

THE DANCE OF THE HONEYBEE: HOW DO HONEYBEES DANCE TO TRANSFER FOOD INFORMATION EFFECTIVELY?*

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A honeybee informs her nestmates of the location of a flower she has visited by a unique behavior called a “waggle dance.” On a vertical comb, the direction of the waggle run relative to gravity indicates the direction to the food source relative to the sun in the field, and the duration of the waggle run indicates the distance to the food source. To determine the detailed biological features of the waggle dance, we observed worker honeybee behavior in the field. Video analysis showed that the bee does not dance in a single or random place in the hive but waggled several times in one place and then several times in another. It also showed that the information of the waggle dance contains a substantial margin of error. Angle and duration of waggle runs varied from run to run, with the range of $\pm 15^\circ$ and $\pm 15\%$, respectively, even in a series of waggle dances of a single individual. We also found that most dance followers that listen to the waggle dance left the dancer after one or two sessions of listening.

Keywords: *Apis mellifera* – waggle dance – foraging – food location – honeybee – social insect

INTRODUCTION

The honeybee (*Apis mellifera*), one of the social insect species, is well known to have the ability to communicate with its nestmates, using the so-called “waggle dance” to inform them of the location of a food source she has visited [3, 10, 12]. In the waggle dance, the dancer walks in a straight line with both her body wagging and wings beating (waggle run), then back to the starting point without wagging or beating. On a vertical comb, the direction of the waggle run relative to gravity indicates the direc-

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tion to the food source relative to the sun in the field. The duration of the waggle run correlates with the distance to the food source. We observed that follower bees keep close contact with the dancer, and may be recruited to visit the food source the dancer is advertising. In the hive, however, it is too dark for followers to “watch” the dance. Hence, they emit a sound by vibrating their wings during the waggle run, which is rapidly attenuated with distance from the dancer [6, 7, 8], suggesting that information can be transferred within only a very limited area in the hive. This means that only a few bees, compared to the total number of the bees in the hive, will receive the information. In spite of this fact, the dance has been considered to be an effective way for honeybees to accumulate their food and maintain their colony. How much benefit do honeybees obtain from doing the waggle dance? What strategies for propagation of information are hidden, and how many bees have to share “the information” to maintain their colony? To address these questions, researchers have applied many mathematical models and computer simulations based on parameters from observations of bee behavior [1, 2, 4, 9, 11]. However, the biological features of dance behavior and followers are not yet fully understood. To obtain better insights into the waggle dance effect, we observed and analyzed honeybee behavior in the field. Here, we will report characteristic features of honeybee dance behavior, dancing patterns of the dancers, precision of dances, and behavior of the followers.

MATERIALS AND METHODS

Behavioral studies were performed in Sapporo, Japan, from 8:30 am to 4 pm on several days in August and September, 2006 (temperature: 25–36 °C in most experiments). Honeybees, *Apis mellifera*, on a comb taken from an original hive were kept in the beekeeping box with a queen for behavioral observation. Bee behavior on the vertical comb was monitored by a video camera (JVC, GR-HD1), with the movie stored on a digital video tape (30 frames/sec) and then analyzed off-line frame by frame. All bees examined here were numbered specifically to distinguish each individual.

RESULTS

Behavioral patterns of dance behavior

A waggle dance consists of one or more waggle runs. Observations of 202 waggle runs in 11 bees (an average of 18.4 runs per bee) revealed that a bee performs the waggle run several times at one place on the comb and then moves to another place before resuming the waggle runs. The locations where waggle runs were observed appear to be “clusters” (Fig. 1). All 20 waggle runs of Bee 10 were observed in two clearly distinguishable areas (Fig. 1, open circle). Until the 13th run she performed in cluster I; then she moved to cluster II and wagged until she stopped. A similar ten-

