

Research Article

Follower Position Does Not Affect Waggle Dance Information Transfer

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It is known that the honey bee waggle dance communicates the distance and direction of some item of interest, most commonly a food source, to nestmates. Previous work suggests that, in order to successfully acquire the information contained in a dance, other honey bees must follow the dancer from behind. We revisit this topic using updated methodology, including a greater distance from the hive to the feeder, which produced longer, more easily-read dances. Our results are not congruent with those of earlier work, and we did not conclude that honey bees must follow a dancer from behind in order to obtain the dance information. Rather, it is more likely that a follower can successfully acquire a dance's information regardless of where she may be located about a dancer.

1. Introduction

The honey bee (*Apis mellifera* L.) waggle dance has been a topic of great interest to biologists for over 50 years, and although it has been well researched during that time, certain aspects related to it remain contested. The waggle dance consists of a vigorous “waggle phase” [1] and brief return phase. The information encoded in the waggle phase communicates the distance and direction of some item of interest, most commonly a food source, to other bees within the hive [2, 3]. When a returning forager performs the waggle dance to alert her nestmates to the existence of a useable food source, other bees crowd around her, touching her with their antennae [4] and at times following her movements through portions of the dance. When a dance follower observes multiple waggle phases in a single dance, the averaging hypothesis states that she incorporates the information into a single flight vector [5].

Judd [6] examined whether there were specific locations relative to the dancer that a follower must occupy in order to successfully receive the information from the dance. He concluded that in fact bees must follow from the rear of a dancer for information transfer to occur.

However, we have not observed following bees vying for the limited positions available at the rear of dancers (Kietzman and Visscher, personal observation). Additionally, bees following from the side of a dancer remain in contact with the dancer for longer periods of time than bees following from other positions [7], which would give those bees a greater opportunity to interpret the dance. Based on our observations, dance followers appear satisfied in any position where it is possible to have antennal contact with the body of the dancer. Also, Judd [6] described a type of “lunging” movement that was of importance to the dance following experience, and it was unclear what this movement entailed. It is possible that the methods he employed did not produce data that were easily interpreted, as the feeding station he employed was located at a mere 150m from the hive, which is very close compared to the distances honey bees will typically travel in search of food [8]. At this distance, bees perform very short waggle runs with much turning during the dance. Due to such constant turning, it would be difficult to determine where the followers were located relative to the dancer. Additionally, it would be difficult for the followers to position themselves in a precise location for any length of time.

This study was conducted using a feeding station located further away from the hive. Data analysis was structured to address the hypothesis that bees would follow more dances from the rear of a dancer, as compared to the null hypothesis that they would follow dances from random positions.

2. Methods

2.1. Overview. This experiment was conducted over the course of three days, from 20 September 2010 to 22 September 2010, in agricultural fields belonging to the University of California, Riverside. Our approach, like that of Judd [6], was to mark an entire two-frame observation colony of honey bees (approximately 2500 individual bees), train scouts to a feeding station, and, with video, observe the dance following behavior of those bees that were successfully recruited.

2.2. Colony Marking. All the bees used in this experiment were marked with numbered tags following the method described by Seeley *et al.* [9]. To do this, approximately 2500 worker bees were shaken from a large hive into a wire mesh box. From there, we shook small groups of approximately 10 bees each into plastic bags and refrigerated them briefly to sedate them. We then transferred them to a cold-well, an open-topped foam box with “blue ice” covered with paper towels at the bottom, so that they would remain chilled. We marked the bees with colored plastic number tags adhered to their thoraxes and dots of colored paint applied to their abdomens with paint pens. Using this system of marking all the bees in the colony could be individually identified. After they were marked, we moved the bees to a different cage to recover. Once all the bees had been marked, we established them as a new colony in a two-deep-sized-frame observation hive together with their original queen.

