

## The Waggle Dance of the Honey Bee: Which Bees Following a Dancer Successfully Acquire the Information?

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Accepted May 25, 1994; revised November 30, 1994

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*During the waggle dance of the honeybee, the dancer is able to tell her nestmates the distance and direction to a rich food source (Frisch, 1967). Little is known about how waggle dance followers are able to read the waggle dance in the darkness of a hive. Initial observations showed that not all of the bees that appear to be dance followers behave the same. Some bees maneuver themselves behind the dancer, while others do not. The paths of a single dancer, trained to an artificial food source, and her followers were traced during the waggle runs. The success of these dance followers was compared to their position relative to the dancer. The results of this study show that during a waggle run a dance follower must position itself within a 30° arc behind the dancer in order to obtain the dance information. The results suggest that bees are using the position of their own bodies to determine direction.*

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**KEY WORDS:** *Apis mellifera*; honey bee; waggle dance; recruitment; communication.

### INTRODUCTION

It has been established that a foraging honey bee is able to communicate to its nestmates the distance and direction to a food source through the waggle dance (von Frisch, 1967; Gould, 1975; Esch and Bastian, 1970). It remains a mystery, however, specifically how the dance followers are able to acquire this information from the dance. To answer this question, one needs to know exactly which bees near a dancer are reading the dance. It is presently thought that many bees can simultaneously extract the information from a dance (see Fig.

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52 of von Frisch, 1967). Evidence from two studies, however, suggests otherwise. Mautz (1971) reports 2.32% of all bees following the dance make it to the feeder. Seeley (1992, Table 2) reported that it took an average of 77 waggle runs to recruit each bee to a food source 400 m away, indicating that dance information is being transmitted to only a small portion of those bees that have been assumed to be dance followers. Bozic and Valentincic (1991) report that not all of the bees near the dance appear to be dance followers. They found two behaviorally different kinds of bees following the dancer which they called followers and attendants, but they had no indication if any of these individuals arrived at the food site advertised by the dancer. If we can determine which bees are getting the information, then this should provide us with some clues about the mechanism of acquiring directional information.

To determine which bees following a dancer are actually receiving the information, I first examined the behavior of dance followers as they followed dancers advertising natural food sources. These observations suggested that a main factor that distinguishes bees behaving differently in the presence of a dancer is their position relative to the dancer. This led to the examination of the position of the dance followers in relation to the waggle run as they followed an individual trained to an artificial food source. The position of the dance followers in relation to the dancer was compared to their success in locating the food source. This experiment reveals the positional differences between the bees that do reach the recruitment target and those that do not. Thus this clarifies which bees near a dancer are actually getting information from the dancer and reveals a possible mechanism for acquiring directional information from the dance.

## MATERIALS AND METHODS

### Study Site

All the observations were made at Liddell Laboratory, Cornell University in Ithaca, New York State. This laboratory is located next to a large, open field. An observation hive was set up inside the building and bees were trained out to a feeder in this field.

### Study Colonies

*Colony 1.* On 9 May 1992, 2500 worker bees were labeled with numbered bee tags on the thorax and paint marks on the abdomen, using the method described by Seeley (1991). This created a colony in which each bee was individually labeled. The bees and their queen were placed in a two-frame observation hive with a wedge at the entrance to force the foragers to enter the hive on one side of the combs.

*Colony 2.* On 24 July 1992, 3500 worker bees were labeled in the same manner described above. They were likewise placed in a two-frame observation hive. The colors used in labeling the bees and their abbreviations are as follows: Blue-B, Red-R, Green-G, Gold-A, Yellow-Y, Orange-O, White-W.

### **Part 1: Analysis of Bees Following Dancers Advertising Natural Food Sources**

Colony 1 was set up in a well-lit room, with the entrance to the observation hive connected to the outdoors through a small tunnel. The bees were allowed to forage freely outside. A videocamera was set up in a fixed position so that it would record the bees' activity over the entire dance floor. Data were collected on 20 and 21 May, both of which were warm, sunny days.

The videotapes were examined to determine the movement of both individual dancers and their followers. A dance follower was provisionally defined as any bee within one bee's body length from the dancer during the dance, regardless of whether the bee faced the dancer. The position and body orientation of the dancer and the dance follower relative to each other were noted at one second intervals. This information was recorded first on a transparent sheet mounted over the video screen using two different-colored markers. The information was then transferred to paper for a permanent record. This produced a plot of the path taken by a dance follower relative to the dancer.

