



Decoding the dance parameters of eastern honeybee, *Apis cerana*

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Abstract – Bees dance to deliver food vectors that contain information regarding distance gauging and spatial orientation. The eastern honey bee, *Apis cerana*, also transmits this vector information through waggle dance. Although many reports have published on this topic, changes in dance parameters of *A. cerana* that occur at different distances are unclear. Herein, we filmed the bees' foraging dance at different distances until the bees stopped collecting food, analyzed these videos frame by frame, and set a feeder in four cardinal directions to record the changes in bees' dance with the azimuth of the sun. The duration and number of waggle runs of the dancers significantly correlated with the distance from hive to feeder. The dance parameter exhibited a linear model with distance. As the sun's azimuth changed, the angle of the waggle run changed counterclockwise. We elucidate how to combine distance and direction to calibrate the spatial distribution of the resource location advertised by dance. Finally, we discuss the dance and navigation of long-distance collection and provide a basis for further understanding of the foraging ecological strategies of eastern honeybee.

Apis cerana / Dance / Waggle phase / Return phase / Angle / Duration of waggle run / Calibration

1. INTRODUCTION

Foraging honeybees use a dance-sun reference system to inform their nest mates about their foraging trip for food and nest vectors (Dyer 2002; Seeley 2012; Menzel 2019). On returning to the hive, the essential components of a foraging trip are repeatedly presented in the form of dances. Bees perform the figure of eight dance according

to the distance of the food source from hive near to far (Frisch 1967). The waggle dance for great distances is also called the marathon dance (Lindauer 1971a, b). These dancing behaviors allow experimenters to study the mechanism of information flow used for a long-range flight.

Successful foragers perform dances in their nests to recruit their mates to profitable sources, including nectar, pollen, water, tree resin, and new nest sites. The wagging dance of bees is divided into the waggle stage and the return stage (Frisch 1967; Tautz 2008; Tan et al. 2012) (Figure 2A and B). In the “waggle stage,” the bee slowly walks forward and shakes its body vigorously from side to side.

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Then, the dancing bee turns left or right, hovers to the starting point, and begins wagging her abdomen again, which is known as the return phase. Numerous studies have reported that the bee dance is directional, that is, the angle of the waggle phase relative to gravity on the vertical comb in the dark hive represents the flight direction in relation to the sun's current azimuth (Dyer 2002; Sherman and Visscher 2002; Young et al. 2021). The duration of the waggle phase is related to the distance between the hive and flower (Visscher and Seeley 1982; Seeley 1986, 2019). The foragers encode information related to flower vector and food quality into the dance (Seeley et al. 2000). After returning to the hive, the foragers dance and regurgitate nectar, while the followers decode the dance. During encoding and decoding, food vectors (Seeley 2012; Collett 2019; Menzel 2021) are passed from the foragers to the colony.

The waggle phase of the dance is considered the core of dance information, which includes the duration, waggles, length of waggle runs, frequency, angle, and angular deviation (Menzel 2019). Numerous studies have depended on our understanding of how bees dance to communicate with nest mates in dark hives (F'Anson Price and Grüter 2015; Collett 2019; Menzel 2021). Although noise was present intra-dance (Couvillon et al. 2012) and inter-dance (Schürch et al. 2016) of the same species, dance duration was linear with distance. This relationship can be used to determine the collection distance of western honeybees in a patchy environment (Visscher and Seeley 1982; Beekman and Ratnieks 2000), as integrative indicators of seasonal foraging challenges (Couvillon et al. 2014a, b) and communicate landscape foraging preferences (Couvillon et al. 2014a, b). In addition to demonstrating food distance, duration can indicate the distance to a colony's new nest site for a swarm (Seeley 1995, 2012).