2.3. Training. The bees were allowed to fly and forage freely during an acclimatization period that lasted one week. Following this, we trained foragers to visit a feeding station baited with 2M sucrose solution lightly scented with anise oil scent drops. The feeding station was first placed directly outside the entrance to the hive and gradually moved further away as a group of 15-20 foragers began visiting it repeatedly. By the end of the two-day training period, the feeding station was located at 400m from the hive. This was the furthest distance used in the experiment and was visited consistently by four foragers. Data collection began directly after the last day of training had been completed using unscented sucrose solution. We recorded the identities of all the visitors to the feeder during the training period.

The feeding station was located at 400 m from the hive on the first day of the experiment and then moved back to 350 m on the second day and 150 m on the third day. We used the 400 and 350 m distances so that the dancers would produce longer waggle runs, which would consequently be easier to analyze. We used the 150 m distance for one day so that the resulting shorter waggle runs would be more similar to the dances observed by Judd [6].

2.4. Dance Following. During the experiment, three trained foragers that reliably danced promptly upon arrival to the

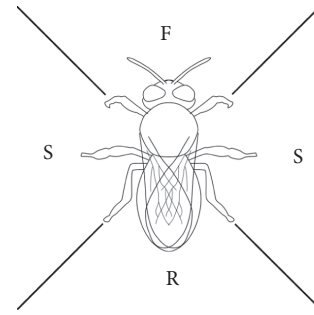


FIGURE 1: The possible positions available to a bee following a waggle dancer (pictured at center). F: the front of the dancer; S: the side of the dancer; R: the rear of the dancer.

hive were allowed to fly freely between the feeding station and the hive. To control for the effects of the presence of other bees at the feeder, which can attract recruits [10], an observer at the feeding station (PKV and undergraduate assistants) captured all other bees that visited the feeder (others familiar with the feeder and new recruits), recorded their identities, and retained them in a cooler until the end of the experiment, so that they could not return to the hive.

At the observation hive, an observer (PMK) recorded the waggle dances that each of the three focal foragers performed and the bees following the dances, using a digital video camera (Sony Handycam DCR-HC20). Other bees that had visited the feeder during the training period were considered nonnaïve and therefore were not included in the data analysis.

2.5. Video Analysis. The list of bees that had arrived at the feeder was used to locate those bees following dances in the video footage. Not all dance followers are active foragers and may instead be following for some other reason, such as waiting to unload nectar from the dancer (reviewed in Seeley 1995); only those that did arrive at the feeder were included in the data analysis. We considered these to have had a successful dance following experience. We defined a follower as any bee facing a dancer and within antennal contact and counted the number of waggle runs that each follower attended. For each waggle run, the position that the follower was in relevant to the dancer was recorded. There were three possible positions (Figure 1) available to the followers, corresponding to the front of the dancer (F), the side of the dancer (S), and the rear of the dancer (R). During the original video analysis, each of these positions was split into three smaller positions, each of a size to be occupied by a single follower bee. This allowed for greater precision during the video analysis, but, to make our statistical analyses more robust, we then pooled the values for the smaller positions into the larger zones pictured in Figure 1.

2.6. Analysis. We first analyzed the data to determine the relationship between the following position used and the number of waggle runs followed by each bee. Because the rear position was of particular interest, the likelihood that a bee following exclusively from a single position would use the rear position as compared to the other possible positions

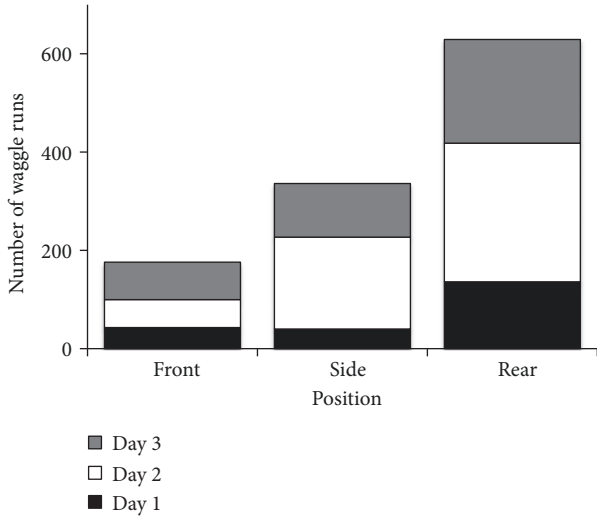


FIGURE 2: The total number of waggle runs followed in each position per day. Each bar pools all of the runs followed in that position for all the days of the experiment.