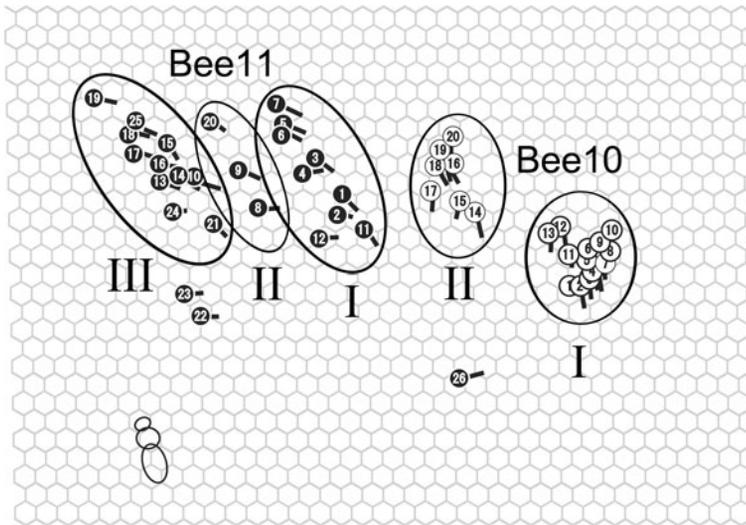


Fig. 1. Locations and orientations of waggle runs of two bees at the same time (Bee 10, open circle; Bee 11, black circle). Starting points are indicated by circles. The numbers in the circles indicate the order of the waggle runs. The direction of the line shows the waggle run direction, and its length shows the distance of the run. For reference, honeycombs and honeybees are illustrated. Twenty-six and 20 runs were observed in Bee 11 and Bee 20, respectively

endency to “dance and move” was observed in other bees (e.g., Fig. 11, Bee 2). However, some bees did not show this tendency. For quantitative evaluation, cluster analysis such as Ward’s method is necessary, and therefore we are now analyzing the dancing place of all bees.

Precision of waggle run

We measured the angles of 358 waggle runs relative to the perpendicular orientation (gravity) of the 20 dancing bees and found that the orientation of the run varied from run to run even in a series of waggle runs performed by same the individual (Fig. 1, Fig. 2A). Angles of 84.9% of waggle runs differed from the mean orientation by $\pm 15^\circ$.

Waggle run durations also varied considerably from run to run, even in a series of waggle runs by the same individual. In Bee 12, for example, the difference in the duration was at most 0.87 sec (1.47 sec in the 4th run and 0.6 sec in the 3rd run), although the mean duration was 1.08 sec. Bee 3 and Bee 6 exhibited long runs (averaging 8.37 sec in Bee 3 and 11.81 sec in Bee 6). In 16 out of 21 runs for Bee 3 and in 9 out of 14 runs for Bee 6, the difference of each run from the mean duration was larger than 1 sec; when translated into the distance the bee was representing, the difference was more than 200 m [12]. Dividing the duration of each single waggle run

by the mean duration of a corresponding series of waggle runs, we found that 56.1% of waggle runs ranged within a mean duration $\pm 15\%$, and 81.3% of them were within $\pm 30\%$ (Fig. 2B).

Behavioral patterns of dance followers

Followers go out to forage after listening to several waggle runs. Even in a series of waggle runs by the same individual, some waggle runs attracted no followers while others attracted up to 10 bees. We observed a positive correlation between the dura-