Moreover, dance duration reflects the existence of ecological dance dialects among bee species. A comparison of the waggle phase duration of the collection of *Apis dorsata*, *A. cerana indica*, and *A. florea* within 500 m revealed a variation of the collection range of bees by decoding

the natural bee dance (Kohl et al. 2020). As the distance increase, the duration of waggle of *A. cerana* increases the most rapidly, followed by that of *A. florea* and *A. dorsata*. Furthermore, honeybee dance communicated distance, as a proxy for availability, changes with season and resource (Couvillon et al. 2015). When dancing for sources near hives, the dance changes greatly, whereas when the distance increases, the dance becomes more precise (Beekman et al. 2015). Observed dance information of *A. mellifera carnica* and *A. florea* suggests that no difference exists in the relative proportions of waggle and round dances between the two species at a given distance (Sen et al. 2004). In Thailand, no obvious dialect difference was observed among *A. florea*, *A. cerana*, and *A. dorsata* (Dyer and Seeley 1991).

The angle of waggle run relative to gravity indicates the direction of the hive to the food source. Most studies have shown that directional information in dance is associated with some inaccuracy (Grüter and Farina 2009). Bees usually exhibit a 10–15° deviation in delivering the direction of a profitable food source, and this deviation becomes significant over 6 km in the bee collection circle (Okada et al. 2008, 2014; Preece and Beekman 2014). This error was considered a complete or partial physical constraint on the bees (Preece and Beekman 2014). In case of a complex and fluctuating nectar and environment, bees can quickly discover nectar sources, which indicates that the imprecise bee dance improves the collection flexibility (George and Brockmann 2019).

Although eastern and western honeybees have many similarities, differences are observed in their foraging decision and information transmission at the individual- or colony-level (Oldroyd and Wongsiri 2006). Relatively few studies have investigated the waggle dance in eastern honeybees during long-distance collection. Therefore, the long-distance collection (known as the marathon dance) of honeybees can enrich the connotation of the animal communication mechanism. We considered *A. cerana* as model insects, trained the bees to the feeder at a known distance, recorded the dance of foragers, and explored the dance

parameters of dancers. We manually analyzed the dance frame by frame for different distances and determined changes in dance in the waggle and the return stages. Then, we recorded the changes in the angle of waggle run with the sun's azimuth at the same distance and same sugar concentration during the day. Accordingly, we further explored the mechanism and connotation of social insects' decision-making and division of labor in food source income and dance language evolution.

2. MATERIALS AND METHODS

2.1. Study site and treatment setup

All experiments and observations were conducted in Caoba Town, Mengzi City, Yunnan Province, during the 0900–1700 in December 2020 and January, July, and August 2021. Three honeybee (*A. cerana*) colonies were placed in an observation hive with glass wall. Each observation hive used a standard Langstroth nest frame and contained a queen and approximately 10,000 worker bees with honey and pollen. We did not complement the colonies for syrup or replace queens during the trial to keep foraging motivation. A bottle inverted on lid with grooves was used as a feeder and sugar could pass freely due to gravity through the feeder. The bees were trained with 2 M of fragrant-free sugar solution and identified with color marks. Unlabeled bees were captured using ventilating bottles at the beginning of the experiment and released at the end of the experiment. To reduce the influence of wind speed and temperature on bee flight, the experiment was stopped when wind speed exceeded 2 m/s and temperature was below 15 °C. The dance video was recorded using a Huawei cellphone camera (P9-IMX286) at a full HD (1920 × 1080 pixels) frame rate of 60 fps. When shooting the video, we used the fishing line with hanging lead block to correct vertical, and the white fishing line in the film did not bend. At the same time, we manually moved the mobile phone to focus on the dancing bees in the dance floor, and made the distance between

the camera lens and the dancing bees almost at 10 cm. We manually analyzed the video frame by frame by using Adobe Premiere Pro CS6.

2.2. Training bees

The bees were trained using the “leapfrog” method, which used a front and a back feeder alternately to stimulate the bees to collect. When more than 20 bees arrived at the back feeder, we gently moved it forward, with bees pass over the front feeder to 10–20 m.

2.3. Experiment 1: waggle dance for different distances

One observation hive was located in the field and the other two are located in the Sericulture and Apiculture Institute of the Yunnan Academy of Agricultural Sciences, which is very close to the straight Yunnan-Vietnam railway (Figure 1). The railway is 2 m above the ground and is surrounded by very sparse shrubs. We also recorded the dance of bees at distances of 50 m and 100 m. After that, every 200-m distance from the hive to the feeder was used as a video test point. The experiment was considered to be complete when no bees visited the feeder for 2 h. The foragers were allowed to collect syrup freely for 10 min, and then, recording was started to collect data when the bees arrived at the feeder at the test point. The assistant at the feeder used a walkie-talkie to report the number or color bees arriving and leaving. Another one was prepared to record the whole dance on the dance floor. At least 20 dancers were recorded from each test point.