### **Part 2: Analysis of Bees Recruited by a Dancer Advertising an Artificial Food Source**

Colony 2 was placed in a room similar to the one above. Twenty bees were trained out to a feeder 150 m from the hive. All the bees visiting the feeder during the training were marked with silver paint to indicate that they had experience at the feeder.

A videocamera was set up at the hive with an internal clock that was synchronized with a clock at the feeder. One person was stationed at the feeder throughout the experiment while another was at the hive to operate the videocamera. A 2.5 M sugar solution flavored with orange was placed in the feeder. All the bees except one (OW11) were captured in plastic bags as they arrived at the feeder. OW11 was chosen because she was determined to be a good dancer before the experiment started. Of the 10 bees that were trained to the feeder prior to the experiment, she was the first bee to start advertising the food source. This bee was then video recorded every time she returned to the hive from the moment she entered it until she left. These recordings also registered every bee that followed her dances as well as the time they followed the dances. The person at the feeder captured every bee arriving at the feeder (hereafter called a "successful follower") and recorded her identity and time of arrival.

The videotapes were examined to find the position relative to the dancer for all the successful followers. This was recorded, as described above, for each waggle run that a successful follower followed. I observed that during each waggle run each successful follower would lunge at the dancer. The orientation of the bee's body while making the lunge, as well as that of the dancer's body, was recorded. The angle between the two bees' bodies is called the "following angle." A bee moving in alignment with the dancer would be at  $0^\circ$ , while a bee perpendicular to the dancer would be at  $90^\circ$ . The same procedure was applied to several bees that followed the dancer but never arrived at the feeder, hereafter called "unsuccessful followers."

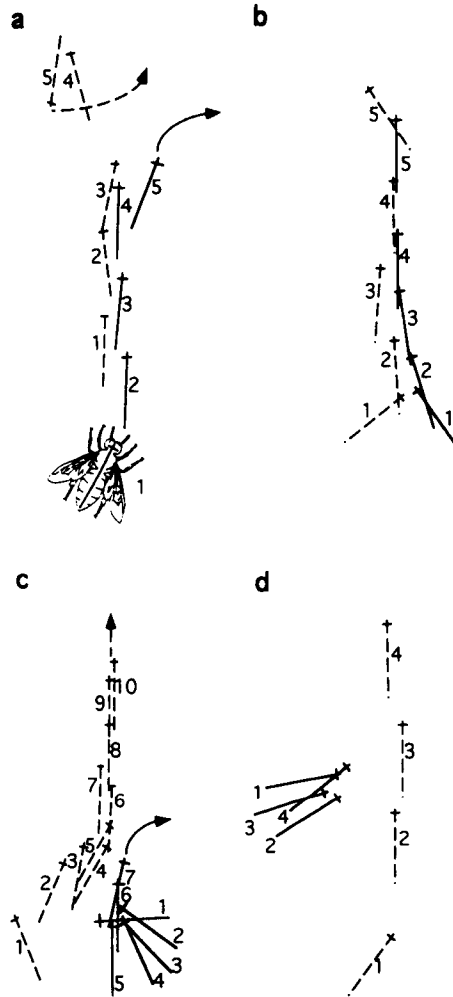
The mean following angles were calculated using the method described by Batchalet (1981). This transforms a circular measure into a linear one, allowing me to compare the mean following angles of the successful and unsuccessful followers with the Mann-Whitney test. The mean following angle of each follower was used to avoid the pooling effect. The number of waggle runs followed by each type of bee was also compared using the Mann-Whitney test.

## RESULTS

### Part 1: Behavior of Bees Following Dancers Advertising Natural Food Sources

A total of 63 followers of 6 dancers was recorded. The duration of the waggle runs of these dancers ranged from 0.5 to 12.5 s. The behaviors of the dance followers fell into two distinct groups. Bees in the first group would maneuver themselves so that they were approximately behind the dancer (Figs. 1a-c). In the longer dances these bees would get directly behind the dancer and then continue to follow her. At the end of the waggle run the followers would position themselves so that they pick up the dancer on the return run. The dance follower seemed to be able to maneuver itself to the dancer in order to follow another waggle run. In many instances more than one bee would try to maneuver itself into the same position behind the dancer. This sometimes led to some bees being pushed away from the dancer. For a single waggle run, a maximum of three bees would be able to complete maneuvering behind the dancer. For example, if five bees all jostled for the same position, generally only one or two of these bees would be able simultaneously to get behind the dancer; the others would lose contact with the dancer or would be forced to the side. In many cases the bees that lost contact with the dancer just wandered off.