was also addressed. Additionally, in the event that the final following experience was of key importance to successfully arrive at the feeding station, the final waggle run followed by each follower was examined and the position used by each bee was recorded. Finally, the most efficient followers or those that only needed to follow 10 or fewer waggle runs before arriving at the feeding station were analyzed to determine whether they had a position preference.

3. Results

On Day 1, 47 bees arrived at the feeder and we identified 16 of them following dances in the resulting video footage. On Day 2, 34 bees arrived at the feeder and 22 were in the footage. Day 3 had the lowest number of visitors to the feeder, 29, and 17 of them were also in the footage. The number of waggle runs followed by each bee varied widely, ranging from as few as a single run to as many as 131. To address this difference, in a later portion of this analysis, we assessed the following experiences of the most efficient bees (those that had followed fewer than 10 waggle runs).

Figure 2 summarizes the total number of waggle runs followed in each position per day of the experiment. We used a generalized linear mixed model to assess the effect of position on the number of waggle runs followed. Because there was no significant effect of the day on the outcome of the model (P value=0.0755), the results from each of the three days were combined into the same model. The number of waggle runs followed from the rear position was significantly different from the number of runs followed from the front position (P value $<2 \times 10^{-16}$). The number of waggle runs followed from the front was also significantly different from the number of dances followed from the side (P value=3.86 $\times 10^{-12}$). A post hoc Tukey test assessed the differences among all pairwise combinations of positions and

TABLE 1: Summary of the differences among all pairwise comparisons of the positions using a post-hoc Tukey test.

Pair	Std. Error	z	p-value
R-F	0.08536	14.921	$<1 \times 10^{-10}$
S-F	0.09314	6.942	$<1 \times 10^{-10}$
S-R	0.06764	-9.270	$<1 \times 10^{-10}$

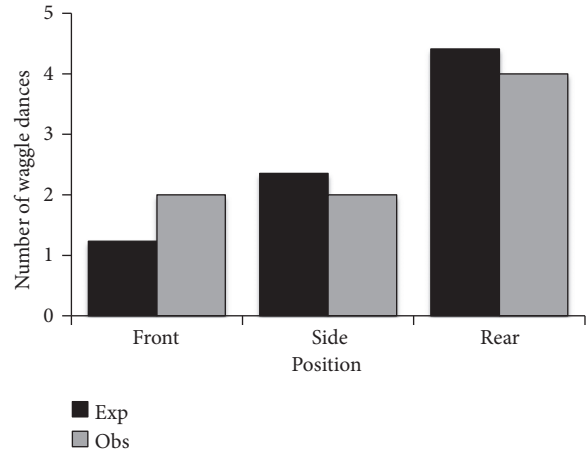


FIGURE 3: The observed and expected number of waggle dances followed in each of the possible positions by bees that followed from a single position.

found significant differences between each. These data are summarized in Table 1.

Of the 55 bees that were observed following dances, 47 followed from at least two of the possible positions. For the question of whether particular positions are more effective for information transfer, recruits that had followed from just a single position are the most informative. To evaluate Judd's assertion that following from the rear was essential in order for followers to successfully interpret the dance information, we performed a Chi-square test on these 8 individuals ($X^2=0.999$, P value=0.067, and $df=2$) (Figure 3). Four of these bees never followed from the rear position, using the front or side positions instead.

To determine whether a follower's final position prior to departing the hive was of particular importance to her dance following experience, we recorded the positions, each of the successful followers used during the last waggle runs they watched (Figure 4). We then compared the number of waggle runs followed in each position using ANOVA (Table 2). There were no significant differences found among the positions (P value=0.3496, $df=2$, and $F=1.2586$).