2.4. Dance decoding

The observation hives had plumb lines made of nylon fishing line with a lead attached to the end. These appeared as thin white lines in the video and gave a vertical frame of reference against which to measure waggle run angles. We manually decode the dance and record dance parameters included the number of waggles, length of waggle runs, duration, angle between

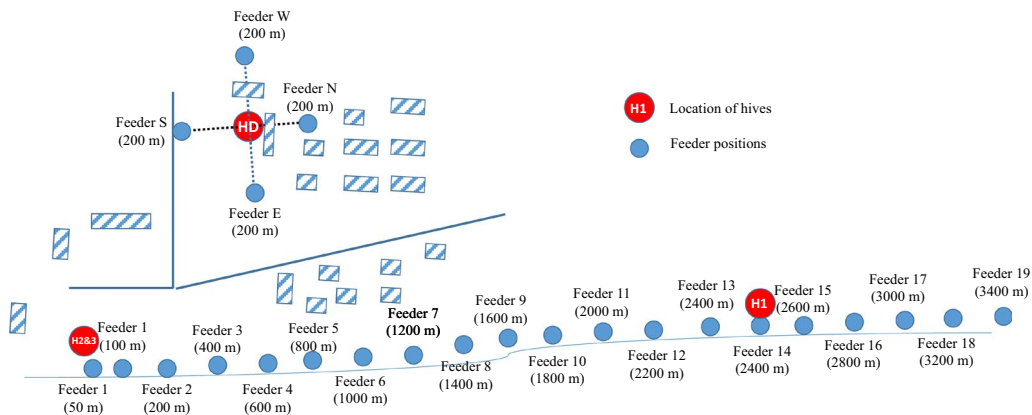


Figure 1. Location view of the test site. Experiment # 1: two-frame observation hives set on the field (hive 1 = 2400 m, the next experiment was not carried out here because the rent was due) and at Sericulture and Apiculture Institute (hive 2 = 2000 m and hive 3 = 3400 m). The experiment was considered to be complete when no bees visited the feeder for 2 h. Experiment # 2: a hive (marked HD) were trained to four cardinal directions at 200 m showing with feeder N, feeder E, feeder S, and feeder W.

the waggle run and gravity, duration, and turn-around of the return stage.

Dances were decoded via frame by frame playback using a modified protocol of Couvillon et al. (2012). We used complete dance circuits as a duration measurement which remained common practice in the decades after von Frisch. The duration was based on the beginning and end of the movement of the blurred dancer’s body and wings, easily visible in the still frame of the video. Data regarding start and end times (hours, minutes, seconds, and frames) were gathered from the timer of the video software, which each frame was 1/60 s. The number of waggles was determined by counting the number of times the bee wagged its tail left or right through the central axis back in the opposite direction and then back to the starting point on the abdomen. The length of waggle run was the distance between the starting and ending points in the waggle phase. In the video, we lined the starting and ending points of the dancer thorax. We also measured the angle of this line clockwise from vertical to the nearest degree.

By measuring the 1134 opposite walls of *A. cerana* worker cells with the same duration of service, we found that the diameter of the worker cell was 4.562837419 cm (unpublished data). The direction of the dance was the angle between the length

of waggle and gravity. The length of waggles and direction of dance were measured using Digimizer (version 5.4.4). With the help of an Excel Macro (Sun 2007, W.F. Towne) and the time of the recording, we calculated the azimuth of the sun.

2.5. Experiment 2: the angle of dance changes with sun’s azimuths

Because the angle of dance changes with sun’s azimuth, we also calibrated the angle of dance in four cardinal directions for a day at a distance of 200 m between the hive and feeder. We trained the bees, and the dances of the bees on the dance floor were filmed for 10 min each and half o’clock. By using the mentioned method, we only analyzed the angle of dance in this experiment.

