposed message for the shaking signal, that it informs other workers it is time to prepare for greater activity? We believe that it can, for the work of Schneider et al. (1986a,b) points to shaking signals playing an important role in activating a colony's workers early in the day at times of consistently good foraging. They report that pre-foraging shaking signals are conspicuous (in what they called 'major peaks of vibration dances') during most days (59 out of 68) of the spring and summer when food is plentiful in central California, but during relatively few days (only 8 out of 20) of the fall and winter when food is much sparser. And when they manipulated the availability of forage for a colony in a flight cage, they found that during several days of no food there was a gradual decline in the production of pre-foraging shaking signals, and that only after 3–4 subsequent days of good food did the production of pre-foraging shaking signals return to its original level. They conclude that at times of consistently plentiful food, foragers produce shaking signals before the foraging begins to prime their colony for later recruitment and foraging. This view of the function of the shaking signal is fully compatible with our view of the message of the shaking signal.

In conclusion, we believe that there is now good, though still incomplete, evidence that the shaking signal informs worker bees to prepare for greater activity, especially in the context of a colony's foraging operation. Certainly it is a communication process that merits deeper investigation. Both the specific constellation of stimuli that cause a worker bee to produce the shaking signal and the full effects of this signal on individual bees and on whole colonies, remain important subjects for future studies.

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