The followers do not necessarily stay with the dancer for the entire waggle run. In the case of one bee following the dancer with 12.5-s waggle runs, the follower remained with the dancer for only about 7 s (Fig. 1c). Indeed, none



**Fig. 1.** Typical patterns of the spatial relations between dancer (dashed lines) and dance follower (solid lines). The bees' positions were recorded at 1-s intervals. Each interval is indicated by a number next to the line. (a, b) Bees that exhibited the alignment behavior in a waggle run that lasted for 4 s. (c) A follower that showed the alignment behavior during a 12-s waggle run. (d) A follower that stayed in the same position.

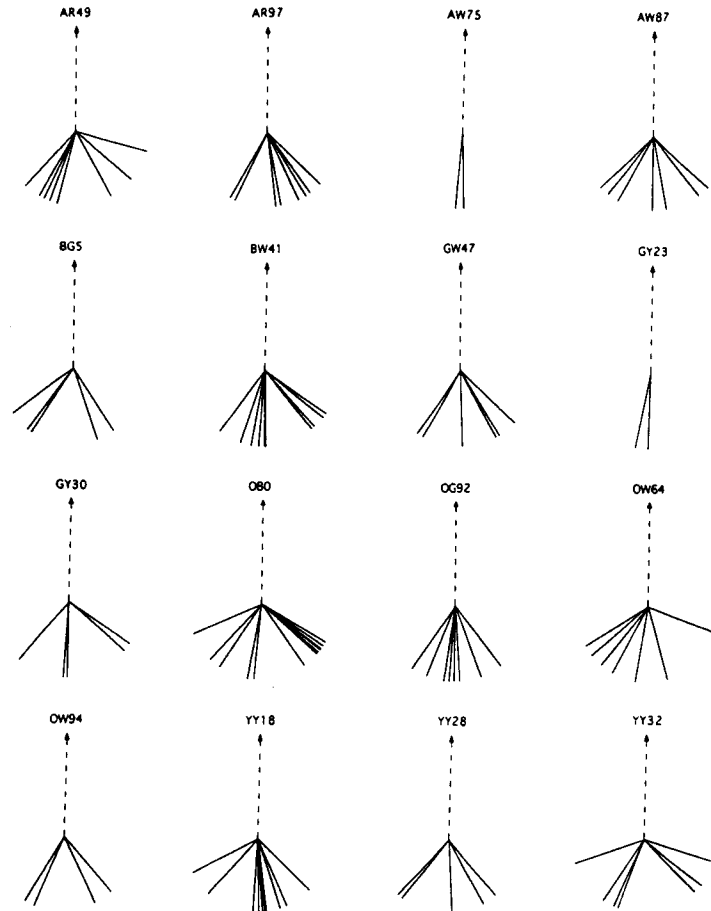
of the eight bees that followed a 12.5-s waggle run stayed with the dancer throughout the waggle run. All the bees remained with the dancer throughout waggle runs if the runs were short, i.e., 4 s or less.

The bees in the second group showed less motion than those in the first group. These bees stayed in the same position in which they started (Fig. 1d). Many times these bees simply remained to the side of the dancing bee throughout the waggle run. Usually these bees would either wander away from the dancer

after the waggle run was over or would remain in the same position on the comb and would not make any attempt to remain near the dancer.

### Part 2: Position of Successful Followers During the Waggle Dance

Sixteen dance followers arrived at the feeder. All of these successful followers behaved similar to the bees in the first group of Part 1, that is, they maneuvered to position themselves behind the dancer. Each successful follower