2.6. Statistics of data

We pooled all the data together for analysis and had obtained $H_1 = 102$ dancers 906 dances, $H_2 = 36$ dancers 465 dances, and $H_3 = 75$ dancers 945 dances. In total, 213 dancers and 2316 dances were used. Because the direction of the dance changed with time, and we also did not shoot video at a fixed time in the first experiment,

so we did not pay attention to the direction of the bee dance at first. In the second experiment to calibrate angular variation with the sun's azimuth, we trained bees to feed in four directions and had obtained Feeder_{North} = 57 dancers 1260 dances, Feeder_{East} = 66 dancers 578 dances, Feeder_{West} = 95 dancers with 1114 dances, and Feeder_{South} = 105 dancers 974 dances, in total of 323 dancers 3926 dances.

We used SPSS 19.0 and R 4.1.3 for our statistical analyses. Referring to the analytical method of Schürch et al. (2013, 2019), the additional packages were loaded into R. The details are as follows: in the linear model fit analysis, we use the duration t and the number of waggles n as response variable respectively, the distance d as a fixed factor, and the colony as a random variable. We used "lme4" v.1.1–30 to calculate the mixed model. Two models were proposed: a random intercept with fixed mean and correlated random intercept and slope. AIC is used to detect these two models. Package "circular" v.0.4–95 manipulated circular data and statistics.

3. RESULTS

3.1. Shape of the calibration curve

Duration of waggle run (Figure 2C) increased with increasing distances (one-way ANOVA, $F = 416.685$, $p < 0.001$); duration at 3400 m (7.2196 ± 0.1109 s) was significantly higher than that at 100 m (0.4713 ± 0.0203 s, Tukey's post hoc test, $p < 0.001$). This significance was maintained using non-parametric statistics (Kruskal–Wallis, $H = 1724.670$, $p < 0.001$). The number of waggles (Figure 2D) also increased along the distance (one-way ANOVA, $F = 592.628$, $p < 0.001$, Kruskal–Wallis, $H = 1881.461$, $p < 0.001$). The length of waggle runs (Figure 2E) increased with increasing distances (one-way ANOVA, $F = 39.890$, $p < 0.001$; Kruskal–Wallis, $H = 623.961$, $p < 0.001$). The waggle frequency of a dancer (Figure 2F) decreased with an increase in distance (one-way ANOVA, $F = 76.662$, $p < 0.001$).

Compared with random intercept, adding random slope to the linear models did not significantly improve the fit for duration of waggle (Table I $AIC_{\text{slope}} = 5915.3$, $AIC_{\text{intercept}} = 5934.1$). Correlated random intercept and slope did significantly improve the linear model fit for number of waggles (Table II $AIC_{\text{slope}} = 17,577$, $AIC_{\text{intercept}} = 17,519$).

3.2. Variation of dance parameters with distance in the return stage

The return time of dancer (Figure 3A) increased significantly with the increase of distance (one-way ANOVA, $F = 23.987$, $p < 0.001$, Kruskal–Wallis, $H = 571.980$, $p < 0.001$); the return time at 3400 m (4.2439 ± 0.4517 s) was significantly higher than that 100 m (1.0711 ± 0.0413 s, Tukey's post hoc test, $p < 0.001$). However, the error of turn-around (Figure 3B) has not significant with the increase of distance (one-way ANOVA, $F = 1.347$, $p = 0.148$, Kruskal–Wallis, $H = 19.718$, $p = 0.349$), and the highest at 2600 m (18.4211%).

3.3. The angle of bee dance in four cardinal directions

In this experiment, we focused on the angle of the dancer's body relative to vertical during the waggle run at the same distance (200 m) on the day. A total of 3926 dances were analyzed. When the feeder at 200 m in the east (Figure 4A), the foragers went against the direction of the rising sun at 0900 in the morning, and the east for honeybees at this time was $330.6944 \pm 2.1370^\circ$. The foragers went along with the sunshine at 1600 in the afternoon, and the east for the bees at this time was $203.1788 \pm 11.9929^\circ$. The south (Figure 4B) for the foragers was $63.5175 \pm 1.3485^\circ$ at 0900 and $308.8968 \pm 1.7221^\circ$ at 1600. The west (Figure 4C) for the foragers was $164.1072 \pm 1.5187^\circ$ at 0900 and $34.4030 \pm 3.5158^\circ$ at 1700, which is opposite to that in the east. The north for the foragers (Figure 4D) was $242.4264 \pm 1.6503^\circ$ and $120.8476 \pm 2.2252^\circ$ at 0900 and 1600, respectively. The dance angles of the four directions were significantly different with time using