There was a very wide range in the number of waggle runs followed by each bee. Of key interest were the individuals that were highly efficient in locating the feeding station. This efficiency was measured in the number of waggle runs observed before departing for the feeding station. We considered individuals that followed 10 or fewer waggle runs to be the most efficient and analyzed their following experiences. Because Day 1 of the experiment had the most efficient recruits of any of the days, we used the efficient

TABLE 2: The waggle runs followed in each position by the most efficient followers of Day 1.

Bee	F	S	R
1	0	3	0
2	2	1	6
3	2	5	1
4	0	1	5
5	0	0	1
6	2	0	2
7	0	3	6
8	1	0	0
9	1	0	6

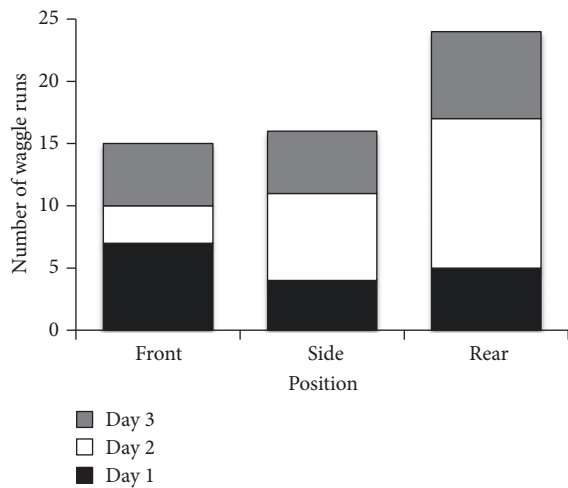


FIGURE 4: The final position followed by each of the successful followers that arrived at the feeding station. Each of the bars pools all of the runs followed in that position for all of the days of the experiment.

followers ($n=9$) from that day for this analysis. A summary of the waggle runs followed in each position by each of the efficient bees from Day 1 is found in Table 2. We compared the number of runs followed per position for the bees using ANOVA. There were no significant differences among the positions (P value=0.07822, $df=2$, and $F=2.839$).

4. Discussion

Far more bees arrived at the feeder than were observed following dances in the video footage, particularly on Day 1. A likely reason for this was that it was often difficult to discern the numbers on the bees' identification tags in the video, and, thus, those bees would not end up being counted. Also, there was no way to control for bees that followed dances during the training period but did not actually land on and feed from the feeder. Such bees would not have been completely naïve with regard to the feeder location but not identified. Regardless, the 55 bees that were possible to analyze in the video provided an adequate sample size from which to draw conclusions.

Although a significantly greater number of individual waggle runs were followed from the rear of the dancer, it should be noted that the overwhelming majority of the followers used at least two positions before departing for the feeding station. Furthermore, of the few bees that followed from a single position, there was no greater likelihood that the rear position would be the position used. If one considers the number of dances followed to equal the number of dances needed to receive the information, it could be argued that following from the rear was actually less efficient than the other positions because bees that followed from this position followed for many more waggle runs (Figure 2).

Next, the analysis of the final waggle run observed before arriving at the feeding station showed that any of the positions could be used. The bees were not specifically following from the rear; rather, it seemed that the positions were selected at random based on what part of the dancer they could conveniently access.

The final component of the analysis involved only the most efficient followers. It is conceivable that if a specific following position was required to receive the dance information it would clearly be used with the greatest frequency by the bees that only needed to follow a small number of waggle runs before locating the feeding station. The results of this analysis showed, however, that there was no single position that was used significantly more times by the most efficient bees.

In his 1995 paper, Judd [6] described a type of “lunging” movement that he believed to be of particular importance to the dance following experience. Throughout the video analysis, we carefully studied this movement whenever it was present. It was observed commonly when the dance floor was not so overcrowded as to not allow space for it. The “lunging” movement seems best described as simply a maneuver performed by bees following from the side of the dancer to help them get into position as she turns for the return phase of the dance. Because the dancer moves forward rapidly during the waggle run and then turns quickly to begin the return phase, bees attempting to remain in contact with her must dart forward or be left behind.