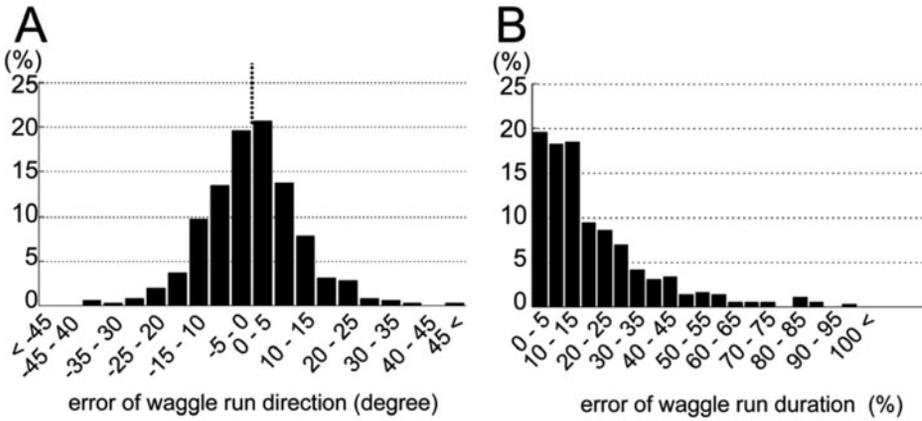


Fig. 2. Distribution of error of angle (A) and duration (B) of runs

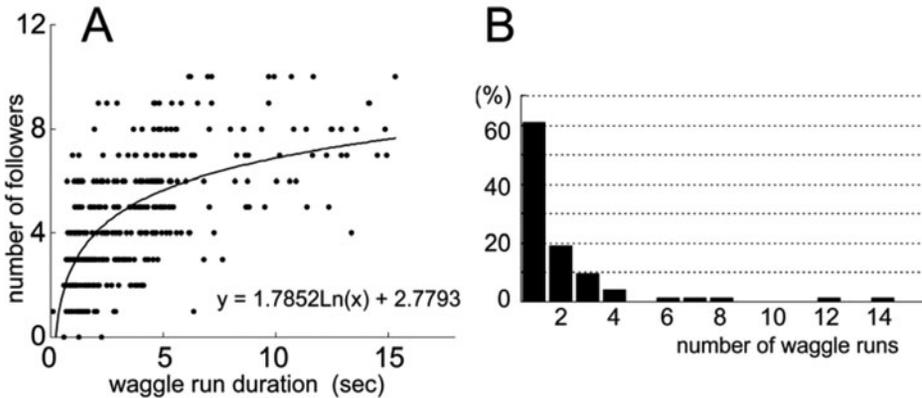


Fig. 3. A: The relationship between waggle run duration and the number of followers. Each dot represents a single waggle run (n = 355). B: The number of bees that followed waggle runs from observation of 62 followers

tion of waggle run and the number of followers. When waggle runs lasted longer than 10 seconds, at least 6 followers were usually attracted (Fig. 3A). In short runs (shorter than 2 sec), wider ranges in the number of followers were observed, from 0 to 9 (Fig. 3A). Some followers left the dancer after listening to only one waggle run, while others followed the dancing bee more than 10 times (Fig. 3B). About 80% of followers observed ($n = 62$, 5 dancers) left dancers after one or two waggle runs (Fig. 3B). Only 5 bees listened to more than 6 consecutive waggle runs (Fig. 3B).

DISCUSSION

We found that dance information is not so precise, containing fluctuation of $\pm 15^\circ$ for direction and $\pm 15\%$ for distance. Furthermore, followers do not listen to all of the waggle runs performed by a dancer (see “Behavioral patterns of the dance follower”). Follower honeybees may receive “ambiguous” information about the orientation and distance of the food source, which entails a non-negligible error for foraging. Our observations show that followers have to forage with imprecise information regarding both orientation and distance in any case. In spite of this fact, bees are considered to use dance information for their effective foraging behavior. An unknown mechanism, thus, for effective collection of food must be hidden in their behavior. A new mathematical model based on our behavioral observations could be helpful to reveal it.

Since the degree of imprecision of dance information depends on the distance of the food source [13] and the successful rate of foraging depends on the number of runs the recruited bee had followed and the relative position of the follower to the dancer [5], we need, as a next step, to control the location of the food source and also trace all of the behavior of the recruited bee from following the dancer to foraging. Incorporating these biological parameters into our mathematical model, we will obtain a better understanding of the effect of the waggle dance.

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