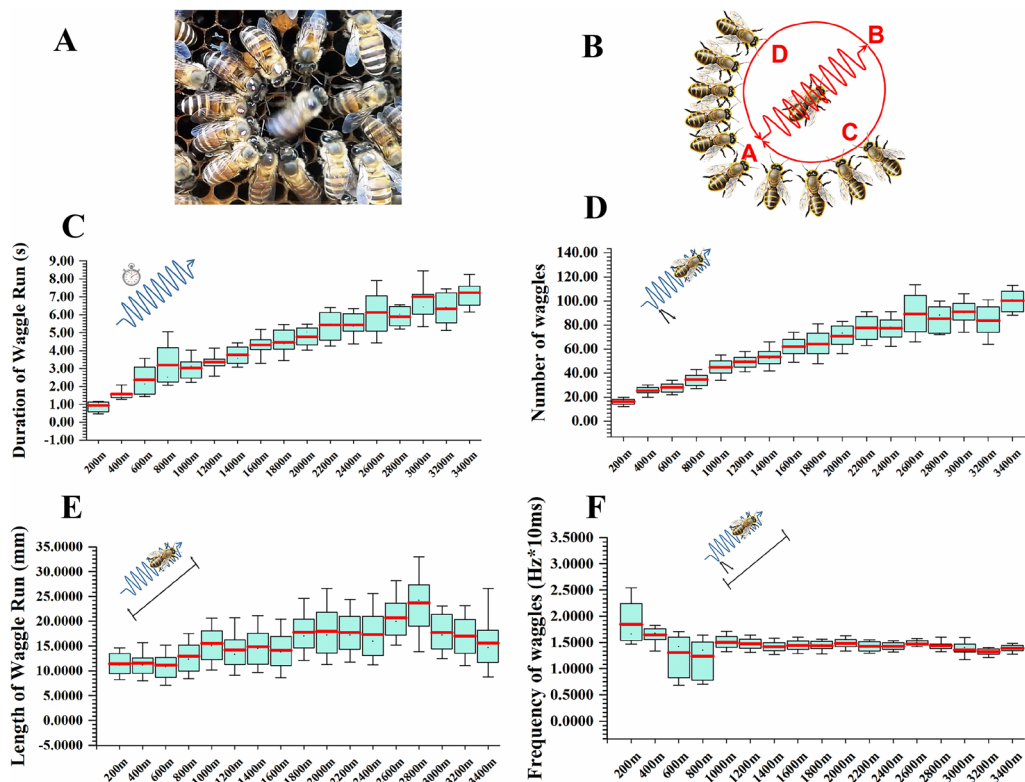


Figure 2. Variation of dance parameters along distance in the waggle stage. **A** is for the wagging dance of *A. cerana* at the hive. **B** is a diagram of the waggle dance. **C–F** are the parameters of the waggle stage. Green box represents the confidence interval, the whisker line represents maximum and minimum values, the red horizontal line represents the mean, and the black circle represents the median. Duration, number, length, and frequency of waggle run have significant with increasing distances by using one-way ANOVA and non-parametric statistics.

homogeneity of means statistics (Watson-Williams test, $F_{\text{North}} = 531.9198$, $p < 0.01$; $F_{\text{East}} = 387.3375$, $p = 2.825758e - 208$; $F_{\text{West}} = 775.8574$, $p < 0.01$;

$F_{\text{South}} = 891.1438$, $p < 0.01$, respectively). In summary, our analysis indicates that the dance angle changed counterclockwise.