A consideration of the dynamics of waggle dancing and following is important here. In a well-populated colony of bees, there is little available space around a dancer. Interested followers, therefore, must crowd in against the dancer wherever space allows. As the dancer moves forward during a waggle run, an empty space is created in her wake and can readily be occupied by followers much more conveniently than the areas next to or ahead of her. We propose that this is a reason for the greater number of dances followed from the rear and not some need that the followers have to position themselves at the rear in order to successfully acquire the dance information. Furthermore, other non-dance-cues are also available to follower bees (reviewed in [9]), and some, such as nectar samples from the food source, would only be available to followers near front of the dancer and not individuals following from the rear.

Von Frisch and Jander (1957) [11] observed that, in spite of variation in waggle run angle and duration within a single dance, followers arrived at a food source with surprising accuracy. Observations of foragers in the field rather than

within the hive reveal that foragers already familiar with a food source can scent mark it using geraniol from the Nasonov gland ([12], reviewed in [13]). Von Frisch (1923) [12] also described a buzzing flight around the food source, which may help nearby foragers unfamiliar with the location of the food source to find it. Thus, foragers in the hive receive information about the location of a food source by following waggle dances, but chemical and behavioral cues in the field aid in guiding them to its exact location (reviewed in [13]).

In conclusion, these results do not support the earlier assertion that dance followers must be positioned to the rear of a dancer in order to receive the dance information. One must consider the crowded conditions of a beehive, where followers must cram themselves in next to a dancer wherever it is possible. In light of that, it is much more likely that the position itself should not matter and rather that a concert of cues both within the hive, such as any physical contact with the dancer, and in the field, such as pheromone usage, act synergistically to help guide a forager to her destination.

Data Availability

The video footage and feeder visit data used to support the findings of this study are available from the corresponding author upon request.

Disclosure

This research was conducted as part of the requirements for the degree of Doctor of Philosophy in Entomology for PMK at the University of California at Riverside. A version of this work was presented as a poster by PMK at the North American Section meeting of the International Union for the Study of Social Insects (IUSSI), held in Greensboro, North Carolina, on October 5-7, 2012. A version was also included as a chapter in the doctoral thesis of Dr. Parry M. Kietzman.

Conflicts of Interest

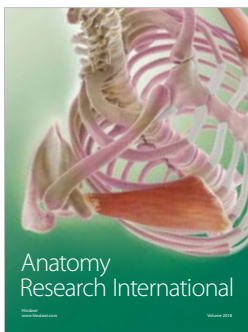
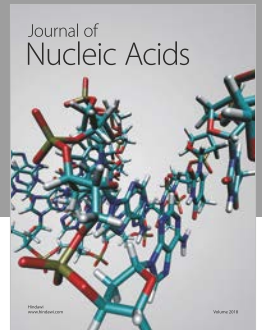
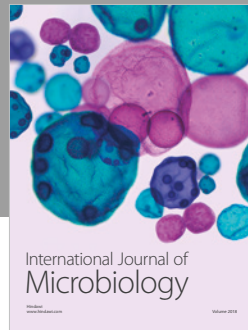
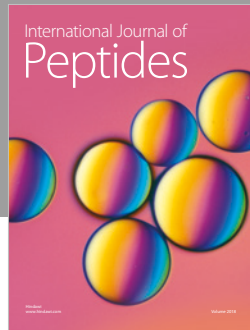
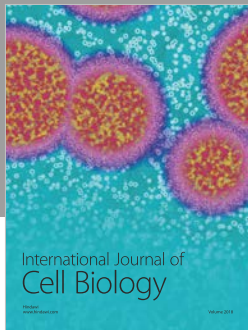
The authors declare that they have no conflicts of interest.

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