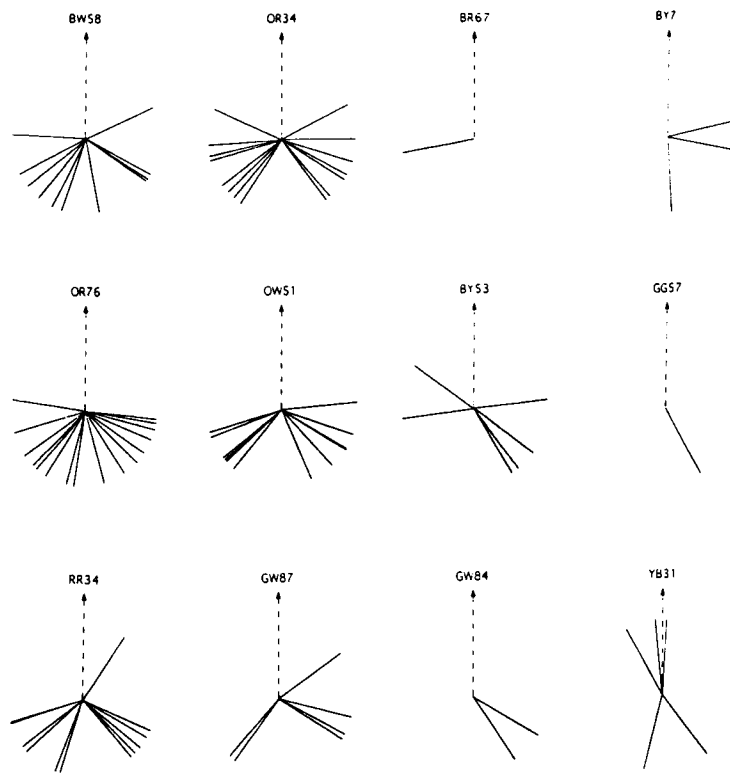


**Fig. 2.** The following angles of all 16 successful followers. The dancer is heading straight up. Each line represents the following angle of the dance follower was during a single waggle run. For example, GW47 followed a total of six consecutive waggle runs. Each pattern comes from the episode of dance following which was recorded immediately before the bee arrived at the feeder.

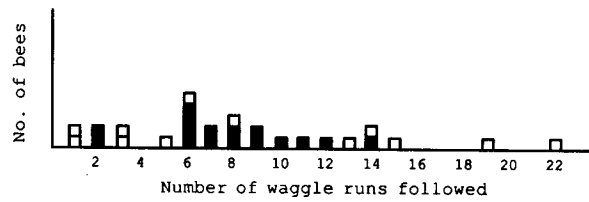
only followed one set of consecutive waggle runs. Figure 2 shows the following angles of each bee as it followed consecutive waggle runs. The patterns of all successful followers were very similar. Although there is some scatter, the following angles were clustered near  $0^\circ$ , corresponding to a position directly behind the dancer. Successful followers followed the dancer for  $7.8 \pm 3.2$  (range, 2–14) consecutive waggle runs.

#### Position of Unsuccessful Followers During the Waggle Dance

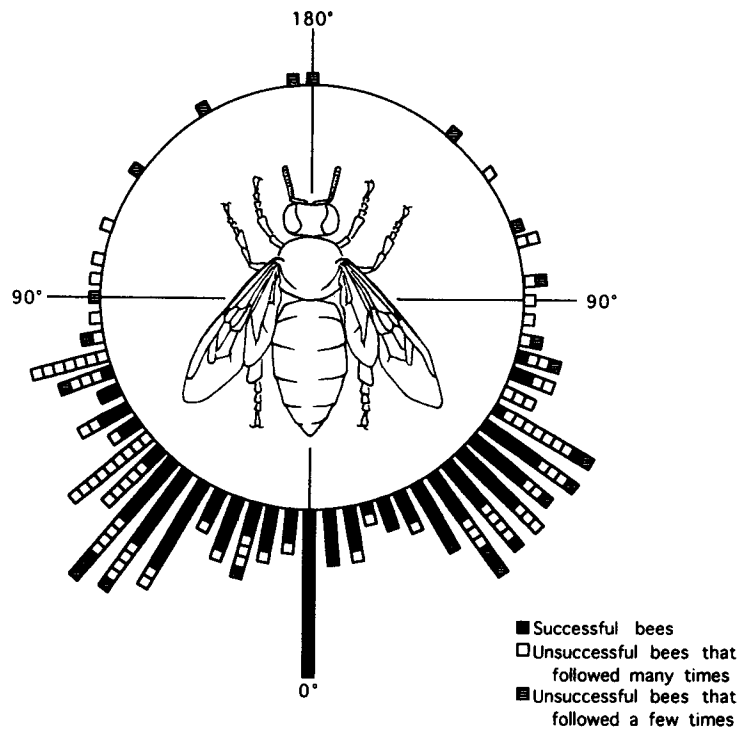
Twelve unsuccessful followers were examined. The number of waggle runs followed and their position relative to the dancer differed from what was observed for the successful followers. To understand the difference, it is important to note that unsuccessful followers fell into two categories, distinguished by the number of waggle runs followed (Fig. 4). Bees in the first group followed significantly



**Fig. 3.** The following angles of all 12 unsuccessful followers. BR67, BY7, BY53, GG57, GW87, GW84, and YB31 all followed only a few waggle runs, while BW58, OR34, OR76, OW51, and RR34 all followed many waggle runs.