Table I Most parsimonious linear model parameter estimates for data sets with a random intercept and random intercept and slope where the effects of distance to the food source on waggle run duration

	Estimate	SE	<i>t</i>	AIC	<i>p</i>
Correlated random intercept and slope	1.0619039	0.6562	1.618	5915.3	<i>1.10E - 05</i>
Distance	0.0018938	0.0001082	17.507		
Random intercept	1.080	0.1680	6.416	5934.1	
Distance	0.0019	0.0000232	81.815		

The final models were derived by Akaike information criterion (AIC) comparison. The terms in italics are significant

Table II Most parsimonious linear model parameter estimates with distance as a linear predictor of number of waggles

	Estimate	SE	<i>t</i>	AIC	<i>p</i>
Correlated random intercept and slope	13.2576	8.8114	1.505	17,577	<i>2.56E-14</i>
Distance	0.0281	0.0023	11.973		
Random intercept	15.09	1.931	7.817	17,519	
Distance	0.02651	2.87E-04	92.42		

Terms in italics are significant

4. DISCUSSION

Our results confirmed that the duration and number of waggle dances of *A. cerana* waggle run duration is a linear function of distance to food source. Several excellent literatures have been published showing that the duration of waggle runs is positively correlated with the foraging distance in western honeybees (Frisch 1967; Srinivasan 2014) although there is a lot of noise (Al Toufaily et al. 2013; Schürch and Couvillon 2013; Schürch et al. 2019). From our observations, the test result was the same as that of a previous study, which indicated that the duration of waggle runs (Figure 2) of eastern honeybee

during long-distance foraging was similar to that of the western honeybee.

The waggle dance is a multicomponent signal for advertisement of food sources and attraction of surrounding bees (Gruter and Farina 2009). The waggle run phase is the most informative part of the bee dance (Lindauer 1971a, b; Weidenmüller and Seeley 1999; Seeley 2012). In this experiment, at a close range to the hive, such as 50 m, the bees showed a very shorter waggle run. With an increase in the foraging distance (Figure 2), the duration, number, and length of waggle runs increase, and the dance of eastern honeybee becomes a figure-eight-shaped dance. When the foraging distance increased to 3400 m (Figure 2C),

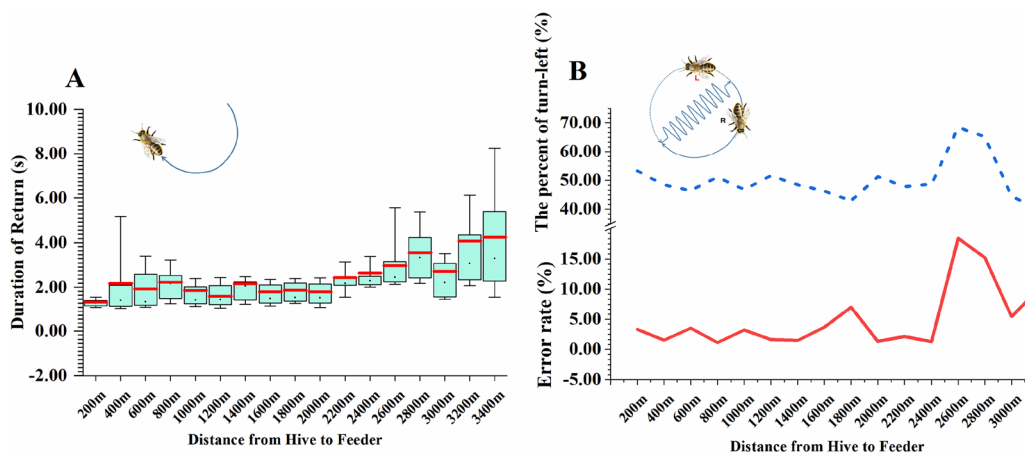


Figure 3. Variation of dance parameters with distance in the return stage. The return time of dancer **A** increased significantly with the increase of distance (one-way ANOVA, $F=23.987$, $p<0.001$), but error of turn-around **B** has not significant with the increase of distance (one-way ANOVA, $F=1.347$, $p=0.148$).

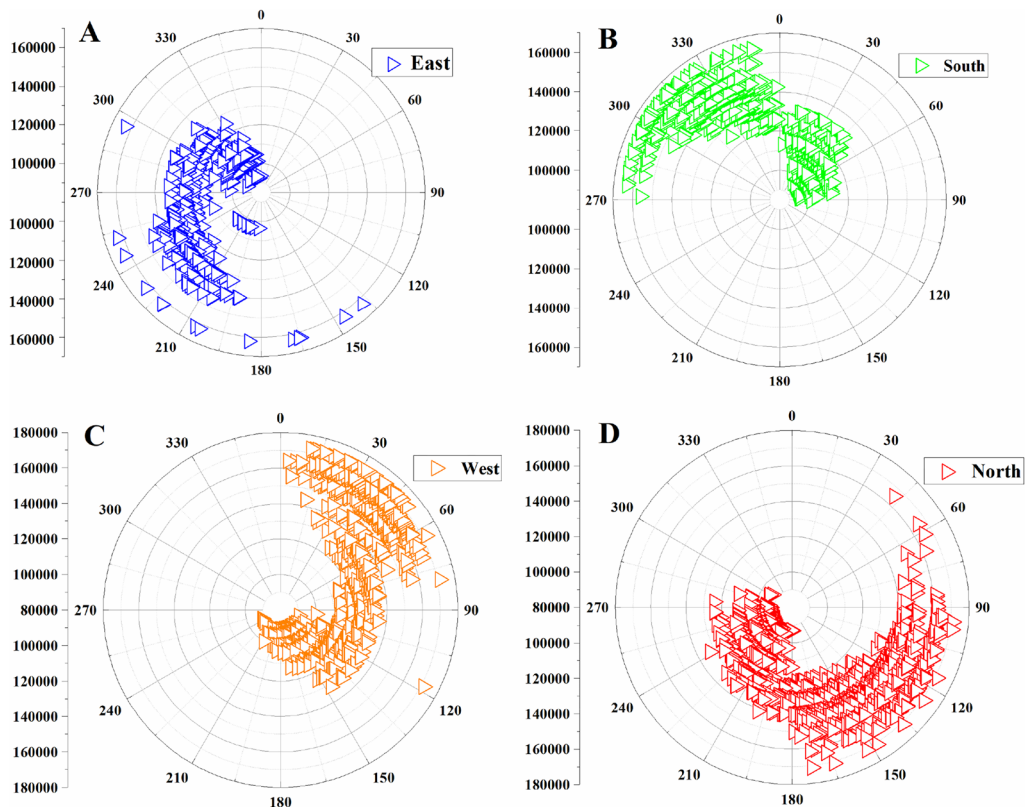


Figure 4. The dance angle changes in four cardinal directions. The dance angles of the four directions were significantly different with time using homogeneity of means statistics (Watson-Williams test, $F_{North} = 531.9198, p < 0.01$; $F_{East} = 387.3375, p = 2.825758e - 208$; $F_{West} = 775.8574, p < 0.01$; $F_{South} = 891.1438, p < 0.01$, respectively).

the duration of waggle run increased to the maximum. At this time, the dance of bees could not attract the bees, and the bees should traded-off between the foraging distance and collection cost.

The number of waggles also act as a parameter representing the distance between the feeding site and hive in accordance with the profitability of the nectar source it represents (Frisch 1967; Seeley 1995). The number of waggles increased with an increase in distance and showed a linear model (Figure 2D, Table II), indicating that the number of waggle run was also more information for implication of food source location. The numbers of waggle run advertise a profitable alternative food source, which is also a crucial component of information collected by bees.

The angle of the dancer’s body relative to gravity during the waggle run indicates the direction of the hive to the food source. Calibration of the dance angle and duration can be used to map the bee collection and integrates with geographic information systems to better understand honey bee foraging ecology (Schürch et al. 2013; Couvillon et al. 2014a, b; Couvillon and Ratnieks 2015). However, the angle calibration of eastern honeybees is rarely reported. In *A. cerana*, the angle of dance varied with sun’s location (Figure 4), in other words, in the morning, east of waggle run is directly above, west is directly below, north is to the left, and south is to the right, and it changes counterclockwise. From our results, the average dance angle of waggle run in a single cardinal direction is not in the

one of four directions, but shows a certain angle. Our experiment took place during winter in the northern hemisphere, when the ecliptic is at an angle to the equator, may account for this phenomenon. Presumably, at the same time and at the same latitude in the northern and southern hemispheres of the eastern bee dance angle showed left–right symmetry.