**Fig. 4.** Comparison of the number of times the bees followed waggle runs between bees that were successful (gray) or unsuccessful (white). The unsuccessful followers fall into two categories distinguished by the number of times the bee followed the dancer. Bees in the first group followed 2-8 waggle runs; those in the second group followed 13-22. These two groups seem to bracket the group of successful followers.



**Fig. 5.** Circular distribution of each following angle for both the successful and the unsuccessful followers. Each following angle was placed in a 5° bin. 0° denotes a bee aligned behind the dancer. Gray bars represent the following angles of the successful followers, white bars the angles of unsuccessful followers that followed many waggle runs, and diagonally striped bars the angles of unsuccessful followers that followed only a few runs. The successful followers were significantly more in line with the dancer (following angle closer to 0°) than both groups of unsuccessful followers. The two unsuccessful groups of bees show no significant difference.

( $P = 0.017$ ) fewer waggle runs:  $3.9 \pm 2.6$  (range, 1–8). Those in the second group followed significantly ( $P = 0.0014$ ) more waggle runs:  $16.8 \pm 3.6$  (range, 13–22). The unsuccessful followers that followed many waggle runs tended to behave similarly to the successful followers, but with less success in positioning themselves directly behind the dancer (Fig. 3). The unsuccessful bees that followed only a few times had an essentially random pattern of position relative to the dancer.

#### Comparing the Positions of Successful and Unsuccessful Followers

Figure 5 shows a comparison of the following angles for the various types of bees. The mean following angle of the successful followers was significantly smaller than that of both groups of unsuccessful followers (df 26,  $P = 0.0001$ , for successful followers versus all the unsuccessful followers; df 19,  $P = 0.0011$ , for successful followers versus unsuccessful followers that followed many times; and df 21,  $P = 0.0019$ , for successful bees and unsuccessful bees that followed only a few times). The two unsuccessful groups of bees show no significant difference in the mean following angle (df 10,  $P = 0.4$ ). Of those bees observed, 90.9% (10 of 11) of the followers having a following angle of less than  $5^\circ$  were successful followers.

### DISCUSSION

The results of these experiments suggest that the position of the bee following the dance relative to the dancer is important in determining whether or not the bee succeeds in locating the food source. In Part 1, it was found that there were two basic behavior patterns of bees near dancers, one in which the bee maneuvered itself behind the dancer and one in which the bee stayed relatively motionless. This difference probably reflects a difference between bees that are actually trying to follow the dance and bees that are simply in the immediate area. If correct, then this implies that the maximum number of bees acquiring information from a dancer at any one time is considerably less than what was originally thought. It appears that although the average number of bees simultaneously orienting to a dancer can be as high as five or six (see Fig. 52 of von Frisch, 1967), at most only one or two bees are simultaneously receiving the dance information.

The second part of the study indicates that just because a bee follows a dance does not guarantee that it will be successfully recruited. In this experiment it was found that a bee has to be within an approximately  $30^\circ$  arc behind the dancer to be recruited successfully. This is contrary to what was proposed by Bozic and Valentincic (1991), who proposed that the dance follower tries to maintain a position perpendicular to the dancer. This study shows that bees that

were unsuccessful failed to get behind the dancer sufficiently (Fig. 5). This correlation between position and success suggests that position plays a key role in determining a bee's ability to acquire information from a waggle dance. The successful followers seemed to need to follow more than one waggle run to get the information. In this study the successful followers attended a mean of 7.8 consecutive waggle runs before leaving the hive. Esch and Bastian (1970) and Mautz (1971) also report successful dance followers following a mean of 6–8 waggle runs.