To obtain the navigation information for long-distance flights from celestial and terrestrial cues, foraging bees employ several strategies. Bees have at least three compass mechanisms for long distance foraging: magnetic compass (De Marco et al. 2008; Towne and Moscrip 2008); celestial or solar compass (Dyer 2002; Dovey et al. 2013), based on sun’s daily rotation and a skylight pattern connected to the sun; and a backup celestial compass (Pahl et al. 2011; Collett 2019; Schürch et al. 2019), based on the memory of the sun’s movements. The interactions of these compass systems have not been fully elucidated. However, celestial compass mostly plays a major role in bee navigation (Menzel et al. 2000), the magnetic compass is a backup in some cases, and the bee’s memory of solar tracks and landscapes is a backup system for overcast navigation (Srinivasan 2011). The eastern bee foragers and followers sense the sun’s azimuth to make changes in the dance. We assume that the bees’ dance creates a time compensation mechanism as the sun’s azimuth changes. Path integration (Collett 2019) theory suggests that path integration provides an animal with a navigation strategy that estimates the position relative to a starting point. In path integration theory, the time compensation of celestial cues plays a vital role (Menzel et al. 2000; De Marco and Menzel 2005; Collett 2019). Desert ants (Knaden 2020; Vega Vermehren et al. 2020) and bees (Menzel 2012; Dovey et al. 2013) produce food–home vectors during the forage–home process. These vectors are located in terrestrial coordinates rather than celestial coordinates, and the foragers adjust the celestial-derived orientation (time compensation) according to the horizontal position of the daytime sun to achieve food–home localization.

Numerous decoded bee dance videos are necessary to truly reflect the information transmission process of eastern bee dance. The waggle dance gave researchers a great opportunity to decode the dance to determine where bees are foraging and possibly use it as an ecological tool to indicate a range of ecological, conservation, and land management issues (Couvillon and Ratnieks 2015). However, manual decoding of the dance is the current method for extracting its spatial information and is time-consuming. Couvillon et al. recommend that any four consecutive waggle runs, not including the first and last runs, may be decoded and has a suitable goodness-of-fit. In this experiment, although it was very time-consuming, we manually decoded the dances of eastern honey bees as much as possible to provide sufficient data of dance parameters. Contributions from robotic bees (Landgraf et al. 2011), advanced mark methods (Wario et al. 2015), and applied software (Wario et al. 2017) may help solve time-consuming problem. Tracking all individuals in a bee colony and automatically detecting and decoding the communication dance should be possible in the future.

Foraging is a basic but costly behavior for most animals, and the costs, such as time investment, energy consumption, and risk assessment, are especially critical for animals that forage relatively far away (Seeley 1995). Information sharing can alter how animals respond to environment-related stimuli, for example, through collective decision-making, or “swarm intelligence,” to the group’s or individual’s benefit (Seeley and Levien 1987). The waggle dance of honeybees, *A. cerana*, is a good example. Encoding and decoding dance is central to finding food resources and decision-making during foraging for colonies, such as deciding which flowers are appropriate for nectar collection and which should be abandoned. Individuals must inform the location of food sources according to their own experience. Moreover, they must adjust the behavior of the colony and its members through the stimulus–threshold–response mechanism in order to improve the colony’s ability to collect food and ultimately enhance the colony’s adaptability.

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AUTHOR CONTRIBUTION

All authors conceived this research and designed experiments; Z.H., C.M., N.D., and Y.L. participated in the design and interpretation of the data; Z.H., C.M., N.D., Y.Z., T.Z., J.Y., L.X., and J.Y. performed experiments and analyses; Z.H. and Y.L. wrote the paper and all authors participated in the revising the paper. All authors read and approved the final manuscript.

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DATA AVAILABILITY

The preprocessed data that support the findings of this study are available from the corresponding author upon reasonable request.

CODE AVAILABILITY

Not applicable.

DECLARATIONS

Ethics approval Not applicable.

Consent to participate Not applicable.

Consent for publication Not applicable.

Competing interests The authors declare no competing interests.

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