The unsuccessful followers in Part 2 fell into two categories, bees that followed many waggle runs and bees that followed only a few. The reason for the lack of success in these two groups may be very different. The bees that followed a mean of 3.9 waggle runs might have been either uninterested or discouraged for some reason. In a few cases these bees positioned themselves in front of the dancer and the dancer just plowed right into them. This may have discouraged these particular followers. The failure of bees in the group that followed many waggle runs might be due to these bees being new foragers. Although they may know in general how to read a dance, they may have to fine tune their skills, especially how to maneuver behind the dancer. One might expect that these unsuccessful followers would leave the hive but be unsuccessful in finding food. Esch and Bastian (1970) describe this very behavior by the unsuccessful foragers that they observed. Unfortunately, the ultimate fate of these following bees could not be determined in this study because I recorded only bees following the dancer and bees reaching the feeder.

#### **How Do the Bees Align Themselves?**

By aligning themselves with the dancer, the followers would be able to measure the angle of the waggle run relative to gravity by sensing the angle of their own bodies. This would allow them to easily determine the direction to the food source, but this requires that bees know that they are directly behind the dancer. How might they do so? The dance is done in the darkness of the hive preventing the use of visual cues.

One possibility stems from the recent work done by Michelsen *et al.* (1987), who show that the waggle dancer emits a near field sound during the waggle run. They have demonstrated that the sound is unevenly distributed around the waggle dancer and is stronger toward the abdomen. The sound intensity probably falls below the bee's threshold of perception beyond about 2 mm from the dancer. This means that a bee to the side of the dancer would hear the dance sound in pulses. For example, as the abdomen swings to the right, bees on the right will be able to detect the sound, but once the abdomen swings to the left these bees will be unable to do so. In contrast, if a bee maneuvers behind the dancer, it will always be in range of the sound emitted by the dancer.

### Importance of Alignment

Since the bees are indeed trying to align themselves behind the waggle dancer, there must be some advantage in doing so. The most likely explanation for this is that the bees are using their own bodies to gain the directional information of the waggle dance. Once behind the dancer during the waggle run, a dance follower will be traveling in the same direction as the dancer. This is supported both by the behavior observed in Part 1 of the study and by the fact that all the successful dance followers had significantly smaller following angles than the unsuccessful dance followers (Fig. 5).

### Conclusions

Based on the results of these experiments, I would like to offer a more precise definition of a waggle dance follower. The actual followers are those bees that try to align themselves with the dancer during the waggle run. The experiments have demonstrated that the bees behaving in this way are the ones who will be able to find the food source advertised in the dance. It is highly possible that the bees are able to use the alignment of their own bodies to measure the direction of the dance.

### ACKNOWLEDGMENTS

Financial support was provided by Grant BNS 89-16006 from the U.S. National Science Foundation to Tom Seeley. I would like especially to thank Tom Seeley for all his help during both the fieldwork and his critical comments on the manuscript. Thanks are also due for Scott Camazine for his help in the field and his valuable comments, Barrett Klein and Cornelia König for their help marking the bees, George Gamboa for his comments on the manuscript, and Barrett Klein for his honey bee illustrations.

### REFERENCES

- Batschelet, E. (1981). *Circular Statistics in Biology*, Academic Press, New York.
- Bozic, J., and Valentincic, T. (1991). Attendants and followers of honey bee waggle dances. *J. Apicult. Res.* **30**: 125-131.
- Esch, H., and Bastian, J. A. (1970). How do newly recruited honey bees approach a food site. *Z. Vergl. Physiol.* **68**: 175-181.
- Gould, J. L. (1975). Honey bee recruitment: The dance-language controversy. *Science* **189**: 685-693.
- Mautz, D. (1971). Der kommunikationseffekt der Schwänzeltänze bei *Apis Mellifica carnica* (Pollm.). *Z. Vergl. Physiol.* **72**: 197-220.
- Michelsen A., Towne, W. F., Kirchner, W. H., and Kryger, P. (1987). The acoustic near field of a dancing honeybee. *J. Comp. Physiol. A* **161**: 633-643.

- Seeley, T. D. (1989). Social foraging in honey bees: How nectar foragers assess their colony's nutritional status. *Behav. Ecol. Sociobiol.* 24: 181-199.
- Seeley, T. D., and Towne, W. F. (1992). Tactics of dance choice in honey bees: Do foragers compare dances? *Behav. Ecol. Sociobiol.* 30: 59-69.
- Seeley, T. D., Camazine, S., and Sneyd, J. (1991). Collective decision-making in honey bees: How colonies choose among nectar sources. *Behav. Ecol. Sociobiol.* 28: 277-290.
- von Frisch, K. (1967). *The Dance Language and Orientation of Bees*, Harvard University Press, Cambridge, MA.